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Rapid evolution of mimicry following local model extinction

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Batesian mimicry evolves when individuals of a palatable species gain the selective advantage of reduced predation because they resemble a toxic species that predators avoid. Here, we evaluated whether—and in which direction—Batesian mimicry has evolved in a natural population of mimics following extirpation of their model. We specifically asked whether the precision of coral snake mimicry has evolved among kingsnakes from a region where coral snakes recently (1960) went locally extinct. We found that these kingsnakes have evolved *more precise* mimicry; by contrast, no such change occurred in a sympatric non-mimetic species or in conspecifics from a region where coral snakes remain abundant. Presumably, more precise mimicry has continued to evolve after model extirpation, because relatively few predator generations have passed, and the fitness costs incurred by predators that mistook a deadly coral snake for a kingsnake were historically much greater than those incurred by predators that mistook a kingsnake for a coral snake. Indeed, these results are consistent with prior theoretical and empirical studies, which revealed that only the most precise mimics are favoured as their model becomes increasingly rare. Thus, highly noxious models can generate an 'evolutionary momentum' that drives the further evolution of more precise mimicry—even after models go extinct.

1. Introduction

When selection is strong, evolutionary change can occur in natural populations rapidly enough to observe [1]. Because selection to avoid being eaten is typically strong [2], a context in which rapid evolution may readily arise is Batesian mimicry. Batesian mimicry occurs when an edible species (the 'mimic') evolves to resemble a conspicuous, noxious species (the 'model'), thereby gaining protection from predation [3–5]. The degree of resemblance between mimics and their models is generally sensitive to changes in model abundance [5,6]; mimetic fidelity can decrease or increase, depending on whether the model becomes relatively more or less abundant, respectively [7,8].

How phenotypic resemblance between mimics and their models changes immediately following model extirpation is unclear, however. Three outcomes are possible. First, mimics may remain *unchanged*. Such an outcome might arise if, for instance, there has not been enough time for mimics to respond to changes in model abundance. Second, *less* precise mimicry may evolve [9,10]. Mimicry may break down following model extirpation, because local predators would no longer experience selection to recognize mimics as dangerous [6,11,12]. Third, *more* precise mimicry may evolve. Greater mimetic precision may evolve after model extirpation if alternative prey are abundant, and if the fitness costs associated with mistaking a model for a mimic were historically greater than those associated with mistaking a mimic for a model (as might be the case with highly noxious models). Indeed, theoretical [13–15] and empirical studies [7,8] have shown that only the most precise mimics receive protection from predation when the model becomes increasingly rare (as would be expected to occur when model extirpation is imminent); thus, selection may
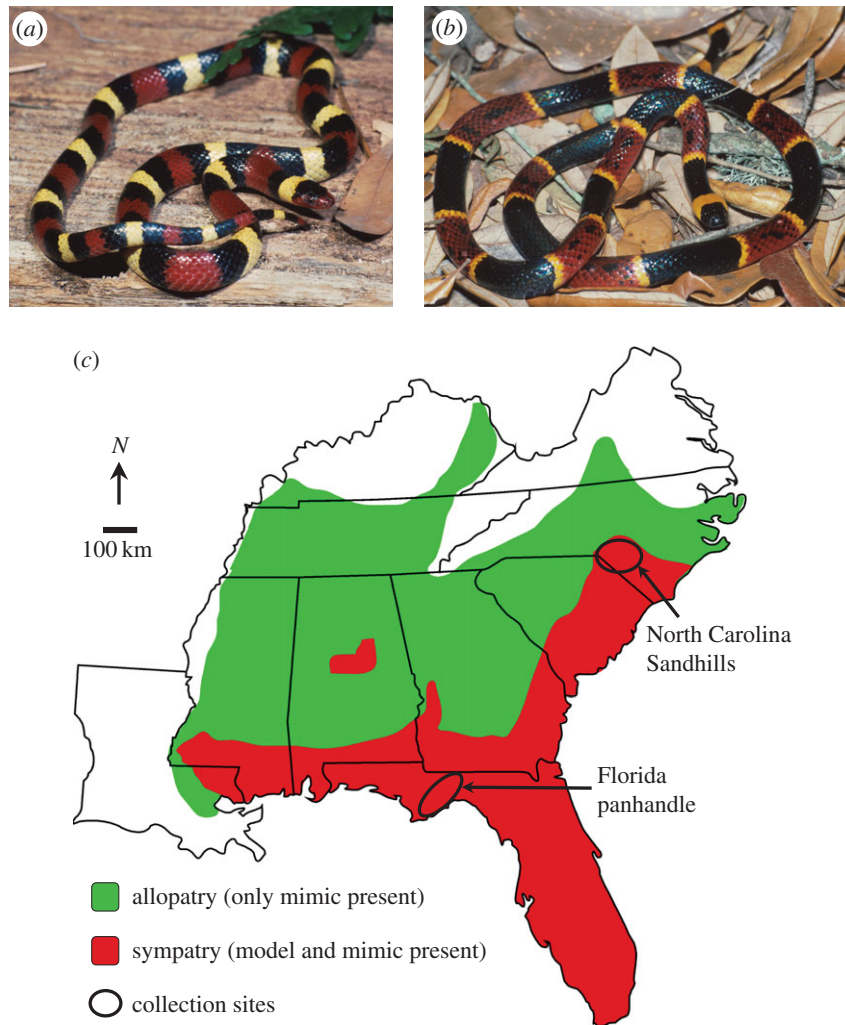
Figure 1. (*a*) Non-venomous scarlet kingsnakes, *Lampropeltis elapsoides*, are Batesian mimics of (*b*) highly venomous eastern coral snakes, *Micrurus fulvius*. (*c*) Historically, *M. fulvius* and *L. elapsoides* co-occurred in the North Carolina Sandhills (as shown here). Around 1960, however, *M. fulvius* was apparently extirpated from this region, but not from the Florida panhandle. (Online version in colour.)

continue to favour the evolution of more refined mimicry, even after the model is gone.

Here, we focus on a well-studied mimicry complex to evaluate whether and how Batesian mimicry evolved following extirpation of the model.

2. Material and methods

(a) Study system

Non-venomous scarlet kingsnakes (*Lampropeltis elapsoides*) resemble venomous coral snakes (*Micrurus fulvius*; figure 1*a,b*). Although both species co-occur in the southeastern US, *L. elapsoides* also occurs further north (figure 1*c*). Field experiments have found that natural predators avoid Plasticine replicas of *L. elapsoides* in sympatry with *M. fulvius* but not in these northern allopatric regions [6], verifying that *L. elapsoides* are Batesian mimics of *M. fulvius*. Moreover, even naive sympatric predators avoid coral snake patterns [16].

Historically, *M. fulvius* reached its northernmost limit in the North Carolina Sandhills [17], a 3900 square kilometres area of gently rolling, sand-covered hills characterized by longleaf pine savannah (figure 1*c*). Local predators include black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), foxes (*Vulpes* and *Urocyon* sp.), raccoons (*Procyon lotor*), hawks (*Buteo* sp.), kestrels (*Falco sparverius*) and loggerhead shrikes (*Lanius ludovicianus*).

Micrurus fulvius has always been considered rare in the Sandhills (only five specimens exist in museums; see the electronic supplementary material), and no recent records exist [17]. Indeed, no specimens have been collected in the Sandhills since 1960 (see the electronic supplementary material), despite extensive activity there by herpetologists [18]. Thus, although the causes are unknown, *M. fulvius* has apparently been extirpated from the Sandhills (or, at the very least, they are so rare that they are *functionally* extirpated). By contrast, *L. elapsoides* are common in the Sandhills [17].

Interestingly, the *L. elapsoides* that most closely resemble *Micrurus* occur in sympatric populations near the sympatry/allopatry border (i.e. 'edge sympatry') [7]. Field experiments have shown that selection for mimicry is strongest in edge sympatry [8]. Because the model is rare in edge sympatry (see above), the probability of mistakenly attacking it is low, and predators are therefore more willing to risk attacking imprecise mimics. Consequently, only precise mimics are favoured in such edge sympatric regions as the Sandhills [7].

(b) Data collection and analysis

To determine whether and how mimicry changed over time, we compared five pre-extirpation *M. fulvius* to 27 post-extirpation *L. elapsoides* from the Sandhills (too few pre-extirpation *L. elapsoides* were available for analysis). These *L. elapsoides* were collected in the 1970s ($n = 5$ individuals), 1980s ($n = 5$), 1990s ($n = 3$), 2000s ($n = 11$) and 2010s ($n = 3$; the electronic supplementary material).

Specimens were photographed using a digital camera (Canon PowerShot SX110; Canon zoom lens, 6.0–60.0 mm, 1 : 2.8–4.3); the width of each ring was measured from digital images using IMAGEJ v. 1.46 [19]. We then calculated the proportions of red and black on the mid-dorsum of each snake from its snout to its cloaca. Previous work showed that these characteristics changed the most as the mimetic pattern breaks down in allopatry [10,11] and that these characteristics are targets of predator-mediated selection [7,8].

We combined the mean proportion of dorsum red and black on mimics and models into a common principal component score. We then subtracted the mean PC1 score for *M. fulvius* from the PC1 score for each individual mimic to calculate a mimic–model dissimilarity score (where a score of zero indicates that *L. elapsoides* and *M. fulvius* were identical in proportion of red and black; for example calculation, see the electronic supplementary material). Using JMP v. 10.0.1, we regressed the dissimilarity score of each *L. elapsoides* against the year it was sampled to determine whether resemblance between *L. elapsoides* and *M. fulvius* changed over time (one outlier was omitted from analysis).

Next, we sought to control for the possibility that any change in *L. elapsoides* colour pattern might reflect not predator-mediated selection favouring mimicry, but some other agent of selection (e.g. a change in light environment following recent anthropogenic changes in habitat). We did so in two ways. First, we assessed whether phenotypic changes similar to those observed among *L. elapsoides* from the Sandhills were observed among *L. elapsoides* from the Florida panhandle, where *M. fulvius* remains abundant (figure 1c). This region is similar to the Sandhills in habitat; moreover, the assemblage of predators is similar across regions. Using the methods above, we compared 23 *M. fulvius* and 23 *L. elapsoides* from the Florida panhandle. The *L. elapsoides* were collected in the 1970s ($n = 13$ individuals), 1980s ($n = 1$), 1990s ($n = 2$), 2000s ($n = 7$; electronic supplementary material). Second, we assessed whether similar phenotypic changes occurred in corn snakes, *Pantherophis guttatus*, a non-mimetic species found in the Sandhills. Like *L. elapsoides*, *P. guttatus* has red and black on its dorsum, but its pattern is characterized by blotches, not rings. Using the methods above, we sampled 82 *P. guttatus* that were collected in the 1970s ($n = 5$ individuals), 1980s ($n = 14$), 1990s ($n = 18$), 2000s ($n = 41$) and 2010s ($n = 4$; electronic supplementary material); these specimens were compared with the five *M. fulvius* from the Sandhills (see above).

3. Results

In 50 years following the apparent extirpation of *M. fulvius*, *L. elapsoides* from the North Carolina Sandhills became more similar to the former in colour pattern ($F_{1,26} = 6.997$; $p = 0.014$; figure 2a). Moreover, these *L. elapsoides* became less variable in colour pattern (Spearman correlation between coefficient of variation in dissimilarity score and decade sampled $= -0.8$; $n = 5$ decades; $p = 0.05$ (one-tailed test)). By contrast, *L. elapsoides* from Florida did not change significantly in mimic–model dissimilarity ($F_{1,22} = 1.417$; $p = 0.247$; figure 2b), nor did *P. guttatus*, a non-mimetic species from the North Carolina Sandhills ($F_{1,81} = 1.028$; $p = 0.314$; figure 2c).

4. Discussion

Theory predicts that mimicry should break down in the absence of models [5]. Indeed, mimicry in *L. elapsoides* breaks down where it occurs in allopatry with its model [10]. However, instead of observing an erosion of mimicry following extirpation of *M. fulvius* from the North Carolina
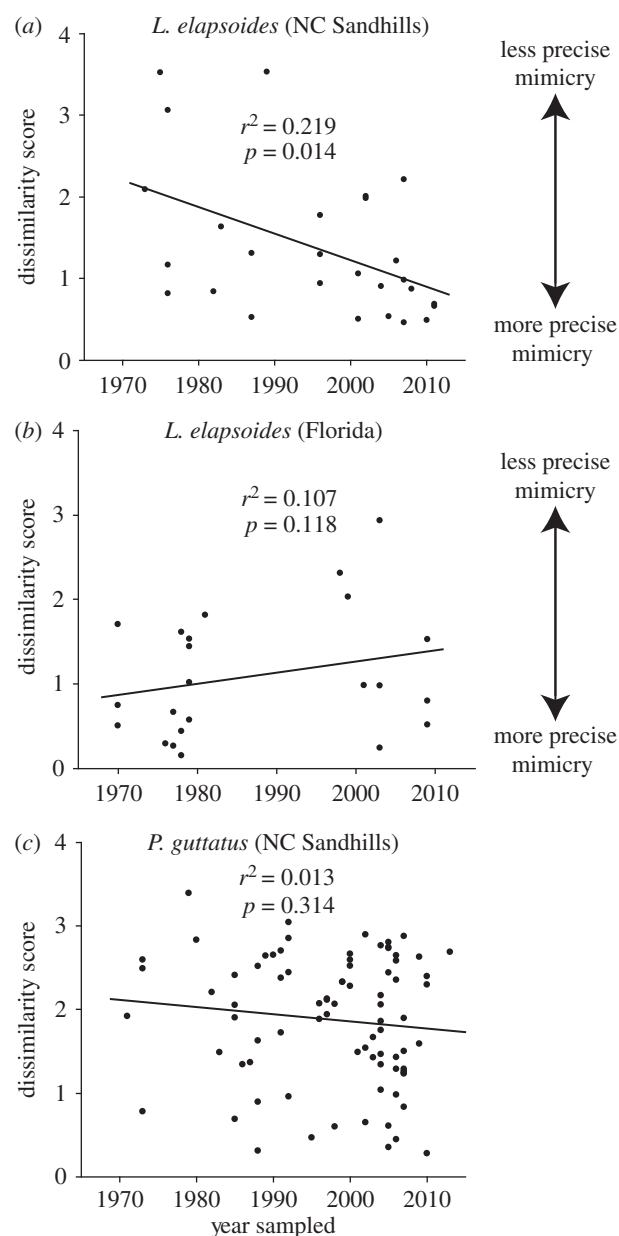

Figure 2. (*a*) Over the past four decades, *L. elapsoides* from the Sandhills (where *M. fulvius* became extirpated around 1960) have become more similar to *M. fulvius*. By contrast, no such trend was found among (*b*) *L. elapsoides* from the Florida panhandle (where *M. fulvius* remains abundant) or (*c*) *P. guttatus* (a non-mimetic species) from the Sandhills.

Sandhills, we observed rapid evolution of more *precise* mimicry (figure 2a). No such pattern was detected among *L. elapsoides* from Florida, where the model has not been extirpated (figure 2b), nor among a non-mimetic species from the Sandhills (figure 2c).

Two lines of evidence suggest that precise mimicry has *evolved* in the Sandhills. First, snakes were sampled over a 38 year interval, twice the maximum lifespan of *L. elapsoides* [20]. Thus, changes occurred across generations. Second, these changes are unlikely to reflect phenotypic plasticity: there is no evidence of plasticity in *L. elapsoides* coloration [21]. Thus, our data (figure 2a) appear to reflect *evolutionary* change.

This rapid evolution of precise mimicry is consistent with theoretical and empirical studies. Theory predicts that selection for mimetic precision should increase as models become scarcer [13–15], as would probably have occurred in the Sandhills. Additionally, field experiments recently

conducted in this population revealed that free-ranging predators only avoid precise (but not imprecise) *L. elapsoides* mimics [7,8]. Thus, predators in the Sandhills continue to exert strong selection for more precise mimicry.

Presumably the generalist predators in the Sandhills [17] are likely to pay a low cost of passing up a palatable meal by mistaking a mimic for a model. By contrast, because *M. fulvius* are highly venomous [22], prior to 1960 (when *M. fulvius* were extirpated), predators were likely to have paid a *high* cost for mistaking a *model* for a *mimic*. This asymmetry in fitness costs explains the strong selection to avoid the model *and* its lookalikes.

Eventually, however, mimicry should break down. How rapidly it does so depends on such factors as the generation times of predators and mimics, the standing variation in coloration among mimics, gene flow between mimics in sympatry versus allopatry [10], and the intensity of selection against mimics.

In sum, our data suggest that, paradoxically, selection imposed on mimics by predators can generate an 'evolutionary momentum' towards more precise mimicry—even after models go extinct.

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