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Batesian mimicry promotes pre- and postmating isolation in a snake mimicry complex

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We evaluated whether Batesian mimicry promotes early-stage reproductive isolation. Many Batesian mimics occur not only in sympatry with their model (as expected), but also in allopatry. As a consequence of local adaptation within both sympatry (where mimetic traits are favored) and allopatry (where nonmimetic traits are favored), divergent, predator-mediated natural selection should disfavor immigrants between these selective environments as well as any between-environment hybrids. This selection might form the basis for both pre- and postmating isolation, respectively. We tested for such selection in a snake mimicry complex by placing clay replicas of sympatric, allopatric, or hybrid phenotypes in both sympatry and allopatry and measuring predation attempts. As predicted, replicas with immigrant phenotypes were disfavored in both selective environments. Replicas with hybrid phenotypes were also disfavored, but only in a region of sympatry where previous studies have detected strong selection favoring precise mimicry. By fostering immigrant inviability and ecologically dependent selection against hybrids (at least in some habitats), Batesian mimicry might therefore promote reproductive isolation. Thus, although Batesian mimicry has long been viewed as a mechanism for convergent evolution, it might play an underappreciated role in fueling divergent evolution and possibly even the evolution of reproductive isolation and speciation.

KEY WORDS: Batesian mimicry, ecological speciation, predation, reproductive isolation.

Batesian mimicry—in which a palatable species (the "mimic") gains protection from predation by resembling an unpalatable or dangerous species (the "model")—has long been used to illustrate how natural selection can promote remarkable convergent evolution between unrelated species (Bates 1862; Wallace 1867; Cott 1940; Wickler 1968; Edmunds 1974; Ruxton et al. 2004; McGhee 2011). However, paradoxically, Batesian mimicry might also promote *divergence*—and possibly even speciation—between populations of a mimic species.

Many (perhaps most) Batesian mimics occur not only in sympatry with their model, but also in allopatry (Pfennig and Mullen 2010). Such populations should experience strong divergent selection: predator-mediated selection should favor the mimetic phenotype in sympatry, but not in allopatry (Pfennig et al. 2001). The transition between selective environments can occur over a narrow spatial scale, thereby promoting local adaptation (Harper and Pfennig 2008; Ries and Mullen 2008). Local adaptation might, in turn, lead to the formation of reproductive isolating mechanisms between such populations and, possibly, "ecological" speciation (Nosil 2012).

For Batesian mimics, at least three factors can act to reduce gene flow between sympatric and allopatric populations (Fig. 1). First, immigrants from one selective environment could be disfavored by predator-mediated natural selection in the alternative environment. For example, individuals bearing the mimetic phenotype (which is locally adapted to the sympatric selective environment) would likely experience enhanced predation if they were to migrate into allopatry. This is because the mimetic phenotype would be conspicuous (Batesian mimics converge on the conspicuous warning signal used by their model; Ruxton et al. 2004),

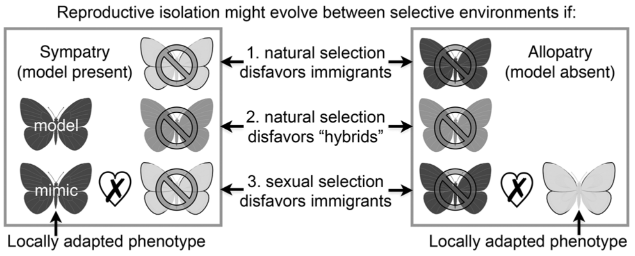

Figure 1. Batesian mimicry might foster ecological speciation by causing barriers to gene flow to arise as a result of ecologically based divergent selection. For example, a mimetic species of butterfly might experience divergent selection on color pattern if it occurs both in the presence of a noxious model (sympatry) and in its absence (allopatry). If these different types of populations become locally adapted to contrasting selective pressures, they might become reproductively isolated from each other owing to at least three different sources of selection (shown here). The present article focuses on sources 1 and 2.

yet unprotected by the presence of the model. Such "immigrant inviability" (sensu Nosil et al. 2005) might serve as a premating isolation mechanism if it lowers the rate of mating encounters between individuals from different selective environments. Indeed, immigrant inviability is thought to play an important role in contributing to reproductive isolation in several systems (Nosil 2012, p. 90). Second, predator-mediated natural selection could also disfavor any "hybrid" offspring produced by matings between sympatric and allopatric individuals: hybrid offspring would likely produce an intermediate phenotype that is poorly adapted to either selective environment. Such ecologically dependent hybrid maladaptation might serve as a postmating isolation mechanism if it acts to reduce gene flow between selective environments (e.g., Rice 1987; Hatfield and Schluter 1999; Rundle 2002; Hendry 2004; Pfennig and Rice 2007). Finally, owing to the previous two factors, selection might favor the evolution of assortative mating by selective environment (e.g., Rundle and Schluter 1998; Rosenblum 2008; Pfennig and Rice 2014; Twomey et al. 2014) via reinforcement (Dobzhansky 1940; Blair 1955; Noor 1999; Servedio and Noor 2003; Coyne and Orr 2004). Such assortative mating could further isolate sympatric and allopatric populations of Batesian mimics.

Whether Batesian mimicry actually initiates reproductive isolation remains untested. This is surprising, given that some of the best support for ecological speciation comes from studies of Müllerian mimicry (e.g., McMillan et al. 1997; Naisbit et al. 2001; Twomey et al. 2014). However, Batesian mimicry may be as widespread as Müllerian mimicry (Kikuchi and Pfennig 2012) and sympatric and allopatric mimics are known to experience strong divergent selection (Harper and Pfennig 2008).

Here, we focus on a well-characterized Batesian mimicry complex to determine if divergent, predator-mediated natural selection disfavors immigrants and sympatric X allopatric hybrids. Our results indicate that such selection may indeed disfavor both immigrants and hybrids, suggesting that Batesian mimicry might promote early-stage reproductive isolation. Thus, although Batesian mimicry has long been viewed as a classic case of convergent evolution, it might play an underappreciated role in diversification.

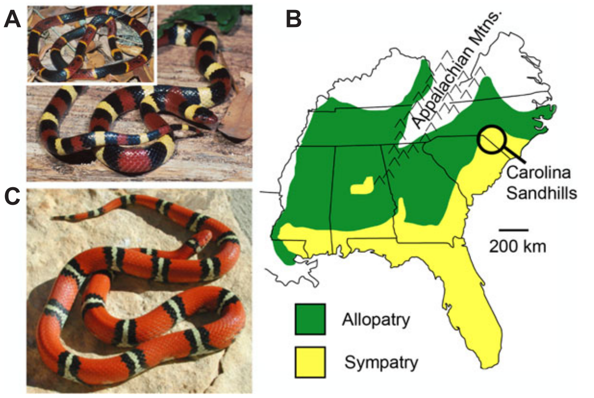

Figure 2. A snake mimicry complex. (A) Nonvenomous scarlet kingsnakes, *Lampropeltis elapsoides*, such as this individual from the Sandhills region of North Carolina, are Batesian mimics of highly venomous eastern coral snakes, *Micrurus fulvius* (inset). (B) *Lampropeltis elapsoides* occur in both sympatry with *M. fulvius* and in allopatry. (C) *Lampropeltis elapsoides* from allopatry, such as this individual from northeastern North Carolina, resemble *M. fulvius* less than *L. elapsoides* from sympatry, reflecting the action of divergent, predator-mediated natural selection on *L. elapsoides* color phenotypes in sympatry versus allopatry. A color version of this figure is available in the online edition of *Evolution*.

Materials and Methods

STUDY SYSTEM

Nonvenomous scarlet kingsnakes (*Lampropeltis elapsoides*) are Batesian mimics of venomous eastern coral snakes (*Micrurus fulvius*; Fig. 2A). Although both species co-occur in the southeastern United States (i.e., in sympatry), *L. elapsoides* also occurs further north (i.e., in allopatry) as a consequence of migration by sympatric *L. elapsoides* into these northern allopatric regions (Fig. 2B). Consistent with Batesian mimicry theory (Wallace 1867; Ruxton et al. 2004), field experiments have found that naturally occurring *sympatric* predators preferentially avoid the mimetic phenotype (Pfennig et al. 2001; Harper and Pfennig 2007, 2008; Kikuchi and Pfennig 2010a,b), whereas *allopatric* predators preferentially attack this phenotype (see *Assessing Immigrant Inviability* below). Presumably because of such divergent selection, allopatric individuals resemble the model less than do sympatric individuals (Fig. 2C; allopatric individuals have more red and less black than do sympatric

Figure 3. Representative replicas of different snake phenotypes used in the field experiments. (Top) Sympatric phenotype, which had the same color proportions and widths of rings as an *L. elapsoides* from sympatry. (Middle) Hybrid phenotype, which had the same color proportions and widths of rings as a sympatric × allopatric hybrid. (Bottom) Allopatric phenotype, which had the same color proportions and widths of rings as an *L. elapsoides* from allopatry (note damage caused by a predation attempt). A color version of this figure is available in the online edition of *Evolution*.

individuals; Harper and Pfennig 2008). Importantly, the direction of this selection shifts over a narrow spatial scale (Harper and Pfennig 2008), fostering local adaptation of color pattern within sympatric and allopatric selective environments.

ASSESSING HYBRID INVIABILITY

To determine if predator-mediated selection disfavors any sympatric × allopatric hybrids that might be formed, we used precolored, nontoxic polymer clay to construct replicas of snakes consisting of three different patterns (Fig. 3): (1) one resembling a sympatric *L. elapsoides*; (2) one resembling an allopatric *L. elapsoides*; and (3) one resembling a sympatric × allopatric hybrid, which are intermediate between allopatric and sympatric *L. elapsoides* in ring width (Williams 1978; Harper 2006). We then placed these replicas in natural areas in both allopatry and sympatry (see Supplemental Information), where they were subjected to predation by naturally occurring, free-ranging predators. Because the replicas consisted of a soft material that took impressions, predation events (and often type of predator) were recorded permanently (e.g., see Fig. 3). This method has been employed successfully to document selection on snake color patterns from both avian and mammalian predators in diverse habitats (e.g., Madsen 1987; Brodie 1993; Brodie and Janzen 1995; Hinman et al. 1997; Pfennig et al. 2001; Wüster et al. 2004; Niskanen and Mappes 2005; Buasso et al. 2006). Clay replicas have also been used to document predator-mediated selection on color patterns in diverse taxa, including salamanders (Kuchta 2005), frogs (Noonan and Comeault 2009), lizards (Husak et al. 2006), and mice (Vignieri et al. 2010).

In placing replicas in the field, we arranged them in pairs (a hybrid and either a sympatric *L. elapsoides* (in sympatric sites) or an allopatric *L. elapsoides* (in allopatric sites)) 1 m apart in the same microhabitat where *L. elapsoides* occur naturally, such as next to logs. We placed 10 such pairs (each approximately 75 m apart) along an approximately 0.75 km transect at each of 16 allopatric sites and 18 sympatric sites. At 34–36 days, we collected the replicas and, based on the presence/absence of tooth and beak marks, scored each as having been attacked or not (as we have done previously; Pfennig et al. 2001, 2007; Harper and Pfennig 2007, 2008; Kikuchi and Pfennig 2010a,b). Three sympatric sites were excluded from the analysis, leaving us with a total of 15 sympatric sites for the analysis (one site was logged, a second site was burned, and at a third site all replicas were likely attacked by a single predator; excluding the last site from the analysis did not qualitatively affect the statistics; the data are presented in the Supplementary Information).

We analyzed attack rates on allopatric × sympatric hybrids against allopatric phenotypes in allopatry and sympatric phenotypes in sympatry. The fate of each replica (attacked or not attacked) was modeled as a function of its phenotype. For both allopatric and sympatric models, the pair and transect in which each replica was placed was included as a random effect to account for the spatial structure of the design (nonrandom predator behavior at different sites could create such structure, and the random effects model controls for this). Specifically, we built generalized linear mixed models with a logit link function using the lme4 package in R 3.02 (R Development Core Team 2013). This package uses the Wald z-test to report P-values for the significance of fixed effects. We also used the likelihood ratio test to confirm the results of the Wald z-tests. In all cases, the two were in agreement, but below (see *Results*) we only present the latter for brevity.

Additionally, for analyses of sympatric sites only, *geographical region* was included as an interaction term in the fixed portion of the model. We placed replicas in two well-defined geographical regions in sympatry: the Sandhills and the coastal plain (the Sandhills are a strip of ancient beach dunes in southern North Carolina and northern South Carolina, which divide the coastal plain from the Piedmont; our analysis included seven Sandhills sites, and eight coastal plains sites). We treated these regions as distinct because recent research has revealed that selection favoring mimicry is particularly strong in the Sandhills of North Carolina (Akcali and Pfennig 2014; see also *Discussion* below).

ASSESSING IMMIGRANT INVIABILITY

Next, we sought to measure immigrant inviability. To do so, we used data from previously published field experiments. Both studies used methods nearly identical to those outlined in the section above on *Assessing Hybrid Inviability*. Moreover, many of the same sites used to assess hybrid inviability were also used in these previous studies to assess immigrant inviability.

Previously, Pfennig et al. (2007) found that the mimetic phenotype (the resident phenotype in sympatry) was attacked by predators in allopatry at a significantly higher rate than expected by chance (see *Results*; note, however, that these earlier authors did not interpret their results in the context of immigrant inviability). Presumably, the mimetic phenotype experiences enhanced predation in allopatry because it is highly conspicuous but unprotected by the model's presence.

However, it is unknown whether immigrant inviability also exists in *sympatry*. Although the allopatric phenotype resembles the model less than does the sympatric phenotype (e.g., see Fig. 2C), this phenotype might nevertheless receive some protection from predation in sympatry (see *Discussion*). To determine if immigrant inviability is present in sympatry, we reanalyzed attack rates on sympatric and allopatric phenotypes in sympatry using data in Kikuchi and Pfennig (2010b). This earlier study compared attacks on a "good mimic" (equivalent to the sympatric phenotype; Fig. 3) relative to those on a "poor mimic" (equivalent to the allopatric phenotype; Fig. 3; the data are presented in the Supplementary Information). Following procedures outlined above in *Assessing Hybrid Inviability*, we modeled the probability of attack as a function of phenotype, with each pair of replicas nested within transect as random effects.

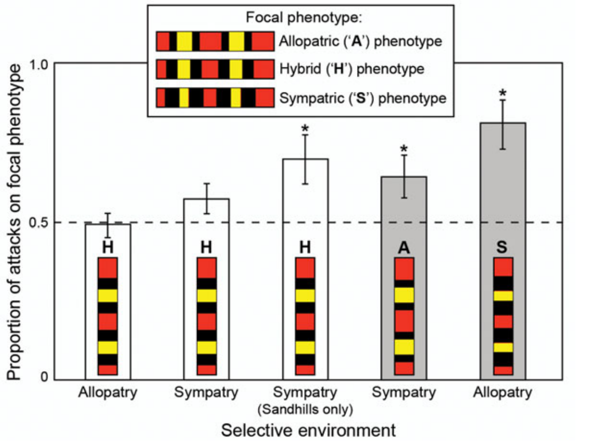

Figure 4. Results of field experiments. Shown is the mean ± SEM proportion of total attacks on the hybrid phenotype (white bars) and immigrant phenotypes (gray bars) in both allopatry and sympatry (and, for the hybrid phenotype, in the Sandhills region of sympatry). *Proportion was significantly greater than random expectation (0.5; dashed line). Data for the sympatric phenotype in allopatry are from Pfennig et al. (2007). Data for the allopatric phenotype in sympatry are from Kikuchi and Pfennig (2010b). A color version of this figure is available in the online edition of *Evolution*.

Results

ASSESSING HYBRID INVIABILITY

In allopatry, attacks on the hybrid phenotype were not significantly different from attack rates on the local, allopatric phenotype (mean ± SEM proportion of attacks on the hybrid phenotype = 0.49 ± 0.04; Wald z-test, $z = 0.864$, $P = 0.387$; Fig. 4). In sympatry, by contrast, patterns of attack rates on the hybrid phenotype were more nuanced: over the entire area of sympatry where we carried out the experiment, we found no evidence of differential attack rates on hybrids versus the local sympatric phenotype (proportion of attacks on the hybrid phenotype = 0.57 ± 0.05; Wald z-test, $z = 1.369$, $P = 0.171$; Fig. 4), nor were overall attack rates different between geographical regions (Wald z-test, $z = 0.452$, $P = 0.651$). However, there was a significant interaction between geographic region and phenotype, with the hybrid phenotype experiencing higher attack rates than the sympatric phenotype in the Sandhills (proportion of attacks on the hybrid phenotype = 0.70 ± 0.08; Wald z-test, $z = -3.616$, $P = 0.0003$; Fig. 4), suggesting that, at least in this region, hybrid inviability was indeed present.

ASSESSING IMMIGRANT INVIABILITY

In our reanalysis of data from sympatry where both sympatric and allopatric phenotypes were exposed to naturally occurring sympatric predators, we found that allopatric phenotypes were attacked significantly more often than sympatric ones (proportion of attacks on the allopatric phenotype = 0.64 ± 0.07; Wald z-test, $z = -2.145$, $P = 0.032$; Fig. 4), suggesting the presence of immigrant inviability in the sympatric selective environment. Together with the results from Pfennig et al. (2007) showing that sympatric phenotypes were attacked in allopatry significantly more often than expected by chance (proportion of attacks on the sympatric phenotype = 0.81 ± 0.08; two-tailed Wilcoxon signed rank test, $P = 0.039$; Fig. 4), we conclude that immigrant inviability exists in *both* selective environments.

Discussion

We evaluated an unexplored route to speciation: Batesian mimicry. Although longstanding theory predicts that mimics should only occur in areas inhabited by their model (sympatry), many mimics violate this prediction and also occupy areas where their model is absent (allopatry). Such populations face opposing selective pressures and should therefore be especially prone to becoming reproductively isolated from each other. In particular, as a consequence of local adaptation within both the sympatric selective environment (where mimetic traits are favored) and the allopatric selective environment (where nonmimetic traits are favored), divergent, predator-mediated natural selection should disfavor any immigrants between these two selective environments, as well as any between-environment hybrids that might be created.

Either factor could act to reduce gene flow between sympatric and allopatric populations, thereby promoting the evolution of reproductive isolation and, possibly, speciation between these selective environments (Fig. 1).

Using field experiments, we measured selection on clay replicas of immigrants and hybrids in different populations of *L. elapsoides*, a Batesian mimic that occurs in sympatry with its coral snake model as well as in allopatry (Fig. 2). We found that: (1) replicas with immigrant phenotypes were disfavored in both sympatry and allopatry, and (2) replicas with hybrid phenotypes were disfavored in one region of sympatry: the Carolina Sandhills (Fig. 4). Depending upon how complete the observed immigrant inviability is (and depending upon whether it acts before immigrants reproduce), it might lower the rate of mating encounters between individuals from different selective environments, in which case it would constitute a premating isolation mechanism. Similarly, the observed ecologically dependent selection against hybrids might act to reduce gene flow between selective environments, in which case it would constitute a postmating isolation mechanism. In either case, our data suggest that Batesian mimicry might indeed foster early-stage reproductive isolation.

We found evidence of hybrid inviability in the Carolina Sandhills only. Previous studies have documented that predator-mediated selection favoring more precise mimicry is especially acute in this region (Harper and Pfennig 2007; Akcali and Pfennig 2014). Presumably, such strong selection reflects the fact that *M. fulvius* has historically been rare in this region (Palmer and Braswell 1995; Beane et al. 2014). Because the probability of mistakenly attacking a coral snake has historically been low in the Sandhills, predators that were more willing to risk attacking imprecise mimics were likely favored (especially during times when prey are scarce), leading to strong directional selection for more precise mimicry (Harper and Pfennig 2007; Akcali and Pfennig 2014). Generally, hybrid inviability might often be present in coevolutionary hotspots where selection favors increasingly precise mimicry.

Although we cannot directly contrast the strength of selection disfavoring immigrants in sympatric versus allopatric environments (because the phenotypes used in our experiments differed between environments), selection might act more strongly against immigrants in the *allopatric* selective environment. Indeed, immigrants were attacked more frequently in allopatry (where 81% of attacks were on the sympatric phenotype) than in sympatry (where 64% of attacks were on the allopatric phenotype; Fig. 4). Such a difference in strength of selection disfavoring immigrants might reflect the fact that the sympatric phenotype in allopatry is conspicuous and entirely undefended, whereas the allopatric phenotype in sympatry should receive *some* protection from predation by resembling the model, especially where the model is common (Harper and Pfennig 2007; Kikuchi and Pfennig 2010a). Predator-mediated selection might similarly differ between sympatric and allopatric selective environments in other Batesian mimicry systems as well.

A number of critical issues remain to be explored to understand Batesian mimicry's role in speciation. Here, we highlight two such issues. First, have sympatric and allopatric populations diverged in mate preferences? In *L. elapsoides*, natural selection disfavors immigrants into both selective environments as well as between-environment hybrids (in at least one region of sympatry). Selection might therefore favor individuals that prefer mates from their own selective environment; that is, assortative mating by population type might evolve. Presently, it is unknown if sympatric and allopatric populations of *L. elapsoides* specifically, or in other Batesian mimics more generally, have indeed evolved mate preferences for members of their own selective environment.

Second, is gene flow between selective environments reduced relative to that within each selective environment? A key prediction of ecological speciation is that there should be enhanced genetic differentiation between population types relative to differentiation within population types, owing to reduced gene flow between adaptively diverging populations (Nosil 2012). Whether gene flow between Batesian mimics in divergent sympatric and allopatric selective environments is reduced relative to that within each selective environment needs to be evaluated.

In sum, although Batesian mimicry has long been regarded as a mechanism of *convergent* evolution (McGhee 2011), it might drive divergence between populations that are locally adapted to different predation regimes (Harper and Pfennig 2008) and, consequently, promote early-stage reproductive isolation that might, ultimately, lead to speciation.

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