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Competition and the evolution of imperfect mimicry

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Abstract Mimicry is widely used to exemplify natural selection's power in promoting adaptation. Nonetheless, it has become increasingly clear that mimicry is frequently imprecise. Indeed, the phenotypic match is often poor between mimics and models in many Batesian mimicry complexes and among co-mimics in many Müllerian mimicry complexes. Here, we consider whether such imperfect mimicry 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. Specifically, for mimicry to be effective, mimics and their models/co-mimics should occur together. Yet, co-occurring species that are phenotypically similar often compete for resources, successful reproduction, or both. As an adaptive response to minimize such costly interactions, interacting species may diverge phenotypically through an evolutionary process known as character displacement. Such divergence between mimics and their models/co-mimics may thereby result in imperfect mimicry. We review the various ways in which character displacement could promote imprecise mimicry, describe the conditions under which this process may be especially likely to produce imperfect mimicry, examine a possible case study, and discuss avenues for future research. Generally, character displacement may play an underappreciated role in fostering inexact mimicry [*Current Zoology* 58 (4): 608–619, 2012].

Keywords Batesian mimicry, Character displacement, Hybridization, Müllerian mimicry, Reproductive interference, Selective trade-off

1 The Problem of Imperfect Mimicry

One-hundred and fifty years ago, Henry Walter Bates described a phenomenon that he maintained was "a most powerful proof of the theory of natural selection" (Bates, 1862, p. 511). Bates had discovered a spectacular type of adaptation known as "mimicry" (Bates, 1862; Müller, 1879; Poulton, 1890; Fisher, 1930 (1999); Cott 1940; Wickler, 1968; Edmunds, 1974; Ruxton et al., 2004). In one common form, now called "Batesian mimicry", an edible species (the "mimic") evolves to resemble a conspicuous, inedible species (the "model"), thereby gaining protection from predation. In another common form, "Müllerian mimicry" (Müller, 1879), multiple defended species ("co-mimics") converge on the same warning signal, thereby sharing the cost of educating predators about their unpalatability. Since Bates' time, mimicry has been widely used to illustrate natural selection's efficacy in promoting adaptation (Fisher, 1930 (1999); Wickler, 1968; Edmunds, 1974; Ruxton et al., 2004; reviewed in Forbes, 2009).

Paradoxically, however, mimicry is frequently imprecise, such that mimics are often (at least to humans) poor replicas of their models/co-mimics (Edmunds, 2000; Ruxton et al., 2004; Gilbert, 2005, e.g., see Fig. 1). Thus, a complete understanding of mimicry requires that we identify the factors that prevent populations from evolving high-fidelity mimicry. Indeed, the existence of inexact mimicry poses a central challenge to mimicry theory (Edmunds, 2000; Sherratt, 2002; Ruxton et al., 2004, pp. 159–161).

One possible explanation for imperfect mimicry is that genetic, developmental, or functional constraints may preclude the evolution of precise 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). Yet, because such constraints can generally be overcome (given enough time and sufficiently strong selection; Maynard Smith et al., 1985), constraints do not offer a universal explanation for imprecise mimicry. Indeed, of the few studies that have thus far examined the proximate bases of mimetic phenotypes, the genetic and developmental mechanisms are similar between mimics and their models/co-mimics, suggesting that imperfect mimicry does not reflect an underlying constraint on signal production (e.g., see Reed et al., 2011; Kikuchi and Pfennig, 2012a). Thus, why are imperfect mimics not further improved by *natural selection*?

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Fig. 1 Variation in degree of mimetic resemblance among coral snake mimics

A. In the southeastern U.S., venomous eastern coral snakes *Micrurus fulvius* serve as models to two species of Batesian mimics. **B**. Scarlet kingsnakes *Lampropeltis elapsoides* and (**C**) scarlet snakes *Cemophora coccinea*. **D**. In the southwestern U.S., venomous Sonoran coral snakes *Micruroides euryanthus* serve as models to several Batesian mimics, including (**E**) Sonoran Mountain kingsnakes *Lampropeltis pyromelana* and (**F**) Western shovel-nosed snakes *Chionactis occipitalis*. Not only do different species of mimics vary in how closely they resemble their model (as illustrated in these examples), but different conspecific populations of mimetic species vary in mimetic fidelity (see main text). A, C, F courtesy of Wayne Van Devender; B, D, E by David Pfennig.

Several nonmutually exclusive (potentially interrelated) selective hypotheses have been proposed to explain imprecise mimicry (Edmunds, 2000; Sherratt, 2002; Gilbert, 2005; Penney et al., 2012). These include: (1) the "jack-of-all trades hypothesis," which posits that imperfect mimics persist because they are under selection to resemble more than one model (Sbordoni et al., 1979; Edmunds, 2000); (2) the "relaxed selection hypothesis," which holds that there is 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); (3) the "selective trade-off hypothesis," which asserts that imperfect mimics represent 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 (see below); (4) the "breakdown hypothesis," which posits that imperfect mimicry may reflect an adaptive breakdown of mimicry, such as what might occur in populations where the ratio of mimics to models increases (Brower, 1960) or where the mimic occurs outside the geographical range of its model (Harper and Pfennig, 2008); (5) the "sensory limitation hypothesis," which holds that selection for improved mimicry might not exist if imperfect mimics exploit limitations in predator cognition (Chittka and Osorio, 2007; Kikuchi and Pfennig, 2010b); and (6) the "kin selection hypothesis," which asserts that, when mimics are imperfect, predators will be more discriminatory and occasionally avoid a mimic by mistaking it for a model, thereby sparing any genetic relatives that share the same imperfect trait (Johnstone, 2002).

Although most of these hypotheses have received some empirical support (e.g., see Gilbert, 2005; Harper and Pfennig, 2007, 2008; Kikuchi and Pfennig, 2010b; Penney et al., 2012), the above list is not exhaustive. Moreover, the precise selective mechanisms that may actually generate imperfect mimicry are unclear. Here, as a general explanation for imperfect mimicry, we propose a novel variation on the selective trade-off hypothesis described above. Specifically, we suggest that imprecise mimicry may reflect a trade-off between two common agents of selection (MacColl, 2011): predation and competition. We outline our hypothesis in the next section.

2 Competition and Imperfect Mimicry

We hypothesize that imprecise mimicry may represent 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 hand.

Our hypothesis can be summarized as follows. First, for mimicry to be an effective deterrent to predation, mimics and their models should occur together in the same location and at the same time (Beatty and Franks, 2012). Yet, as we describe in the next section, co-occurring, phenotypically similar species often compete with each other for resources, successful reproduction, or both (throughout this paper, "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, 2009; Pfennig and Pfennig, 2010, 2012). As an adaptive response to minimize such costly interactions, competitively mediated selection may favor individuals that differ from their heterospecific competitors (reviewed in Schluter, 2000; Dayan and Simberloff, 2005; Pfennig and Pfennig, 2009; Pfennig and Pfennig, 2012). Consequently, interacting species may diverge phenotypically through an evolutionary process known as "character displacement" (*sensu* Brown and Wilson, 1956; see also Grant, 1972; Schluter, 2000; Dayan and Simberloff, 2005; Grether et al., 2009; Pfennig and Pfennig, 2009; Pfennig and Pfennig, 2012). Such divergence between mimics and their models/co-mimics may thereby result in imperfect mimicry (Fig. 2).

Before we develop this hypothesis, we first review the theory and evidence for character displacement.

3 Competition and Species Divergence: Theory and Evidence

Competition for limited resources, such as food or habitat, is a ubiquitous feature of living systems and an important agent of divergent selection (Darwin, 1859 (2009); Lack, 1947; Schluter, 2000; Pfennig and Pfennig, 2010, 2012). Regardless of whether such competition occurs through direct contests (Peiman and Robinson, 2010) or through more subtle means, such as when two or more species share a resource that is limited (Schoener, 1983; Grover, 1997), competitive interactions are always—by definition—costly (on average) to all parties involved (*sensu* Odum, 1959; Pianka, 2000). Indeed, in some cases, resource competition may become so severe that it may cause one of the species to go locally through competitive exclusion (e.g., Gause, 1934; Connell, 1961b, a).

Heterospecifics compete for more than just resources, however. They also potentially experience "*reproductive*

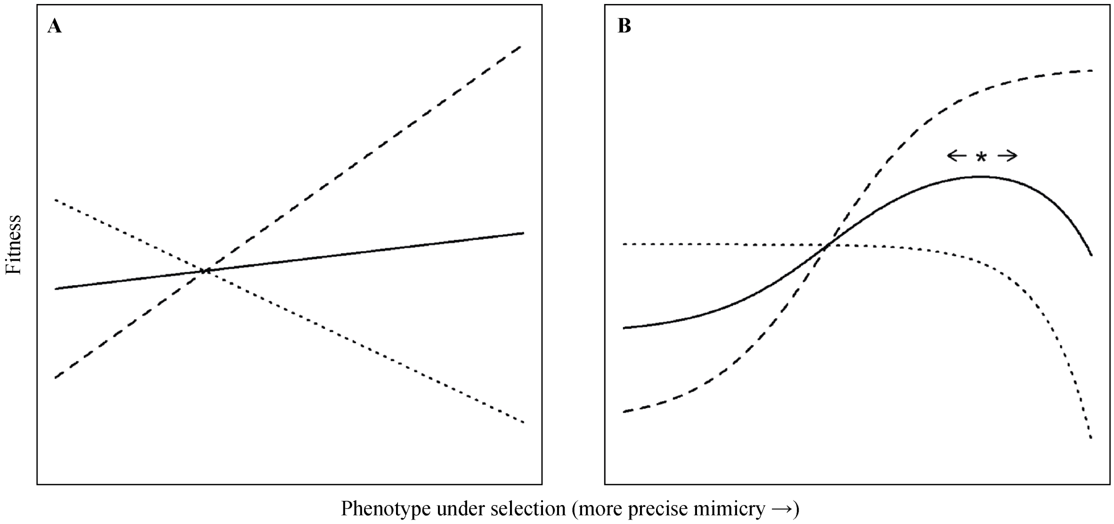

Fig. 2 How competitive interactions between mimics and their models/co-mimics may foster imperfect mimicry

Mimics always reap the fitness benefit of reduced predation (dashed line), but they may also experience a cost—increased competitive interactions with their model/co-mimics (dotted line). The net fitness associated with a particular degree of mimicry is depicted by a solid line. **A**. If benefits and costs vary linearly with the degree of mimetic resemblance, then, depending on the relative magnitudes of these costs and benefits, directional selection will either favor perfect mimicry or preclude mimicry's evolution altogether (the former situation is depicted here). **B**. Both theoretical and empirical studies have shown, however, that benefits of mimicry typically level off as the mimic approaches its model phenotypically (e.g., see Sherratt, 2002; Caley and Schluter, 2003). Additionally, competition typically rapidly increases in frequency and intensity with increasing phenotypic similarity between competitors (see main text), meaning that the costs of competition should cause fitness to decrease exponentially with more precise mimicry. The net fitness effect is an optimum at imperfect mimicry (denoted by the asterisk). Depending on the relative strength of predator- versus competitively mediated selection, the shape of the adaptive landscape may change to alter the position of this optimal degree of mimicry (arrows).

competition" (*sensu* Pfennig and Pfennig 2009) if they engage in hybridization (Barton and Hewitt 1989; Harrison 1993; Arnold 1997) or interfere with each other's ability to attract and locate a high-quality mate; e.g., through signal interference (Pfennig 1998, 2000). As with resource competition, the costs of reproductive competition can become so severe that they may cause a species to go locally extinct; in this case, through "reproductive exclusion" (Gröning and Hochkirch, 2008; e.g., see Kishi et al., 2009).

The likelihood and costs of competition are not uniform across all possible pairwise combinations of interacting species. Generally, competition is most severe between the most phenotypically similar individuals. For example, resource competition is most likely to occur—and is most costly—between individuals that express resource-use phenotypes most closely resembling those of their heterospecific competitor (Pacala and Roughgarden, 1985; Pritchard and Schluter, 2001; Gray and Robinson, 2002; Schluter, 2003; Pfennig et al. 2007b; Violle et al. 2011). Moreover, species that are more similar in reproductive characters are generally more likely to hybridize and interfere with each other during reproduction (Liou and Price, 1994).

As an adaptive response to competition, selection should favor traits that maximize access to resources or successful reproduction while simultaneously minimizing investments associated with obtaining resources/reproduction. A common response is for competing species to diverge in the resources or reproductive trait "space" that they each utilize and thereby minimize the likelihood and costs of competitive interactions. If such divergence leads to trait evolution, and if it arose in direct response to competitively mediated selection, then character displacement is said to transpire (Grant, 1972; Howard, 1993; Schluter, 2000; Dayan and Simberloff, 2005; Pfennig and Pfennig, 2009; Pfennig and Pfennig, 2010, 2012). Character displacement can involve either traits associated with resource use—in which case, "ecological character displacement" occurs—or traits associated with reproduction (e.g., sexual traits or female mate preferences)—in which case, "reproductive character displacement" occurs.

Before proceeding, we must stress two points. First, character displacement may cause species to converge in trait expression if doing so minimizes resource or reproductive competition (e.g., as when two species converge on similar signaling to demarcate feeding territories; Grether et al., 2009). Second, character displacement is not the only evolutionary explanation for why sympatric species often differ; such differences may alternatively arise through "species sorting," in which species that already differ are more likely to coexist (Case and Sidell, 1983; e.g., see Losos, 1992).

Yet, divergent character displacement is commonplace, and it provides a compelling explanation for why even closely related sympatric species typically differ phenotypically, especially in traits associated with resource use and reproduction (reviewed in Howard, 1993; Schluter, 2000; Dayan and Simberloff, 2005; Pfennig and Pfennig, 2009; Pfennig and Pfennig, 2010, 2012). In the sections below, we consider the possible role of character displacement in promoting imperfect mimicry. But first, we examine the evidence for competition between mimics and their models/co-mimics.

4 Evidence for Competition between Mimics and Their Models/Co-mimics

Several studies have documented competition among the members of the same mimicry complex (reviewed in Rainey and Grether, 2007). In the context of Müllerian mimicry, such studies have been motivated by recent theory, which suggests that the costs of negative ecological interactions, such as competition, can be offset by the benefits of positive ecological interactions, such as mutualisms (Gross, 2008). Müllerian mimicry complexes provide an ideal setting in which to evaluate this hypothesis, because Müllerian co-mimics are a particular type of mutualist that share the mortality costs of predator education concerning their unprofitability as prey (Ruxton et al., 2004; Rowland et al., 2007). Moreover, because Müllerian co-mimics must be phenotypically similar and sympatric with each other (in order for mimicry to be effective), there is a priori reason to expect that they would engage in competitive interactions with one another.

In a recent test of this facilitation hypothesis, Elias et al. (2008) studied a diverse community of Neotropical ithomiine butterflies, which are Müllerian mimics. They found that co-mimics have converged in habitat use more than expected by chance (Elias et al., 2008). Furthermore, they found that such convergence could not be explained simply in terms of how closely related co-mimics were to each other (Elias et al., 2008). Thus, these data suggest that co-mimics likely compete (at least for habitat). Elias et al. (2008) therefore concluded that the benefits of Müllerian mimicry outweigh the negative effects of spatial overlap in habitat. A limitation of this study, however, was that it only considered whether co-mimics overlapped in habitat utilization. Although habitat is often a limited resource (Schoener, 1983), the degree to which these butterflies compete within the overlapping habitat is unclear.

Another empirical test of the facilitation hypothesis, however, found a pattern opposite to that predicted by the theory. In particular, Alexandrou and colleagues (2011) evaluated the relative importance of competition versus Müllerian mimicry in determining the local community structure in a species-rich group of neotropical catfish that have converged on both an effective predator deterrent—retractable venomous spines—and a similar warning signal—bold color patterns. The researchers identified 52 different species belonging to 24 different mimicry rings, each composed of two or three sympatric species that shared the same warning coloration. They found that the vast majority of co-mimics differed in resource use, indicating that the benefits of mutualism do not outweigh the need for potential competitors to partition resources (Alexandrou et al., 2011). Interestingly, co-mimics were also less closely related than expected by chance (Alexandrou et al., 2011), suggesting that species-specific dietary differences arose through species sorting (generally, more closely related species should be more ecologically similar and therefore compete more intensely; reviewed in Losos, 2008; Wiens et al., 2010; for experimental support, see Burns and Strauss, 2011). Thus, although the degree to which long-term coexistence can be explained by positive ecological interactions remains unclear, both of the above studies indicate that Müllerian co-mimics compete for resources.

Müllerian co-mimics also risk engaging in deleterious reproductive interactions with each other. For example, many butterfly species of the genus *Heliconius* have converged on the same wing color patterns, owing to Müllerian mimicry (Turner, 1981; Mallet and Gilbert, 1995). However, not only is wing coloration used to signal unpalatability to potential predators, it is also used to signal to prospective mates. For instance, male *H. cydno* and *H. pachinus* use wing color to discriminate conspecific from heterospecific mates (Kronforst et al., 2006). Yet, such convergence in wing color pattern increases the risk of hybridization among co-mimics (Estrada and Jiggins, 2008). Thus, such mistakes in mate choice may favor reproductive character displacement as a means of reducing these costly reproductive interactions.

Above, we focused on Müllerian mimicry. Although few studies have examined competition in Batesian mimicry complexes, resource competition is also likely to arise between Batesian mimics and their models. This is because the simultaneous occurrence of mimics and their models (required for mimicry to be most effective; see Beatty and Franks, 2012) may often necessitate that the two species occupy similar ecological niches, which would potentially cause them to compete with each other for scarce resources. Additionally, as in Müllerian mimicry complexes, if a signal used to dupe potential predators is also used in mate choice, then reproductive competition may occur between the mimic and its model, which could also favor signal divergence.

Thus, prior studies have revealed that Müllerian co-mimics do compete with each other and that, in some cases, the costs of these competitive interactions may be sufficiently great to shape the community structure of the mimicry complex. Although less is known concerning competition in Batesian mimicry complexes, Batesian mimics also likely compete with their models for both resources and successful reproduction.

5 When should Competition Promote Imperfect Mimicry?

Until now, we have not discussed the conditions under which competitively mediated selection should promote imperfect mimicry. In this section, we explicitly consider these conditions.

Generally, for imperfect mimicry to be selectively favored, the ratio of costs to benefits of maintaining a certain degree of mimicry should vary nonlinearly with how perfect the mimetic phenotype is. This is most easily illustrated by envisioning a scenario with linear costs to benefits associated with varying degrees of phenotypic resemblance between a mimic and its model/co-mimics (Fig. 2A). Imagine that on a phenotypic scale ranging from 1–10, where 1 is far from mimicry and 10 is perfect mimicry, moving 1 unit closer to mimicry always gives the same fitness advantage (say, an increase in selection coefficient of 0.2). At the same, if mimicry entails a cost of -0.1 in selection for every unit that a population evolves towards mimicry, the net selection for mimicry will always be 0.1, and imperfect mimicry should ultimately give way to perfect mimicry (Fig. 2A). However, if the selective benefit conferred by mimicry decreases as a population approaches perfect mimicry (Sherratt, 2002; Holen and Johnstone, 2004), but the costs increase rapidly (due to competition, in our hypothesis), there may be an equilibrium point of maximum fitness that is displaced away from perfect mimicry (Fig. 2B).

Such evolution of more or less precise mimicry is likely a dynamic process that depends on a number of factors that influence the strength of both predator-mediated selection and competitor-mediated selection. These factors—which we depict in Fig. 3—can vary both spatially and temporally. Such variation may, in turn, lead to spatial or temporal variation in the strength of selection favoring more or less precise mimicry. Ultimately, however, more imprecise mimicry should evolve whenever predator-mediated selection is weak relative to competitively mediated selection.

Predator-mediated selection should depend, of course, on the abundance of predators, but it should also depend on at least four other factors: the degree of phenotypic overlap between the focal species and its model/co-mimics; the ability of predators to discriminate between the mimic and its model/co-mimics; the availability of alternative prey; and the toxicity of the model/co-mimics (Fig. 3). The strength of competitively mediated selection, by contrast, should depend on three factors (Pfennig and Pfennig, 2012).

First, as with predator-mediated selection, competitively mediated selection depends on the degree of overlap in phenotypes between mimics and their models/co-mimics (Fig. 3). As noted above, the more similar species are in resource-use traits (be they morphological, physiological, or behavioral traits), the more likely they are to compete for resources. Likewise, the more similar species are in reproductive traits (e.g., female preferences or male secondary sexual traits), the more likely they should be to also interfere with each other during reproduction and engage in hybridization.

A second factor determining the strength of selection to avoid resource competition or reproductive interactions with a heterospecific is the actual fitness costs of individual competitive interactions. These fitness costs can vary in different situations or for different types of interactants. For example, in times and places where resources are relatively abundant, competitive interactions are not likely to be costly, and selection to avoid these competitive interactions will therefore be weak. Additionally, species that are closely related may pay lower costs of hybridization (Arnold 1997). When such costs are low, character displacement (and, hence, imprecise mimicry) should be less likely to occur.

Finally, even when interactants are phenotypically similar and competition between them especially costly, selection favoring character displacement will be weak if heterospecific competitors are rarely encountered (Pfennig and Murphy, 2002; Tynkkynen et al., 2004; Pfennig and Pfennig, 2005; Goldberg and Lande, 2006; Anderson and Grether, 2010). Thus, when mimics encounter their models/co-mimics frequently, the strength of competitively mediated should be stronger, and character displacement (and imperfect mimicry) should generally be more likely to occur. Essentially, selection arising from interspecific competition is expected to act in a frequency- or density-dependent manner (of course, changing densities and frequencies of models and mim-

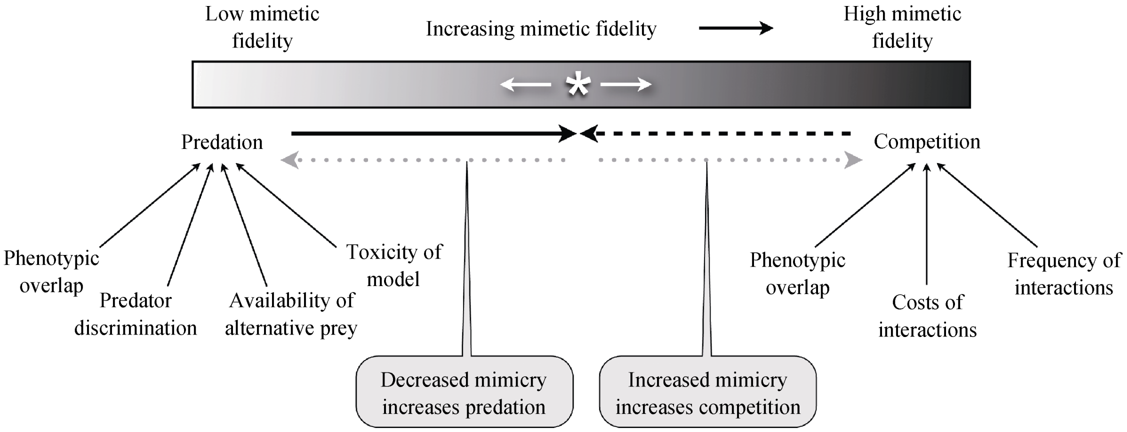

Fig. 3 The evolution of imprecise mimicry is a dynamic process that depends on several factors

In the presence of a noxious/dangerous species, predation-mediated selection may favor mimicry (solid heavy arrow). However, because such phenotypic convergence may heighten competition between mimics and their models/co-mimics (dotted right-facing arrow), competitively mediated selection may favor phenotypic divergence—i.e., imprecise mimicry (dashed heavy arrow). Yet, imprecise mimicry may, in turn, increase predation pressure on the focal species (dotted left-facing arrow), which may (again) favor increased mimicry. The optimal degree of mimicry (denoted by the asterisk) likely varies for different species and populations, depending on factors that influence the relative strength of predator- versus competitively mediated selection.

ics will also affect the strength of *predator*-mediated selection [Sherratt, 2008]). Thus, whether or not mimicry is favored, and how precise it will evolve to be, depends partly on the densities and relative frequencies of mimics and their models/co-mimics.

Imprecise mimicry may arise via either reproductive or ecological character displacement. Reproductive character displacement may generate imprecise mimicry when displays aimed at potential predators are also used to signal to prospective mates, as may be the case in many mimicry systems (Estrada and Jiggins, 2008). Indeed, Müllerian co-mimics may frequently risk costly hybridization with each other (Estrada and Jiggins, 2008). Moreover, even when the incidence or costs of hybridization are low, Müllerian co-mimics might interfere with each other's ability to identify high-quality mates (see above). Additionally, Batesian mimics and their models may similarly run the risk of hybridizing or interfering with each other's reproductive signals, thereby imposing significant costs on each other. Thus, selection may often act to favor reproductive character displacement as a means of reducing costly reproductive interactions between mimics and their models/co-mimics.

Imprecise mimicry may also evolve via ecological character displacement. One way in which imperfect mimicry may arise is when the signal that is used to alert predators is in some way environmentally dependent, such that its production requires some limited resource (e.g., a food item or a particular habitat). In these situations, mimics and models may be thrust into competition with each other for access to this resource. For instance, many toxic fish species alert potential predators of their noxiousness through warning coloration (reviewed in Cott, 1940; Edmunds, 1974), and other species (be they toxic or not) sometime mimic these colors (e.g., Moland et al., 2005; Alexandrou et al., 2011). Moreover, in many fish species, coloration is diet dependent, such that dietary components (e.g., carotenoids) are incorporated into these displays (e.g., Seehausen and van Alphen, 1998; Boughman, 2001). In such a system, if ecological character displacement causes a shift in diet, then the production of mimetic phenotypes may be affected if, in the post-displacement population, the dietary components used to generate the mimetic signal are no longer available or are too costly to obtain.

Competition for space may also promote imprecise mimicry. For instance, mimics and their models/co-mimics may compete for the microhabitat where they can most effectively display their aposematic/mimetic signal to potential predators (e.g., certain butterflies compete for "sunspots" on the forest floor where their coloration may be more visible; Davies, 1978). If this space competition becomes sufficiently costly to outweigh the benefits of an incremental decrease in predation risk, then ecological character displacement may promote a habitat shift, thereby precluding complete signal convergence and precise mimicry.

In sum, although the evolution of more or less precise mimicry is likely a dynamic process (Figs. 2, 3), generally, imprecise mimicry may be most likely to evolve when predator-mediated selection is weak relative to competitively mediated selection. More specifically, competitively mediated selection may favor the evolution of imprecise mimicry when the signal used to dupe predators is also in mate choice, or when, in order to produce a signal needed to dupe potential predators, mimics and their models/co-mimics require the same limited resource whose supply is scarce relative to demand.

6 A Case Study

To illustrate our hypothesis, we discuss a possible case study: a well-known Batesian mimicry complex involving a coral snake and its mimic (coral snake mimicry has been studied for nearly 150 years; see Wallace, 1867; Savage and Slowinski, 1992; Brodie and Brodie, 2004; Greene and McDiarmid, 2005).

The mimicry complex that we focus on here includes two species—the nonvenomous scarlet kingsnake *Lampropeltis elapsoides* and the highly venomous Eastern coral snake *Micrurus fulvius*—both of which co-occur in the southeastern U.S. from Florida to southern North Carolina (Fig. 1A, B). An important feature of this complex is that the geographical range of *L. elapsoides* also extends further north than that of *M. fulvius*; i.e., populations of the mimic also occur in allopatry (Conant and Collins, 1998). Previous studies revealed that free-ranging natural predators avoid plasticine replicas of *L. elapsoides* in sympatry with *M. fulvius* but not in allopatry (Pfennig et al., 2001; Pfennig et al., 2007a; Kikuchi and Pfennig, 2010a), demonstrating that *L. elapsoides* are indeed Batesian mimics of *M. fulvius*.

These two species likely compete with each other for two key resources: food and habitat. As evidence of food competition, *L. elapsoides* deviates from the normal diet of closely related heterospecifics (i.e., other species of snakes in the *L. triangulum* complex), which feed primarily on small rodents, and shifts instead to feeding on small snakes and lizards (Pyron and Burbrink, 2009), which is the same diet as *M. fulvius* (Palmer and Braswell, 1995). Indeed, the two species show a high degree of overlap in diet, especially at the edge of the sympatry/allopatry boundary; i.e., at the northern limit of *Micrurus fulvius*'s geographical range (Palmer and Braswell, 1995). Moreover, they occupy similar microhabitats (Palmer and Braswell, 1995), suggesting that they also likely compete for habitat (e.g., shelter and basking sites).

Interestingly, *L. elapsoides* from different locations vary in how closely they resemble *M. fulvius*, and such geographical variation in mimetic fidelity may reflect character displacement. In particular, the most precise mimics occur at the edge of the sympatry/allopatry boundary ("edge sympatry"). By contrast, relatively imprecise mimics occur in "deep sympatry" (i.e., Florida). Moreover, the relative abundances of the two species also vary geographically. Specifically, although *M. fulvius* is rare at edge sympatry (Harper and Pfennig, 2007), this species is relatively abundant in deep sympatry. Indeed, *M. fulvius* are approximately twice as abundant as *L. elapsoides* in Florida (Harper and Pfennig, 2007).

The observed geographical variation in mimetic fidelity has been ascribed to the relaxed selection hypothesis, which holds that there is little selective benefit to refine mimetic resemblance, if (for example) the model is especially common (see above). By contrast, when mimics are relatively abundant, the likelihood of attacking a model by mistake decreases. In such conditions, predators should be willing to sample all but the best mimics, resulting in selection for more precise mimicry. In support of this hypothesis, field experiments have revealed that, whereas slightly imperfect mimics are selected against by predator-mediated selection at edge sympatry (Harper and Pfennig, 2007), such selection against imperfect mimics is relaxed in deep sympatry, where the model is much more abundant (Kikuchi and Pfennig, 2010a).

However, instead of (or in addition to) relaxed selection, geographical variation in mimetic fidelity may reflect character displacement. In particular, the most precise mimics occur at edge sympatry, where *M. fulvius* is rare, and where the strength of competitively mediated selection imposed by the model on the mimic should therefore be relatively weak. By contrast, the most imprecise mimics occur in deep sympatry, where *M. fulvius* is relatively common. In deep sympatry, *L. elapsoides* should experience much stronger competition from *M. fulvius*, because the latter are relatively abundant. Therefore, there should be much stronger competitively mediated selection acting on *L. elapsoides* to diverge from *M. fulvius* in deep sympatry (recall from the previous section that competitively mediated selection acting on mimics should be especially strong in areas where their model is more abundant). Indeed, not only are mimics more imprecise in deep sympatry than in edge sympatry, mimics in deep sympatry also appear to diverge from their model in *diet*: although the two species show a high degree of diet overlap at edge sympatry (Palmer and Braswell, 1995), the two species appear to be much less similar in diet in deep sympatry (Bartlett and Bartlett, 2003; Jensen et al., 2008).

At present, it is unknown whether competitively mediated selection acting on *L. elapsoides* is stronger in deep sympatry than in edge sympatry. Moreover, even if such selection were stronger in deep sympatry, additional studies are needed to clarify how competitively mediated selection acting on *L. elapsoides* to diverge from *M. fulvius* ecologically could promote morphological divergence. One possibility is that both species may derive from their diet a critical substance used to manufacture pigments needed to produce the distinctive "coral-snake" phenotype. If so, by diverging from *M. fulvius* in diet, *L. elapsoides* in deep sympatry may be unable to produce a high-fidelity mimetic phenotype. However, although *L. elapsoides* and *M. fulvius* share identical color production mechanisms, none of their color pigments appear to be environmentally derived (Kikuchi and Pfennig, 2012a). Further study is needed to determine whether and how competitively mediated selection promotes imperfect mimicry in some populations but not in others in this system.

7 Conclusions and Future Directions

The hypothesis that competitively mediated selection could promote phenotypic divergence between mimics and their models/co-mimics—thereby contributing to imperfect mimicry—is well grounded conceptually. Empirical tests are generally lacking, however. We especially need studies that measure between mimics and their models/co-mimics: (1) niche overlap (for both ecological and "reproductive" niches; *sensu* Yoshimura and Clark, 1994); (2) the mode, magnitude, and direction of selection acting on resource-use and reproductive traits in such species; and (3) the incidence and costs of hybridization and signal interference. Also needed are controlled mate choice tests, in which mimics are offered a choice between conspecifics and models/co-mimics (e.g., see Estrada and Jiggins, 2008).

However, a number of other issues require clarification. Here, we conclude by briefly mentioning a related set of issues that promise to be particularly fruitful areas for future research.

First, data are urgently needed to clarify whether there is a *net* fitness cost of mimicry the more closely a mimic matches its model/co-mimics phenotypically. As described above, theory (Gross, 2008) suggests that the costs of competition can be mitigated by the benefits of Müllerian mimicry. However, empirical tests of this facilitation hypothesis have thus far been mixed (e.g., see Elias et al., 2008; Alexandrou et al., 2011). Thus, the dynamics of factors that govern the relationship between the benefits of Müllerian mimicry and the costs of competition remain unclear.

Additionally, greater effort should go into measuring the net fitness benefits of mimicry in *Batesian* mimicry complexes—from both the mimic's and the *model's* perspectives. Indeed, Batesian mimicry may provide greater opportunity than Müllerian mimicry for studying competitively mediated selection's possible role in promoting imperfect mimicry for the simple reason that, in Batesian mimicry complexes, only the mimic—not the model—realizes any selective benefits of mimicry (from the model's perspective, mimicry is always costly, because it increases the model's predation risk; Ruxton et al., 2004). Therefore, whereas only competition should serve as an agent of selection promoting divergence (and, hence, imprecise mimicry) among mimics, both competition *and predation* should act on models to diverge from their mimic (Gavrilets and Hastings, 1998). In other words, imprecise mimicry may often reflect situations in which models are moving away from their mimics, and such phenotypic divergence on the part of models may be especially likely to occur in situations where competitively mediated selection is strong.

A related issue requiring clarification is whether competitively mediated selection, by itself, could actually favor greater mimetic fidelity between a Batesian mimic and its model. Indeed, circumstances may exist in which *greater* phenotypic similarity between a Batesian mimic and its model could yield a *competitive advantage* to the mimic. Such a situation may have occurred in Batesian mimicry complexes involving harmless hoverflies and stinging Hymenoptera (i.e., bees and wasps; reviewed in Gilbert, 2005).

Hoverflies are generally thought to have evolved hymenopteran mimicry because it affords them protection from predation (see references in Rashed and Sherratt, 2007). However, these resemblances may also confer a *competitive* advantage to mimetic hoverflies (Rashed and Sherratt, 2007). Specifically, a hoverfly that resembles an aggressive, stinging insect may intimidate potential competitors (including bees, wasps, mimetic or non-mimetic flies) that seek to forage on the same flower, thereby benefiting from reduced competition (Rashed and Sherratt, 2007). Although empirical tests have thus far failed to support this "competitive mimicry" hypothesis (Rashed and Sherratt, 2007), it nevertheless remains a compelling explanation for hoverfly mimicry. More research is needed to test this hypothesis, as well as to determine if other circumstances exist under which character displacement may promote convergent trait evolution between mimics and their models.

A further issue requiring additional evaluation is whether alternative avenues exist—other than imprecise mimicry—whereby mimics can reduce costly reproductive interactions with models/co-mimics. Above, we suggested that, as an adaptive response to such costly interactions, selection may favor divergence between species in mating signals/preferences; this divergence is what leads to imperfect mimicry. However, rather than favoring phenotypic divergence, selection may favor the use of entirely different traits in mate recognition. For example, selection may alternatively favor mimics that use a different sensory modality for mate choice; i.e., a communication channel that is both undetectable to predators and different from that used by its models/co-mimics. Because females often rely on multiple cues in mate choice (Candolin, 2003; Hebets and Papaj, 2005), such switches to an alternative sensory modality may occur readily (Hankison and Morris, 2003). By evolving a "private" communication channel, high-fidelity mimicry may be possible without the attendant costs of reproductive competition with other species.

More generally, costly interactions with other species—whether these interactions involve competition for resources or reproduction—can be viewed as a "constraint", which (like most other constraints) can be overcome, given enough time and sufficiently strong selection (see above). Additional studies are needed to evaluate these ideas in the context of mimicry.

Finally, although we have focused throughout this paper on Batesian and Müllerian mimicry, the ideas that we have presented here may apply more generally to other forms of mimicry (Kikuchi and Pfennig, 2012b), including aggressive mimicry. Future studies are also required to investigate the role of competition in promoting imprecise mimicry in other contexts.

In conclusion, as we mark the 150th anniversary of Bates' discovery of mimicry (Bates, 1862), mimicry continues to be an active and important field of inquiry (Ruxton et al., 2004; Forbes, 2009). Clarifying why selection produces remarkable mimicry—and why it often does not—promises to continue to provide novel insights into the evolutionary process.

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