

## SHORT COMMUNICATION

**Geographic variation in mimetic precision among different species of coral snake mimics**C. K. AKCALI\*†  & D. W. PFENNIG\*

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**Abstract**

Batesian mimicry is widespread, but whether and why different species of mimics vary geographically in resemblance to their model is unclear. We characterized geographic variation in mimetic precision among four Batesian mimics of coral snakes. Each mimic occurs where its model is abundant (i.e. in 'deep sympatry'), rare (i.e. at the sympatry/allopatry boundary or 'edge sympatry') and absent (i.e. in allopatry). Geographic variation in mimetic precision was qualitatively different among these mimics. In one mimic, the most precise individuals occurred in edge sympatry; in another, they occurred in deep sympatry; in the third, they occurred in allopatry; and in the fourth, precise mimics were not concentrated anywhere throughout their range. Mimicry was less precise in allopatry than in sympatry in only two mimics. We present several nonmutually exclusive hypotheses for these patterns. Generally, examining geographic variation in mimetic precision – within and among different mimics – offers novel insights into the causes and consequences of mimicry.

**Introduction**

Batesian mimicry evolves when a palatable species (the 'mimic') gains the selective advantage of reduced predation because it resembles a toxic species (the 'model') that predators avoid (Bates, 1862; Ruxton *et al.*, 2004). A long-standing assumption of mimicry theory is that natural selection should favour mimics that precisely resemble their models (Ruxton *et al.*, 2004). However, variation in the degree to which mimics resemble their models (i.e. 'mimetic precision') is common, and explaining why this variation exists can provide key insights into the causes and consequences of mimicry (reviewed in Kikuchi & Pfennig, 2013).

Most studies that have examined variation in mimetic precision have focused on variation between species. For example, colubrid snakes (Pough, 1988), hover flies (Penney *et al.*, 2012; Taylor *et al.*, 2013,

2016a), myrmecomorphic spiders (Pekár *et al.*, 2011) and velvet ants (Wilson *et al.*, 2013) have been shown to vary interspecifically in mimetic precision. Fewer studies have rigorously characterized geographic variation *within* species. Examples include colubrid snakes (Greene & McDiarmid, 1981; Harper & Pfennig, 2007, 2008), red-backed salamanders (Kraemer *et al.*, 2015) and sedge sprites (Iserbyt *et al.*, 2011).

Although there are several nonmutually exclusive selective reasons for why mimics vary in resemblance to their model (reviewed in Kikuchi & Pfennig, 2013), studies of geographic variation in mimetic precision within species have revealed two types of patterns. First, mimetic precision has been shown to vary with the frequency of local models (Harper & Pfennig, 2007; Iserbyt *et al.*, 2011). Generally, mimetic precision should increase as the mimic: model ratio increases (Oaten *et al.*, 1975; Sherratt, 2002; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2013). This outcome occurs because in regions where the model is common, predators should experience strong selection to avoid anything that remotely resembles the model, thereby weakening selection for precise mimicry. In contrast, where the model is rare, selection on predators to avoid the model should be

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relaxed. Consequently, only precise mimics should receive any protection from predation; thus, selection for precise mimicry is expected to be strong in such regions. Because species tend to be rarer at the edges of their range due to selective or demographic constraints (Geber, 2008; Steen & Barrett, 2015), mimics that occur at the edge of their model's range (i.e. 'edge sympatry') should be more precise than those in the centre of their model's range (i.e. 'deep sympatry'). This pattern – known as 'mimicry on the edge' – has been documented in colubrid snakes (Harper & Pfennig, 2007).

Second, the precision of mimics has been shown to decrease in locations where their model is absent; that is, in allopatry (Harper & Pfennig, 2008; Ries & Mullen, 2008). Although long-standing theory predicts that mimics should only occur in regions inhabited by their model (Wallace, 1870; Ruxton *et al.*, 2004), many species of mimics violate this prediction and also occupy regions where their model is absent (Pfennig & Mullen, 2010). Although mimics might benefit from being conspicuous in the absence of models if, for instance, predators innately avoid such signals, mimics that occur in such locations are generally expected to experience selection against mimetic phenotypes because such phenotypes are typically aposematic and thus conspicuous to potential predators (Ruxton *et al.*, 2004). Therefore, mimics are expected to resemble their models less precisely in allopatry, with the degradation of the mimetic phenotype increasing as the distance from the sympatry/allopatry boundary increases. This pattern – dubbed 'mimetic breakdown' – has been reported in colubrid snakes (Harper & Pfennig, 2008) and butterflies (Ries & Mullen, 2008).

How general mimicry on the edge and mimetic breakdown are among mimicry complexes – as well as the underlying causes of such geographic patterns in mimetic precision – is unknown. Here, we characterize geographic variation in mimetic precision among four Batesian mimics of coral snakes. We address three questions. First, how common is mimicry on the edge? Second, how widespread is mimetic breakdown? Finally, what are the possible causes of any such geographic variation in mimetic precision?

## Materials and methods

### Study system and geographic sampling

Several species of harmless colubrid snakes mimic highly venomous New World coral snakes. We focused on four such mimics (Fig. S1). In the south-eastern USA, scarlet kingsnakes (*Lampropeltis elapsoides*) and scarlet snakes (*Cemophora coccinea*) mimic eastern coral snakes (*Micrurus fulvius*). In the southcentral USA, Western milk snakes (*Lampropeltis gentilis*), *C. coccinea*, and the recently described Texas scarlet snake (*Cemophora lineri*; Weinell & Austin, 2017) mimic Texas coral

snakes (*Micrurus tener*). All of the *C. coccinea* and *C. lineri* that co-occurred with *M. tener* were considered to be one mimic (Western *C. coccinea*) as the two species do not differ in any mimetic traits and share the same model. All of the *C. coccinea* that co-occurred with *M. fulvius* were called Eastern *C. coccinea*. All four mimics (*L. elapsoides*, Eastern *C. coccinea*, *L. gentilis* and Western *C. coccinea*) occur in regions where models are abundant (deep sympatry), rare (edge sympatry) and absent (allopatry).

We sampled 2880 snakes, nearly all of which were from museum collections (Table S1): 2053 mimics (841 *L. elapsoides*, 963 Eastern *C. coccinea*, 130 *L. gentilis*, and 119 Western *C. coccinea*) and 827 models (523 *M. fulvius* and 304 *M. tener*). Our sampling regime included most of the geographic range of each model and mimic species within the USA.

### Quantifying mimetic precision

Specimens were photographed using a digital camera (Canon PowerShot SX130 IS; Canon Zoom Lens, 6.0–60.0 mm, 1 : 2.8–4.3); the length of each ring was measured from digital images using ImageJ v. 1.46 (Abramoff *et al.*, 2004). Digital measurements of photographs is one of the most consistent and accurate methods to make length measurements on live and preserved snakes (Astley *et al.*, 2017). We then calculated the proportions of red and black on the mid-dorsum of each snake, from snout to cloaca. We limited our analysis to red and black because these are the predominant colours on both models and mimics and because including all three colours (black, red, and yellow/white) would remove the independence of the characteristics. In addition, previous work has revealed that the proportions of red and black change the most as the mimetic pattern breaks down in allopatry (Pfennig *et al.*, 2007; Harper & Pfennig, 2008) and that these characteristics are targets of predator-mediated selection in the USA (Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b; Pfennig *et al.*, 2015).

Mimetic precision was assessed using previously described methods (Akcali & Pfennig, 2014; Fig. S6; see Figs S9 and S10 for additional sample photographs). Specifically, we combined the proportion of dorsum red and black on mimics and models into a common principal component (PC1) using JMP v. 10.0.1. A 'dissimilarity score' (D) was then computed by taking the absolute value of the difference between the PC1 scores of mimics and models. Thus, higher values of D correspond to less precise mimicry, whereas lower values of D correspond to more precise mimicry.

### Assessing mimicry on the edge

Geographic variation was visualized by constructing phenotypic rasters for each mimic and model using

local inverse distance-weighted (IDW) interpolation of PC1 scores of georeferenced mimic and model specimens. A critical assumption of IDW is that the interpolated traits are spatially autocorrelated (Cromley, 1992). To test for spatial autocorrelation within each mimic and model in PC1, we computed Moran's  $I$ , a commonly used measure of spatial autocorrelation in ecology (Legendre & Fortin, 1989). We calculated values of Moran's  $I$  at varying distances at a 50-km interval up to the highest possible spatial extent. We tested for the significance of the Moran's  $I$  statistic for PC1 locally (at each distance class) as well as globally (at all distance classes) after Bonferroni correction. Spatial outliers were removed prior to conducting IDW analyses in mimics or models that did not meet the assumption of global spatial autocorrelation in PC1 when they were included.

Phenotypic rasters for each mimic and model included all specimens from sympatry, and additionally, for mimics, all allopatric specimens within 30 km of the sympatry/allopatry boundary (Figs S7 and S8). All IDW analyses were conducted at a 1-km resolution, a power function of one, and a fixed radius of inference of 150 km, as spatial autocorrelation tended to be low beyond 150 km (Fig. S2). Although parameter selection can affect the outcome of IDW analyses, most species were sampled thoroughly enough such that estimated surfaces were robust to major changes in parameter values. To visualize geographic patterns of mimic-model resemblance, we took the absolute value of the difference between mimic and model rasters. The resulting raster was then clipped to a geographic range polygon of sympatry. Geographic range data for each mimic and model species (except for *L. gentilis*) were downloaded from the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org), accessed on 1 July 2015). Geographic range polygons were modified by hand according to our own knowledge of species distributions prior to being used in analyses. The geographic range polygon for *L. gentilis* was constructed by hand based on the distribution of vouchered specimens (Werler & Dixon, 2000). All analyses were performed in ArcMap 10.1.

To statistically determine whether mimics exhibit mimicry on the edge, we extracted interpolated PC1 values of models at the location of each mimic specimen and used these values to compute  $D$  scores for each mimic specimen. We then tested for differences in  $D$  between deep sympatric ( $D_{DS}$ ) and edge sympatric ( $D_{ES}$ ) mimics at 50-km intervals from the sympatry/allopatry boundary using two-tailed  $t$ -tests. The sympatry/allopatry boundary was estimated from published accounts (Mount, 1975; Palmer & Braswell, 1995; Werler & Dixon, 2000; Trauth *et al.*, 2004; Jensen *et al.*, 2008) supplemented by recent vouchered records from the VertNet database (<http://portal.vertnet.org/search>) that had accurate locality information. Because  $D_{ES}$  was subtracted from  $D_{DS}$ , positive values indicate that deep

sympatric mimics are more dissimilar (and thus more imprecise) than edge sympatric mimics; negative values indicate that edge sympatric mimics are more precise than deep sympatric mimics; and values close to 0 indicate that edge sympatric and deep sympatric mimics do not differ in  $D$ . The total number of distance classes used varied among mimics and depended on the spatial extent of the sampled specimens. We plotted differences in  $D$  calculated at each distance class against distance from the sympatry/allopatry boundary to visualize how  $D$  changes in sympatry. Thus, mimics with consistently positive differences in  $D$  show 'mimicry on the edge', whereas mimics with consistently negative differences in  $D$  show the opposite pattern – imprecise mimics on the edge.

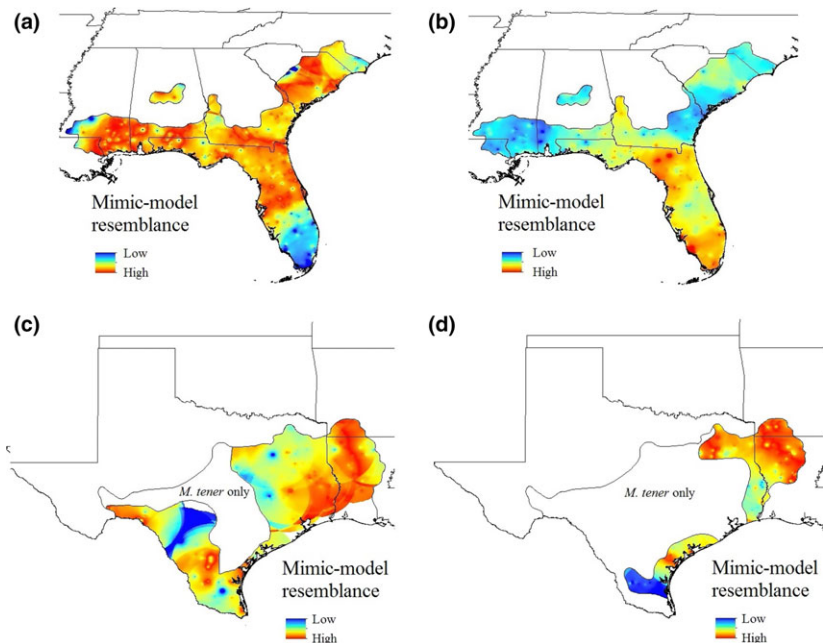
### Assessing mimetic breakdown

To determine whether mimicry breaks down in allopatry, we compared the  $D$  of sympatric mimics (*L. elapsoides*,  $N = 699$ ; Eastern *C. coccinea*,  $N = 663$ ; *L. gentilis*,  $N = 78$ ; Western *C. coccinea*,  $N = 73$ ) and allopatric mimics (*L. elapsoides*,  $N = 142$ ; Eastern *C. coccinea*,  $N = 300$ ; *L. gentilis*,  $N = 52$ ; Western *C. coccinea*,  $N = 46$ ) to their models (*M. fulvius*,  $N = 525$ ; *M. tener*,  $N = 304$ ) using two-tailed  $t$ -tests. Mimicry was considered to break down in allopatry if the  $D$  scores of allopatric mimics were significantly higher than the  $D$  scores of sympatric mimics. To determine whether mimicry degrades with increasing distance into allopatry, we used regression analyses to assess the relationship between the mimetic precision of each snake and distance from the sympatry/allopatry boundary.  $D$  scores for sympatric mimics and allopatric mimics < 30 km from the sympatry/allopatry boundary were generated using the methods described in the previous section.  $D$  scores for allopatric mimics > 30 km from the sympatry/allopatry boundary were generated by comparing the PC1 value of each mimic specimen to the mean PC1 value of their model.

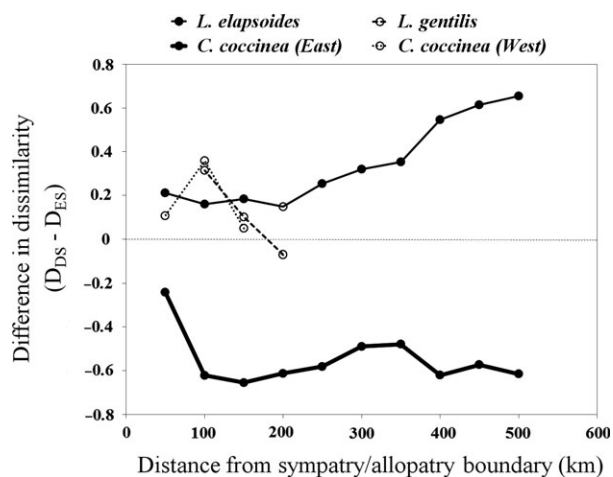
## Results

### Assessing mimicry on the edge

PC1 for all snake species met the assumption of spatial autocorrelation at local and global scales (Fig. S2). Spatial outliers were removed from Western *C. coccinea* prior to conducting IDW analyses to meet spatial autocorrelation assumptions (Fig. S2). Patterns of geographic variation in mimetic precision in sympatry were highly variable among coral snake mimic species (Fig. 1). The difference between  $D_{DS}$  and  $D_{ES}$  was positive in *Lampropeltis elapsoides*, indicating that this species exhibited mimicry on the edge (Figs 1a and 2). In contrast, the difference between  $D_{DS}$  and  $D_{ES}$  was negative in Eastern *C. coccinea* (Fig. 2). Thus, Eastern *C. coccinea*



**Fig. 1** Geographic variation in the resemblance of coral snake mimics (a, *Lampropeltis elapsoides*; b, Eastern *Cemophora cocinea*; c, *Lampropeltis gentilis*; d, Western *C. cocinea*) to their models (a, b, *Micrurus fulvius*; c, d, *Micrurus tener*) in sympatry. Warmer (red) values correspond to low dissimilarity (i.e. precise mimicry); cooler (blue) values correspond to high dissimilarity (i.e. imprecise mimicry).



**Fig. 2** Difference in dissimilarity between deep sympatry (DS) and edge sympatry (ES) mimics of *Lampropeltis elapsoides*, Eastern *Cemophora cocinea*, *Lampropeltis gentilis* and Western *C. cocinea* at varying distances from the sympatry/allopatry boundary. Significant differences (two-tailed *t*-tests;  $P < 0.05$ ) between deep sympatry and edge sympatry are indicated by filled symbols (nonsignificant differences are indicated by open symbols).

did not exhibit mimicry on the edge; instead, the best mimics of Eastern *C. cocinea* were located deep in sympatry (Fig. 1a, b). On the other hand, *L. gentilis* and Western *C. cocinea* did not vary throughout their geographic ranges in sympatry with their model: differences in D were not significant at any distance (Fig. 1c, d and 2).

### Assessing mimetic breakdown

Patterns of mimicry between sympatry and allopatry were also highly variable among coral snake mimic species (Figs 3 and 4). *Lampropeltis elapsoides* and Eastern *C. cocinea* both exhibited mimetic breakdown: mimics in allopatry were more imprecise than those in sympatry (Fig. 4). However, *L. elapsoides* and Eastern *C. cocinea* differ in how their mimetic pattern breaks down over space. In *L. elapsoides*, D is spatially bimodal: D is high deep in sympatry (in southern Florida), low close to the sympatry/allopatry boundary and then becomes high again in allopatry ( $F_{2,840} = 23.047$ ;  $P < 0.0001$ ; Fig. 3a). In Eastern *C. cocinea*, D gradually increases from sympatry to allopatry ( $F_{1,962} = 43.792$ ;  $P < 0.0001$ ; Fig. 3b). *Lampropeltis gentilis* tended to be more precise in allopatry than in sympatry (Fig. 4), with D gradually decreasing across the sympatry/allopatry boundary ( $F_{1,129} = 3.266$ ;  $P = 0.0731$ ; Fig. 3c). Western *C. cocinea* mimics did not differ in D between sympatry and allopatry (Fig. 4) and did not exhibit any spatial variation across the sympatry/allopatry boundary ( $F_{1,118} = 0.635$ ;  $P = 0.4272$ ; Fig. 3d).

### Discussion

Different species of coral snake mimics exhibited different patterns of geographic variation in mimetic precision. Mimicry in *L. elapsoides* was most precise at the edge (Figs 1a and 2) and broke down sharply in allopatry (Figs 3a and 4); mimicry in Eastern *C. cocinea* was

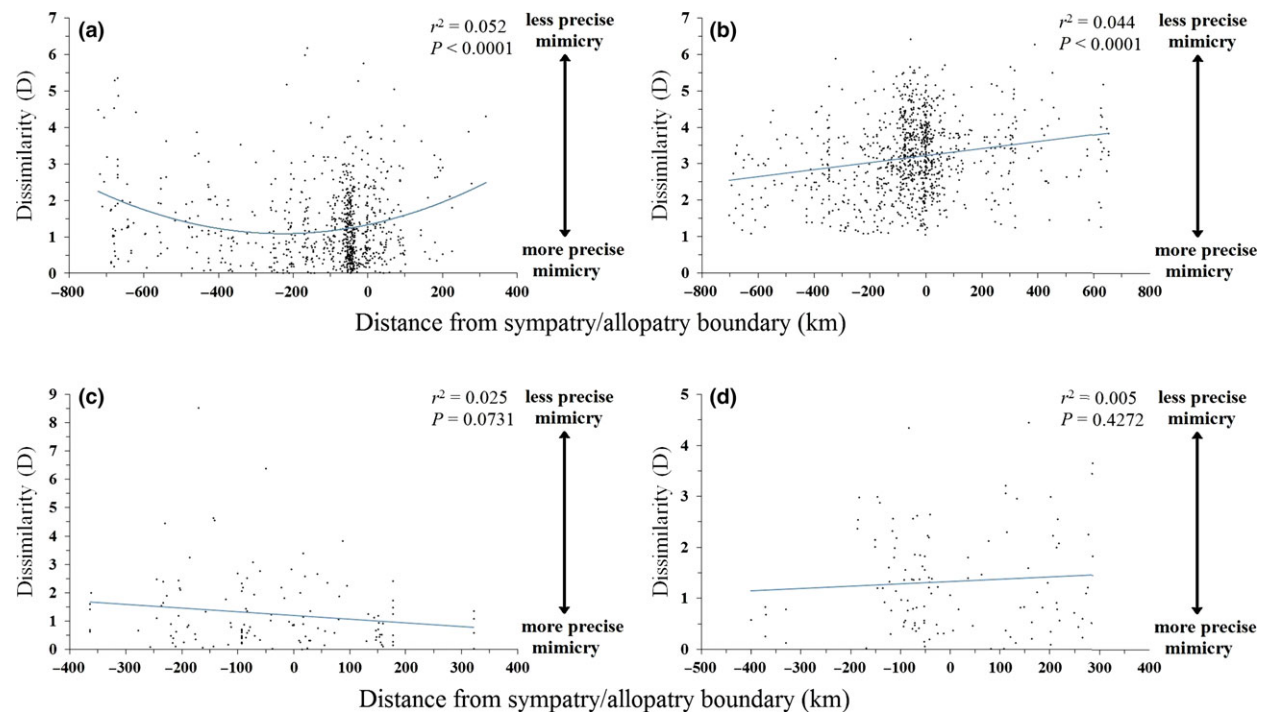
most precise in deep sympatry (Figs 1b and 2) and broke down gradually across the sympatry/allopatry boundary (Figs 3b and 4); mimicry in *L. gentilis* did not vary in sympatry (Figs 1c and 2) and became more precise across the sympatry/allopatry boundary (Figs 3c and 4); and mimicry in Western *C. coccinea* was mostly invariant throughout its range (Figs 1d, 2, 3d, and 4).

Such variable patterns suggest that the causes of geographic variation in mimetic precision likely differ between species. This finding has important implications for mimicry studies. If geographic patterns of mimicry are variable among mimic species more generally, then the field of mimicry would benefit from case studies that conduct more empirical tests of alternative mechanisms that could contribute to explaining such variation (e.g. Harper & Pfennig, 2007, 2008).

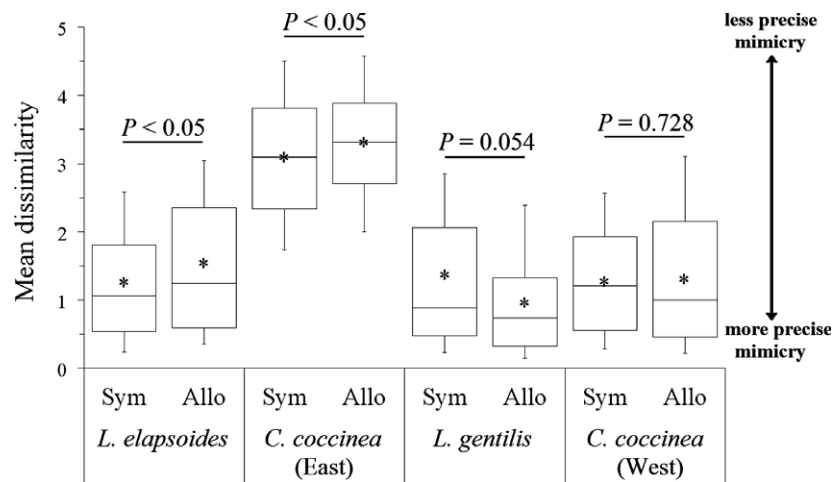
One question to consider is whether these differences in geographic variation in mimicry between species could be explained by the fact that the genetic control of mimetic colour pattern varies among the mimics in our study. Currently, nothing is known of the genetic control of mimetic colour pattern in any of our study species. However, genetic crossing studies of several nonmimetic colubrid snakes, such as kingsnakes (Zweifel, 1981), gopher snakes (Bechtel & Whitecar, 1983), rat snakes (Bechtel & Bechtel, 1985), corn snakes (Bechtel & Bechtel, 1989) and garter snakes (King,

2003), have revealed two major findings: (i) the inheritance of colour and pattern traits tends to be under simple genetic control, and (ii) the genetic control of colour and pattern are independent, but intimately connected, suggesting that loci for colour and pattern traits are genetically linked or in linkage disequilibrium. However, a recent study of a polymorphic coral snake mimic (*Sonora semiannulata*; Davis Rabosky *et al.*, 2016a) has found no evidence that loci for red and black pigmentation are linked or are in linkage disequilibrium. Given that colour and pattern traits are under simple genetic control in a wide variety of nonmimetic and mimetic colubrid snakes, we consider it unlikely that species-specific variation in the genetic control of colour and pattern explains differences in geographic variation in mimicry between the mimic species in our study.

Another important question that follows from our study is how generalized these variable geographic patterns in mimetic precision within sympatry may be across New World coral snake mimics – especially in the tropics, where mimic, model, and colour pattern diversity are higher (Davis Rabosky *et al.* 2016b). It is possible that the patterns of geographic variation in mimetic precision of *L. elapsoides*, *L. gentilis* and *Cemophora* are atypical among New World coral snake mimics because these mimics occur at the northern edges of



**Fig. 3** Geographic variation in mimetic dissimilarity ( $D$ ) of (a) *Lampropeltis elapsoides*, (b) Eastern *Cemophora coccinea*, (c) *Lampropeltis gentilis* and (d) Western *C. coccinea* to their models as a function of the distance from the sympatry/allopatry boundary (i.e. 0). More negative values are deeper into sympatry, and more positive values are deeper into allopatry.



**Fig. 4** Mean dissimilarity of *Lampropeltis elapsoides*, Eastern *Cemophora coccinea*, *Lampropeltis gentilis* and Western *C. coccinea* in sympatry (sym) and allopatry (allo) with their models. Stars indicate means. Box plots show 10th, 25th, 50th (median), 75th and 90th percentiles. Statistical significance was determined using two-tailed *t*-tests ( $P < 0.05$ ).

the distribution of coral snakes, whereas the majority of coral snake mimics that occur in the tropics co-occur with multiple models and are exposed to more diverse predator communities. However, many species of closely related, mimetic *Lampropeltis* occur throughout the New World (Ruane *et al.*, 2014), yet all of these species share the same colour pattern with the mimic species in our study and quantitatively vary in the same traits (C.K. Akcali, unpublished data). Additionally, New World coral snake mimics (as well as their models) from Central and South America show quantitative variation in several colour pattern traits between and within different geographic areas – even in species that are known to exhibit discrete morphs in different populations as well as among polymorphic populations (C.K. Akcali, D.W. Kikuchi, and D.W. Pfennig, unpublished manuscript). Thus, the variable geographic patterns in mimetic precision observed *within* sympatry among the northerly species in our study likely represent a common condition among coral snake mimics generally. Whether the patterns of variation *between* sympatry and allopatry observed in our study are common among coral snake mimics generally cannot be answered as regions of complete allopatry with coral snakes in the tropics are nonexistent.

How general our results will prove to be beyond coral snake mimics is uncertain. Most studies of variation in mimetic precision in insects have examined variation between species (Penney *et al.*, 2012; Taylor *et al.*, 2013; Wilson *et al.*, 2013; Taylor *et al.* 2016b). The few studies that have examined variation in mimetic precision within species in insects (Iserbyt *et al.*, 2011) and other vertebrates (Kraemer *et al.*, 2015) did not examine multiple mimic species. Thus, more analyses of intraspecific variation in mimetic precision need to be conducted in more species in other groups to determine how common such variation is in nature. Indeed, studies of more diverse taxa would also help clarify whether hotspots and coldspots *generally* occur in the

geographical mosaic of coevolution between Batesian mimics and their models (*sensu* Thompson, 2005), as we found in our study (Fig. 1).

Our results suggest several more intriguing questions deserving of future study. For example, why are mimics not always most precise in regions where models are rare, such as at range edges, as predicted by theory (Harper & Pfennig, 2007; Iserbyt *et al.*, 2011; Kikuchi & Pfennig, 2013)? Eastern *C. coccinea* were most precise in deepest sympatry, which is the opposite pattern found in its co-mimic, *L. elapsoides* (compare Fig. 1a, b). A possible explanation is that these two species affect each other's mimicry evolution via character displacement (*sensu* Brown & Wilson, 1956). Phenotypically similar species, such as co-mimics for example (Elias *et al.*, 2008), often compete for resources, successful reproduction, or both, and, as an adaptive response to minimize such costly interactions, selection might cause interacting species to diverge – in both phenotype and habitat (Pfennig & Pfennig, 2012). Such divergence between co-mimics may thereby result in the evolution of imprecise mimicry in one of the mimic species that loses the competition for the mimetic 'niche' (e.g. the microhabitat where the model occurs; Pfennig & Kikuchi, 2012).

Alternatively, *C. coccinea* might fail to show mimicry on the edge if there is a selective trade-off between mimicry and thermoregulation: mimics that occur at higher latitudes might need more black coloration to achieve optimal body temperatures more rapidly (as in hoverflies; see Taylor *et al.*, 2016b). Contrary to this expectation, however, all snake species – both mimics and models – either had less black on their patterns at higher latitudes or did not vary significantly with latitude (Fig. S3). Additionally, although mimics with more black did tend to resemble their models more poorly, mimics with little black on their patterns were just as poor mimics as those with more black on their patterns (Fig. S4).

Lastly, mimics might fail to show mimicry on the edge if selection on smaller mimics is relaxed as a consequence of their lower nutritional content. In other words, there might be a relationship between mimic-model dissimilarity ( $D$ ) and the nutritional content (i.e. body size) of mimics (as in hoverflies; see Penney *et al.*, 2012) that could obscure the effect of model abundance. However, none of the mimic species are known to vary ontogenetically in their coloration, and there is no evidence of plasticity in their coloration (Kikuchi & Pfennig, 2012). Moreover, there was no significant relationship between body size and  $D$  in any of the mimic species (Fig. S5).

Two additional, related questions are as follows: why are *L. gentilis* more precise in allopatry than in sympatry, and why does mimicry fail to break down in Western *C. coccinea*? A possible answer to both questions is that selection might maintain – and even favour – precise allopatric mimicry if predators migrate between sympatric and allopatric regions (Poulton, 1909). For example, migratory birds that exhibit innate (Smith, 1975, 1977) or learned avoidance of coral snakes (e.g. due to their co-occurrence with coral snakes on their overwintering grounds) might subsequently avoid conspicuous lookalikes in areas where coral snakes do not occur (i.e. allopatry). Indeed, the diversity and abundance of raptors that migrate from sympatry with coral snakes into allopatry appears to be higher west of the Mississippi River than in the south-eastern USA (Sauer *et al.*, 2014). Additionally, gene flow among mimics from sympatry into allopatry might also maintain precise allopatric mimicry. For example, gene flow has been shown to be one of the major reasons why mimics of *L. elapsoides* persist in allopatry, despite selection against mimicry in allopatry (Pfennig *et al.*, 2001, 2007; Harper & Pfennig, 2008).

Regardless of why mimicry fails to break down in allopatry, these findings have important implications for Batesian mimicry's role in local adaptation and, potentially, speciation (Pfennig & Mullen, 2010; Pfennig *et al.*, 2015; Davis Rabosky *et al.*, 2016b). Generally, populations of mimics that occur in sympatry with their model vs. those in allopatry are expected to experience contrasting selective pressures (Pfennig *et al.*, 2001). In addition, mimics could also experience contrasting selective pressures if mimics occur on different background substrates in sympatry and allopatry (e.g. *L. elapsoides* would primarily be viewed against deciduous leaf litter by predators in allopatry and against pine needles in sympatry). If these opposing selective pressures lead to the evolution of different locally adapted phenotypes (i.e. mimetic phenotypes in sympatry and nonmimetic phenotypes in allopatry; Harper & Pfennig, 2008; Ries & Mullen, 2008), then selection might further favour the evolution of reproductive isolating barriers – and, possibly, speciation – between such populations (Nosil, 2012). Indeed, at least two isolating

barriers appear to have evolved between sympatric and allopatric populations of *L. elapsoides* (Pfennig *et al.*, 2015). However, if mimicry does not generally break down in allopatry, then Batesian mimicry might not play an important role in promoting local adaptation and speciation. Additional studies are needed to determine how common mimetic breakdown is.

In sum, characterizing variation in mimicry and explaining why such variation exists is critically important for understanding how the complex adaptation of mimicry evolves. Our data suggest that the causes of geographic variation in mimicry differ among mimic species. More detailed case studies of single mimicry complexes are needed to evaluate whether there are any general explanations for the causes of variation in the precision of mimicry in nature.

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## Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

**Figure S1** Coral snake mimics and coral snakes of the southeastern and southcentral United States.

**Figure S2** Moran's  $I$  spatial correlograms for PC1 in *Lampropeltis elapsoides*, Eastern *Cemophora coccinea*, *Lampropeltis gentilis*, Western *C. coccinea*, *Micrurus fulvius*, and *Micrurus tener*.

**Figure S3** Geographic variation in the proportion of dorsum black of (a) *Lampropeltis elapsoides*, (b) Eastern *Cemophora coccinea*, (c) *Lampropeltis gentilis*, (d) Western *C. coccinea*, (e) *Micrurus fulvius*, and (f) *Micrurus tener* as a function of latitude.

**Figure S4** Dissimilarity (D) of (a) *Lampropeltis elapsoides*, (b) Eastern *Cemophora coccinea*, (c) *Lampropeltis gentilis*, and (d) Western *C. coccinea* as a function of proportion of dorsum black.

**Figure S5** Dissimilarity (D) of (a) *Lampropeltis elapsoides*, (b) Eastern *Cemophora coccinea*, (c) *Lampropeltis gentilis*, and (d) Western *C. coccinea* as a function of snout-vent length (SVL).

**Figure S6** Sample measurements and dissimilarity (D)

calculations in two *Lampropeltis elapsoides* specimens.

**Figure S7** Geographic variation in the proportion of red and black and sympatric specimens (specimens in sympatry and within 30 km of the sympatry-allopatry boundary) that were sampled in *Lampropeltis elapsoides* (a), *Micrurus fulvius* (b), and Eastern *Cemophora coccinea* (c).

**Figure S8** Geographic variation in the proportion of red and black and sympatric specimens (specimens in sympatry and within 30 km of the sympatry-allopatry boundary) that were sampled in *Lampropeltis gentilis* (a), *Micrurus tener* (b), and Western *Cemophora coccinea* (c).

**Figure S9** Photographs of *Lampropeltis elapsoides* (a), *Micrurus fulvius* (b), and Eastern *Cemophora coccinea* (c) specimens that illustrate the range of variation in phenotype in each species.

**Figure S10** Photographs of *Lampropeltis gentilis* (a), *Micrurus tener* (b), and Western *Cemophora coccinea* (c) specimens that illustrate the range of variation in phenotype in each species.

**Table S1** Phenotypic and location data for each model and mimic specimen sampled.

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