

# Coevolutionary arms races in Batesian mimicry? A test of the chase-away hypothesis

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Reciprocal selection on harmless Batesian mimics and their defended models has long been hypothesized to spawn coevolutionary arms races. Mimics are thought continuously to experience selection to resemble their models better. Models are thought continuously to experience ‘chase-away’ selection for phenotypes that let them escape from these ‘parasitic’ mimics, especially when the cost of having mimics is high. Although abundant evidence suggests that models affect the evolution of mimics, evidence that mimics affect selection of models is meager in natural systems. Here, we tested whether mimics affect selection of models in a snake mimicry complex. Specifically, we tested whether models show phenotypic signatures of chase-away selection in regions that vary in levels of mimetic parasitism and whether models experience chase-away selection in regions where there are many mimics. Contrary to the predictions of the chase-away hypothesis, we found no evidence that models exhibit phenotypic signatures of chase-away selection or that models experience either directional or disruptive selection favouring extreme phenotypes. The absence of chase-away in a mimicry complex that appears to be primed for it suggests that chase-away in natural systems might be weak, rare or of a different character than has been predicted by theoretical studies of Batesian mimicry.

ADDITIONAL KEYWORDS: aposematism – chase-away – coevolution – *Micrurus* – mimicry – predation.

## INTRODUCTION

Coevolutionary arms races, in which a species evolves defenses against its antagonists, spurs these antagonists to invest in countermeasures, in turn spurring the focal species to evolve even greater defenses, have long been recognized as important mechanisms of evolutionary change (Ehrlich & Raven, 1964; Dawkins & Krebs, 1979; Thompson, 1994). A relatively understudied context in which coevolutionary arms races have been conjectured to arise is Batesian mimicry (Thompson, 1994; Joron & Mallet, 1998), wherein harmless prey (‘mimics’) evolve phenotypic resemblances to defended species that predators avoid (‘models’). Given that the fitness of such mimics depends on the presence of their models, Batesian mimics are predicted to have a close phenotypic resemblance to their models (Fisher, 1930; Ruxton *et al.*, 2004). Likewise, because the efficacy

of model warning signals is reduced as the precision and number of mimics increases (this is often referred to as ‘mimetic load’), models are expected to evolve increasingly distinctive phenotypes that differentiate them from mimics (Poulton, 1890; Sherratt & Franks, 2005; Franks *et al.*, 2009). This reciprocal interaction between mimics and models might, in turn, lead to a coevolutionary arms race (Van Valen, 1973), where mimics continuously experience selection to converge on their models to decrease predation, whereas models continuously experience selection to evolve new phenotypes to escape ‘parasitic’ mimics. Such a process has been dubbed ‘chase-away’ (Fisher, 1930; Gavrillets & Hastings, 1998; Joron & Mallet, 1998; Franks *et al.*, 2009). Models of chase-away evolution predict that: (1) mimics should experience selection to resemble their models when they are imprecise; and (2) models should experience selection to evolve away from mimics when the mimetic load is high.

There is a marked discrepancy in the empirical support for each of these two predictions of chase-away

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selection in Batesian mimicry complexes. Although there are many reasons why mimics might not closely resemble their models (Kikuchi & Pfennig, 2013; Sherratt & Peet-Paré, 2017), numerous studies have shown that mimics can, and often do, experience selection for precise mimicry (Brodie & Brodie, 1980; Brodie, 1993; Ohsaki, 1995; Pfennig *et al.*, 2001; Caley & Schluter, 2003; Harper & Pfennig, 2007). In contrast, evidence that models experience chase-away selection is scarce. One study of mimetic avian brood parasites found convincing evidence that models do evolve away from their mimics (although in this case, the signal receiver and the model are one and the same, and mimics are aggressive, not prey; Spottiswoode & Stevens, 2012). An additional study of a salamander–newt mimicry complex found that toxic newts are likely to experience greater selection for conspicuousness in the presence of their salamander mimics (Kraemer *et al.*, 2015). If conspicuousness is a component of newt warning signals, then this would support chase-away selection. Beyond these studies, there is little evidence of chase-away selection acting on models in Batesian mimicry complexes. This lack of empirical support from natural systems is surprising, given that chase-away dynamics are predicted by many theoretical models of mimicry (Oaten *et al.*, 1975; Gavrillets & Hastings, 1998; Holmgren & Enquist, 1999; Franks & Noble, 2004; Franks *et al.*, 2009). Furthermore, laboratory experiments (e.g. Rowland *et al.*, 2010) have suggested that avian predators may behave in ways that select for chase-away evolution.

We focused on natural populations of a well-characterized Batesian mimicry complex to test for signatures of chase-away. Using morphological analyses, we found that models do not show phenotypic signatures of chase-away selection, and in a field experiment, we found no evidence that models experience chase-away selection. Thus, chase-away might be rarer or of a different character than predicted.

## MATERIAL AND METHODS

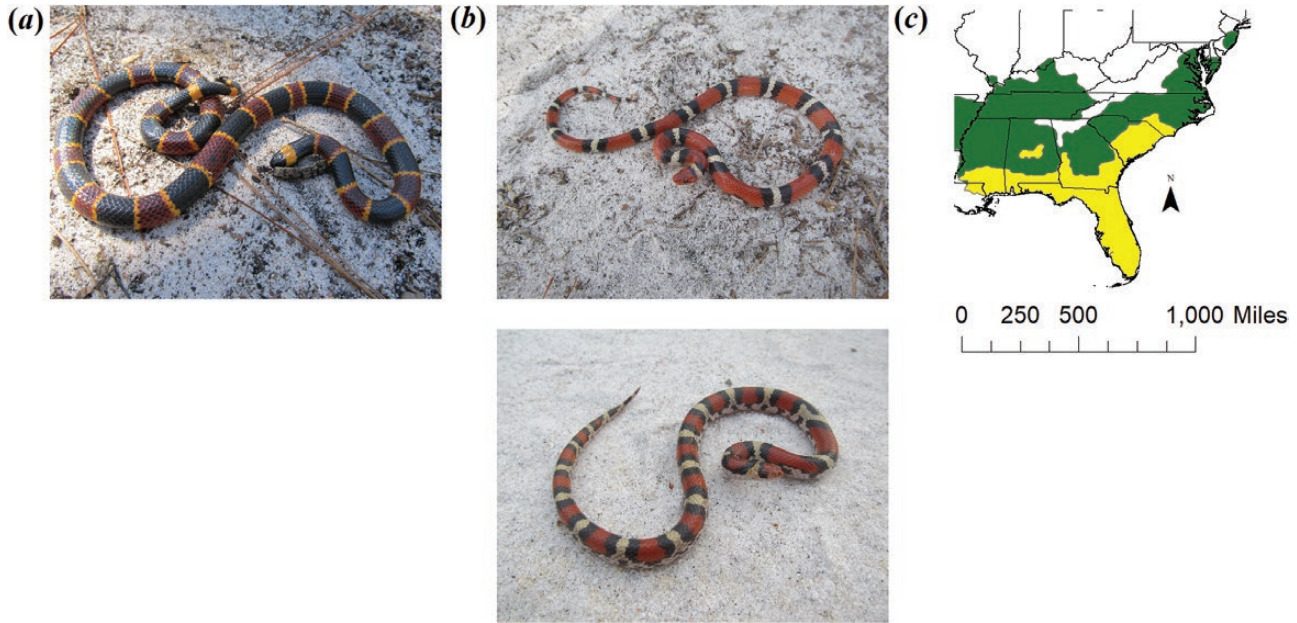
### STUDY SYSTEM

The highly venomous, brightly coloured eastern coral snake (*Micrurus fulvius*) serves as a model for the non-venomous scarlet kingsnake (*Lampropeltis elapsoides*) and scarlet snake (*Cemophora coccinea*) (Fig. 1). Although all three species co-occur in the southeastern USA, both *L. elapsoides* and *C. coccinea* occur well beyond the range of their model (Fig. 1). Consistent with Batesian mimicry theory, field experiments have shown that mimetic phenotypes of *L. elapsoides* are favoured only where *M. fulvius* occurs (i.e. in sympatry) and not where *M. fulvius* is absent (i.e. in allopatry) (Pfennig *et al.*, 2001, 2007; Harper & Pfennig, 2008).

There are at least four reasons to expect chase-away in this mimicry complex. First, the strength of selection on mimics varies geographically. Specifically, selection for precise mimicry is strong on the sympatry–allopatry boundary, as previous field experiments have shown that precise mimetic phenotypes receive more protection from predation than imprecise mimetic phenotypes in this region (Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b; Pfennig *et al.*, 2015). In contrast, selection for precise mimicry is relaxed in deep sympatry (Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a). Second, the ratio of mimics to models varies geographically. On the sympatry–allopatry boundary, mimics greatly outnumber *M. fulvius*; in contrast, the ratio of mimics to *M. fulvius* is low in deep sympatry (Palmer & Braswell, 1995; Harper & Pfennig, 2007). Third, the rate of evolution of mimic colour patterns varies geographically. In at least one population on the sympatry–allopatry boundary, mimics are in the process of rapidly evolving more precise mimicry, whereas mimics in deep sympatry are not evolving at the same rate or in the same direction (Akcali & Pfennig, 2014). Fourth, even within a region (e.g. deep sympatry), mimics vary geographically in mimetic precision, suggesting that different populations might be at different stages of chase-away evolution (Akcali & Pfennig, 2017).

### ASSESSING PHENOTYPIC SIGNATURES OF CHASE-AWAY SELECTION

Chase-away selection should be stronger on the sympatry–allopatry boundary, where mimetic load is high and where mimics experience strong selection for precise mimicry. In contrast, chase-away selection should weaken further away from this boundary as mimetic load attenuates. Thus, if *M. fulvius* has evolved away from the phenotype of its mimics, then it should vary geographically in phenotype (i.e. populations of *M. fulvius* should be at different stages of chase-away evolution), given that chase-away selection should vary geographically depending on the mimetic load. We quantified the phenotypes of 537 *M. fulvius* throughout their range using previously described methods (Akcali & Pfennig, 2014, 2017). Specifically, we measured the proportions of red and black on the mid-dorsum of each snake. We limited our analysis to red and black because these are the predominant colours on both models and mimics, and including yellow would remove the independence of these characters. Previous work has also shown that the proportions of red and black change the most in mimetic snakes (Pfennig *et al.*, 2007; Harper & Pfennig, 2008; Akcali & Pfennig, 2017) and that these characteristics are targets of predator-mediated selection in one mimetic species (*L. elapsoides*) in the southeastern USA (Harper &



**Figure 1.** A coral snake mimicry complex. A, B, the venomous eastern coral snake (*Micrurus fulvius*; A) serves as a model for two non-venomous snake species, the scarlet kingsnake (*Lampropeltis elapsoides*; B, top panel) and the scarlet snake (*Cemophora coccinea*; B, bottom panel). C, both mimics occur well beyond the range of their model in the southeastern USA. Sympatry and allopatry refer to the presence and absence of the model, *M. fulvius*. Range data were downloaded from the IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org)) and were subsequently modified based on point occurrence data obtained from various museums ([www.vertnet.org](http://www.vertnet.org)).

Pfennig, 2007; Kikuchi & Pfennig, 2010a, b; Pfennig *et al.*, 2015). For analysis, we combined the proportion of dorsum red and black on models into a common principal component (PC1). We compared the mean and variance of PC1 between different regions using ANOVA and Levene's test, respectively. We tested for differences in PC1 at varying 25 km distances (from 0 to  $\geq 500$  km) from the sympatry–allopatry boundary [a 25 km interval was chosen so that the smallest number of snakes in a distance class (15 snakes at 225–250 km) was greater than the number of distance classes]. If *M. fulvius* has experienced chase-away evolution, then *M. fulvius* should differ in phenotype between regions where the mimetic load is high (e.g. along the sympatry–allopatry boundary) vs. where the mimetic load is low (e.g. deep sympatry).

#### ASSESSING CHASE-AWAY SELECTION

To determine whether *M. fulvius* experiences chase-away selection, we measured predation rates on different colour pattern phenotypes using artificial snake replicas. This technique has been used successfully to study predation in the field in many taxa and in many regions (Bateman *et al.*, 2017), including the *M. fulvius* mimicry complex (Pfennig *et al.*, 2001, 2007, 2015; Harper & Pfennig, 2007; Kikuchi & Pfennig,

2010a, b). Experiments were conducted in southern North Carolina and adjacent South Carolina, USA, where *M. fulvius* reaches its northernmost extent (Powell *et al.*, 2016) and where it experiences its highest known mimetic load (Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a). Separate experiments were conducted in the spring and autumn to evaluate the temporal consistency of selection (*M. fulvius* is most active in spring and autumn; Jackson & Franz, 1981).

All replicas were constructed with precoloured, non-toxic polymer clay (Sculpey III), following previously described protocols (Kikuchi & Pfennig, 2010a, b; Pfennig *et al.*, 2015). Replicas bearing three phenotypes of *M. fulvius* were constructed, each of which varied in the proportion of red and black (recall from above that proportions of red and black are targets of predator-mediated selection in this region): (1) a phenotype with average amounts of red and black on *M. fulvius* from the Carolinas ('mean phenotype'); (2) a phenotype with 25% more red and 25% less black than the average Carolina *M. fulvius* ('red phenotype'); and (3) a phenotype with 25% more black and 25% less red than the average Carolina *M. fulvius* ('black phenotype'). The red and black phenotypes are found in natural populations of *M. fulvius* (Akcali & Pfennig, 2017). Thus, these two phenotypes represent extreme, but possible, phenotypes found in natural populations

of *M. fulvius*. We constructed 200 replicas per phenotype per season (1200 replicas total).

We hypothesized a priori that finding any one of the following three outcomes would suggest that chase-away selection is acting on the colour pattern of *M. fulvius*: (1) evidence of directional selection favouring the red phenotype (i.e. the red phenotype receives more protection from predation than both the mean and black phenotypes); (2) evidence of directional selection favouring the black phenotype (i.e. the black phenotype receives more protection from predation than both the mean and red phenotypes); or (3) evidence of disruptive selection favouring both the red phenotype and the black phenotype (i.e. the red and black phenotypes both receive more protection from predation than the mean phenotype). Outcomes that would not be consistent with chase-away selection would be: (4) evidence of stabilizing selection favouring the mean Carolina *M. fulvius* phenotype (i.e. the mean phenotype receive more protection from predation than the red and black phenotypes); or (5) evidence of no selection (i.e. all phenotypes being equally protected from predation).

Each of the three phenotypes was arranged into triads (each triad consists of one of each phenotype) in the field 2 m apart (Pfennig *et al.*, 2001, 2007, 2015; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b). We placed ten such triads along a transect at each of 20 sites per season. Triads were separated within transects by ~50–75 m. After 28–30 days, replicas were collected and scored as having been attacked or not (and whether by a mammal or bird) based on the presence or absence of tooth and beak marks (Pfennig *et al.*, 2001, 2007, 2015; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b). Previous studies have shown that mammals exhibit avoidance responses to coral snake colour patterns (Gehlbach, 1972) and that mammalian

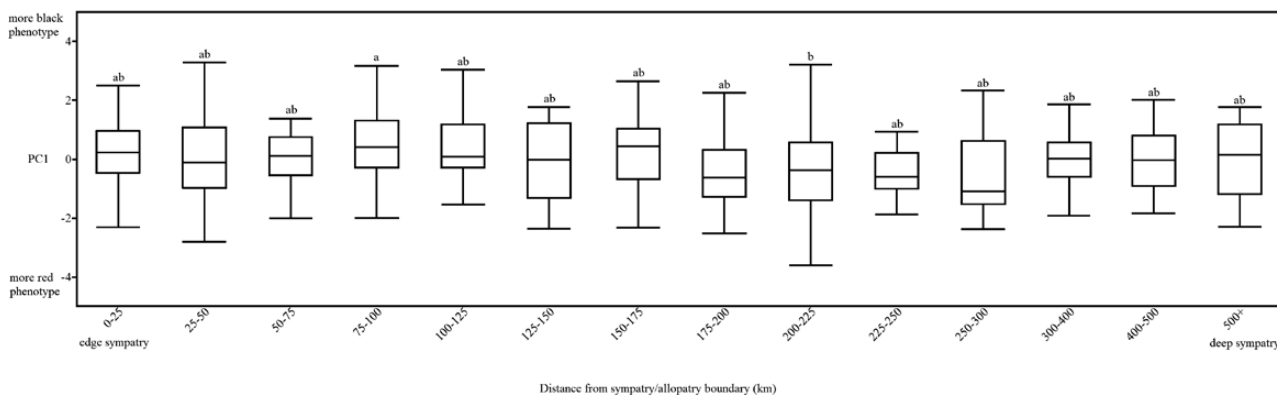
predators (i.e. black bear, *Ursus americanus*; common raccoons, *Procyon lotor*; grey foxes, *Urocyon cinereoargenteus*; and Virginia opossums, *Didelphis virginiana*) preferentially avoid coral snakes and their mimics, compared with other snakes (Pfennig *et al.*, 2001, 2007, 2015; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b; Akcali *et al.*, unpubl. data).

Attack data were analysed with generalized linear mixed models to compare the fitness of the mean Carolina *M. fulvius* phenotype with that of the other two phenotypes across seasons. Specifically, we used a logistic regression, with predation on each replica coded as a binary response variable, the interaction of season and phenotype (both factors) as fixed effects, and the triad within each transect as random effects. The random effects account for spatial autocorrelation in predation. We used the likelihood ratio test (LRT) to verify the significance of fixed effects (Bolker, 2008). In the LRT, the predictor of interest is compared with a model that does not include it; a significant difference in model fit between the two is interpreted as support for the inclusion of the predictor. We used  $\chi^2$  tests to analyse the relative rates of predation by birds and mammals between spring and autumn and the absolute difference in total predation pressure between seasons. Analyses were conducted in R (R Core Team, 2016).

## RESULTS

### ASSESSING PHENOTYPIC SIGNATURES OF CHASE-AWAY SELECTION

*Micrurus fulvius* varied phenotypically in different regions (ANOVA,  $F_{13,536} = 2.533$ ,  $P = 0.0022$ ; Tukey–Kramer HSD,  $P < 0.05$ ; Fig. 2); however, phenotype did not depend on distance from the sympatry–allopatry boundary. Individuals from deepest sympatry



**Figure 2.** Comparison of principal component 1 (PC1; relative proportions of red and black on the dorsum) for *Micrurus fulvius* (the model) at varying distances from the sympatry–allopatry boundary with its mimics. Box plots show tenth, 25th, 50th (median), 75th and 90th percentiles. Means with different superscripts are significantly different ( $P < 0.05$ ; Tukey–Kramer HSD).

(where the mimetic load is low) did not differ significantly in PC1 from individuals from the sympatry–allopatry boundary (where the mimetic load is high; Fig. 2). Moreover, variation in phenotype did not vary with distance from the sympatry–allopatry boundary (Levene’s test,  $F = 0.7242$ ,  $P = 0.7398$ ).

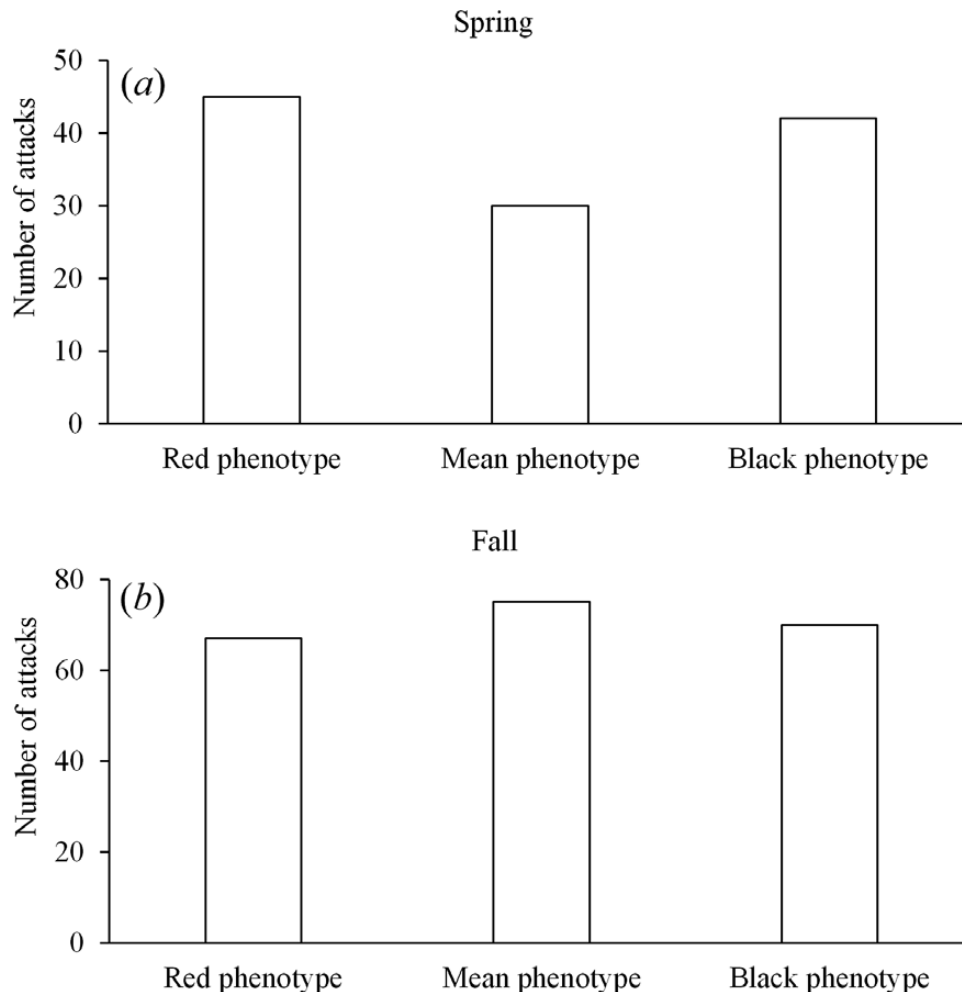
#### ASSESSING CHASE-AWAY SELECTION

Although there was a non-significant trend towards stabilizing selection in the spring (fewer attacks on the mean phenotype), the three phenotypes were equally likely to be attacked; all three phenotypes were also equally likely to be attacked in the autumn (LRT;  $\chi^2_{d.f.=4} = 7.32$ ,  $P = 0.12$ ; Fig. 3). Interestingly, there were more replicas attacked in the autumn than the spring (LRT;  $\chi^2_{d.f.=1} = 7.87$ ,  $P = 0.005$ ; Fig. 3), with attacks by both avian and mammalian predators higher in the autumn (LRT;  $\chi^2_{d.f.=1} = 28.46$ ,  $P < 10^{-4}$ ;

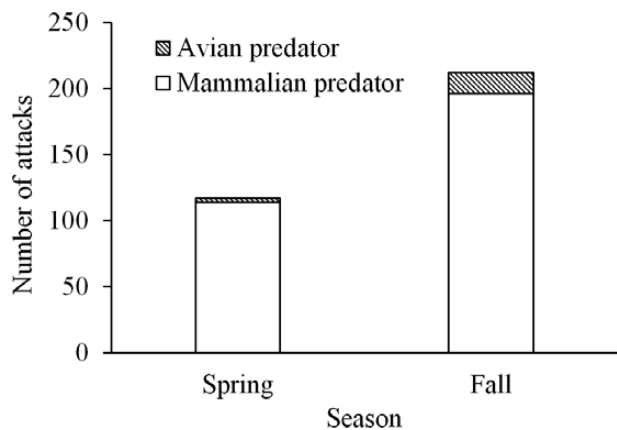
Fig. 4). However, the relative proportion of avian to mammalian predation did not differ between seasons (LRT;  $\chi^2_{d.f.=1} = 2.53$ ,  $P = 0.11$ ).

#### DISCUSSION

We evaluated whether a Batesian mimic and its model participate in a coevolutionary arms race. Batesian mimics and their models have long been hypothesized to be linked in such interactions. Given that the efficacy of model warning signals is reduced as the accuracy and the number of mimics increases, models are expected to evolve increasingly distinctive phenotypes that differentiate them from these ‘parasitic’ mimics. Thus, if chase-away evolution occurs, then models should differ in phenotype between regions where the mimetic load is high (e.g. along the sympatry–allopatry boundary) vs. where it is low (e.g. deep sympatry).



**Figure 3.** Results of field experiments. A, B, the number of attacks on each replica type of *Carolina Micrurus fulvius* in spring 2017 (A) and autumn (Fall) 2017 (B).



**Figure 4.** Number of avian and mammalian attacks on red, black and mean phenotypes of North Carolina *Micrurus fulvius* in the spring and the autumn (Fall) of 2017.

Moreover, if chase-away selection occurs, then models should experience selection to escape from mimics when the mimetic load is high (e.g. when mimics are relatively abundant and under selection for more precise mimicry). Our data are inconsistent with both predictions and do not support the hypothesis that Batesian mimics negatively impact the fitness of their models.

Previous work has shown that both *L. elapsoides* and *C. coccinea* (Batesian mimics of *M. fulvius*; Fig. 1) vary geographically in mimetic precision depending on the local abundance of *M. fulvius* (Harper & Pfennig, 2007; Akcali & Pfennig, 2017). Furthermore, previous work has shown that selection for mimicry varies geographically, with selection favouring precise mimicry being strongest at the sympatry–allopatry boundary (Fig. 1; Pfennig *et al.*, 2001, 2015; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010a, b). These findings therefore confirm that the mimetic load does indeed influence the evolution of mimics. However, in the present study, we did not find the converse; mimetic load did not influence the evolution of models. In particular, we found that *M. fulvius* did vary geographically (Fig. 2), but *M. fulvius* from regions with high and low mimetic loads did not differ, suggesting that chase-away evolution has not occurred separately in different regions in response to variation in mimetic load. Moreover, we found that the three phenotypes used in our experiments received similar protection from predation in both the spring and the autumn (Fig. 3). If this pattern of selection is consistent across years, then the Batesian mimics in our system (*L. elapsoides* and *C. coccinea*) are likely to have a negligible influence on the evolution of the colour pattern of their model (*M. fulvius*). Thus, our data suggest that mimics and models do not coevolve in this mimicry complex, and that chase-away is unlikely to explain the pronounced

geographical variation in mimic–model similarity documented by Akcali & Pfennig (2017).

Predator generalization is theoretically central to driving chase-away, where models that resemble mimics most in phenotype face higher risks of predation (Holmgren & Enquist, 1999; Franks *et al.*, 2009). Therefore, one possible explanation for our finding that attack rates did not differ significantly among phenotypes is that their pattern differences were too small to be detected by predators. In other words, predators could have generalized across all replicas. However, previous field studies have demonstrated that predators from these same sites respond to even smaller differences in mimic phenotypes (Kikuchi & Pfennig, 2010a, b; Pfennig *et al.*, 2015). Alternatively, predators might have detected differences, but the extreme aposematic phenotypes that we selected were not distinctive enough from the mean phenotype to provide any increased protection from the mimetic load, i.e. our extreme phenotypes might not have represented a coevolutionary ‘escape’ from mimics. We also consider this possibility unlikely given that a previous field study (Pfennig *et al.*, 2001) conducted at nearby sites suggests that predators do not avoid an even more distinctive phenotype [red, black and yellow striped (rather than banded) pattern] that does not normally occur on any snakes from the southeastern USA. Although it is conceivable that regions of signal space exist that would allow *M. fulvius* to escape from mimics, these peaks in signal space, if they do exist, are likely to be separated by valleys of low fitness and thus unlikely to be easily evolvable.

The question remains as to whether chase-away selection plays an important role in shaping the colour patterns of coral snakes and their mimics generally. The pattern of selection that we documented on *M. fulvius* might be atypical: *M. fulvius* is the most northerly distributed coral snake and has only two mimic species. Most coral snakes occur in the Neotropics, with many more species of mimics (Davis Rabosky *et al.*, 2016b). Chase-away selection might be present in such regions, where model, mimic and colour pattern diversity are much higher. However, our data suggest that chase-away is unlikely to play a widespread role in coral snakes and their mimics. The effect of chase-away on models is predicted to be strongest in regions with a high mimetic load and, although the mimetic load has not been well characterized for many diverse tropical assemblages of coral snakes, there might be few locations where coral snakes experience as high a mimetic load as the region where our study took place. In this region, coral snakes are exceptionally rare, whereas mimics are abundant, and these mimics are relatively precise (Palmer & Braswell, 1995; Harper & Pfennig, 2007; Akcali & Pfennig, 2017). In the Neotropics, in contrast, the difference in the abundance of coral snakes

and their mimics is reduced, and many of these mimics resemble coral snakes imprecisely (Pough, 1988). Thus, the failure to detect chase-away selection in a model that appears to be primed to experience chase-away selection suggests that chase-away is unlikely to contribute to the evolution of colour patterns in coral snakes and their mimics [note, however, that coral snake species sometimes show substantial geographical variation in colour pattern (Greene & McDiarmid, 1981), suggesting that mimics might, in at least a few instances, play a role in driving diversification of coral snake colour patterns].

More generally, chase-away dynamics might be rare among Batesian mimicry complexes, for at least two reasons. First, mimics should experience stronger selection to converge on their models than models experience to evolve away from their mimics (Nur, 1970). Hence, mimics should always evolve faster than their models. This also means that chase-away selection would be most likely to be present if models experience especially strong fitness trade-offs between phenotypes. For this reason, chase-away might be widespread in egg mimicry complexes involving avian brood parasites and their hosts. In such complexes, hosts face extreme fitness consequences (e.g. the loss of an entire clutch of eggs) if they fail to recognize and reject foreign eggs (Spottiswoode & Stevens, 2012). In the context of defensive mimicry, systems in which aversion of aposematic prey is learned by predators should more readily exhibit chase-away dynamics because learning requires sampling, which might increase the strength of directional selection for distinctive model phenotypes (Franks *et al.*, 2009). In contrast, systems in which predators exhibit innate aversion of aposematic prey (as might occur in coral snakes; Smith, 1975, 1977) should generally reduce the likelihood that chase-away would occur, especially over short time scales (Franks *et al.*, 2009).

A second reason why chase-away dynamics are likely to be rare in Batesian mimicry complexes is that the warning signals of models (like those of all aposematic species) are generally expected to be under strong stabilizing selection (Fisher, 1930). Indeed, theory predicts that predation will select for uniformity of warning signals, thereby enhancing the ability of predators to recognize and learn to avoid such signals (Ruxton *et al.*, 2004). Consequently, once a warning signal has initially evolved, predator-mediated selection is expected to favour the most common (conspicuous) phenotype (Lindstedt *et al.*, 2011). Such stabilizing selection to maintain the effectiveness of the warning signal might offset any directional or disruptive (chase-away) selection to evolve away from parasitic mimics.

Finally, another crucial issue to explore is the significance of temporal variation in predation on the

evolution of aposematism. We found that attacks were higher in the autumn than in the spring (Fig. 4). This might reflect an increased abundance in the autumn of young (potentially, naïve) predators. Indeed, this pattern is consistent with other studies in seasonal environments (Mappes *et al.*, 2014) that have found that an increase in naïve predators at certain times of the year can make aposematism selectively disadvantageous, because uneducated predators make up a larger proportion of the predator community in the autumn and winter. This result is also interesting when considering that the model, *M. fulvius*, has a slightly higher surface activity peak in autumn than in spring (Jackson & Franz, 1981), whereas the mimics tend to be more surface active during the spring months (Palmer & Braswell, 1995). Thus, frequency dependence on the mimic and model patterns might be responsible for driving temporal variation in selection, as has been documented in other coral snake mimicry complexes (Cox & Davis Rabosky, 2013; Holmes *et al.*, 2017). The ultimate effect of this temporal variation in predation depends on whether the avoidance of coral snake colour patterns is innate or learned. Which predators in the southeastern USA exhibit innate or learned avoidance of coral snake colour patterns remains to be evaluated.

This study is also consistent with a growing body of evidence that coral snake mimicry often fails to meet general predictions of mimicry theory that frequently apply to other well-characterized mimicry complexes, such as butterflies (Kunte, 2009), hoverflies (Penney *et al.*, 2012) and spiders (Ceccarelli & Crozier, 2007). Coral snake mimics are more species rich and abundant than models in much of the New World (Davis Rabosky *et al.*, 2016b). In addition, the genetic architecture of colour pattern in coral snake mimics might facilitate the rapid gain and loss of coral snake coloration (Davis Rabosky *et al.*, 2016a). Here, we show that mimics do not appear to affect the evolution of models as would be expected from predictions of chase-away theory.

In sum, although chase-away has long been thought to contribute to the evolution of Batesian mimicry complexes, its general importance in Batesian mimicry, especially of coral snakes, remains unclear. More work in natural systems is needed to assess the significance of chase-away mechanisms in the evolution of mimics and models generally.

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## REFERENCES

- Akcali CK, Pfennig DW. 2014.** Rapid evolution of mimicry following local model extinction. *Biology Letters* **10**: 20140304.
- Akcali CK, Pfennig DW. 2017.** Geographic variation in mimetic precision among different species of coral snake mimics. *Journal of Evolutionary Biology* **30**: 1420–1428.
- Akcali CK, Pérez-Mendoza HA, Salazar-Valenzuela D, Guayasamin JM, Pfennig DW.** Unpubl. data.
- Bateman PW, Fleming PA, Wolfe AK. 2017.** A different kind of ecological modelling: the use of clay model organisms to explore predator–prey interactions in vertebrates. *Journal of Zoology* **301**: 251–262.
- Bolker BM. 2008.** *Ecological models and data in R*. Princeton: Princeton University Press.
- Brodie ED Jr, Brodie ED III. 1980.** Differential avoidance of mimetic salamander by free-ranging birds. *Science* **208**: 181–182.
- Brodie ED III. 1993.** Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution* **47**: 227–235.
- Caley MJ, Schluter D. 2003.** Predators favour mimicry in a tropical reef fish. *Proceedings of the Royal Society B: Biological Sciences* **274**: 1955–1961.
- Ceccarelli FS, Crozier RH. 2007.** Dynamics of the evolution of Batesian mimicry: molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. *Journal of Evolutionary Biology* **20**: 286–295.
- Cox CL, Davis Rabosky AR. 2013.** Spatial and temporal drivers of phenotypic diversity in polymorphic snakes. *The American Naturalist* **182**: E40–E57.
- Davis Rabosky AR, Cox CL, Rabosky DL. 2016a.** Unlinked Mendelian inheritance of red and black pigmentation in snakes: implications for Batesian mimicry. *Evolution* **70**: 944–953.
- Davis Rabosky AR, Cox CL, Rabosky DL, Title PO, Holmes IA, Feldman A, McGuire JA. 2016b.** Coral snakes predict the evolution of mimicry across New World snakes. *Nature Communications* **7**: 11484.
- Dawkins R, Krebs JR. 1979.** Arms races between and within species. *Proceedings of the Royal Society of London B: Biological Sciences* **205**: 489–511.
- Ehrlich P, Raven P. 1964.** Butterflies and plants: a study in coevolution. *Evolution* **18**: 586–608.
- Fisher RA. 1930.** *The genetical theory of natural selection*. Oxford: Clarendon Press.
- Franks DW, Noble J. 2004.** Batesian mimics influence mimicry ring evolution. *Proceedings of the Royal Society B: Biological Sciences* **271**: 191–196.
- Franks DW, Ruxton GD, Sherratt TN. 2009.** Warning signals evolve to disengage Batesian mimics. *Evolution* **63**: 256–267.
- Gavrilets S, Hastings A. 1998.** Coevolutionary chase in two species systems with applications to mimicry. *Journal of Theoretical Biology* **191**: 415–427.
- Gehlbach FR. 1972.** Coral snake mimicry reconsidered: the strategy of self-mimicry. *Forma et Functio* **5**: 311–320.
- Greene HW, McDiarmid RW. 1981.** Coral snake mimicry: does it occur? *Science* **213**: 1207–1212.
- Harper GR, Pfennig DW. 2007.** Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society B: Biological Sciences* **274**: 1955–1961.
- Harper GR, Pfennig DW. 2008.** Selection overrides gene flow to break down maladaptive mimicry. *Nature* **451**: 1103–1106.
- Holmes IA, Grundler MR, Davis Rabosky AR. 2017.** Predator perspective drives geographic variation in frequency-dependent polymorphism. *The American Naturalist* **190**: E78–E93.
- Holmgren NMA, Enquist M. 1999.** Dynamics of mimicry evolution. *Biological Journal of the Linnean Society* **66**: 145–158.
- Jackson DR, Franz R. 1981.** Ecology of the eastern coral snake (*Micrurus fulvius*) in northern peninsular Florida. *Herpetologica* **37**: 213–228.
- Joron M, Mallet JLB. 1998.** Diversity in mimicry: paradox or paradigm? *Trends in Ecology & Evolution* **13**: 461–466.
- Kikuchi DW, Pfennig DW. 2010a.** High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test. *Proceedings of the Royal Society B: Biological Sciences* **277**: 1041–1048.
- Kikuchi DW, Pfennig DW. 2010b.** Predator cognition permits imperfect coral snake mimicry. *The American Naturalist* **176**: 830–834.
- Kikuchi DW, Pfennig DW. 2013.** Imperfect mimicry and the limits of natural selection. *Quarterly Review of Biology* **88**: 297–315.
- Kraemer AC, Serb JM, Adams DC. 2015.** Batesian mimics influence the evolution of conspicuousness in an aposematic salamander. *Journal of Evolutionary Biology* **28**: 1016–1023.
- Kunte K. 2009.** The diversity and evolution of Batesian mimicry in *Papilio swallowtail* butterflies. *Evolution* **63**: 2707–2716.
- Lindstedt C, Eager H, Ihalainen E, Kahilainen A, Stevens M, Mappes J. 2011.** Direction and strength of selection by predators for the color of the aposematic wood tiger moth. *Behavioral Ecology* **22**: 580–587.
- Mappes J, Kokko H, Ojala K, Lindström L. 2014.** Seasonal changes in predator community switch the direction of selection for prey defences. *Nature Communications* **5**: 5016.
- Nur U. 1970.** Evolutionary rates of models and mimics in Batesian mimicry. *The American Naturalist* **104**: 477–486.
- Oaten A, Pearce CEM, Smyth MEB. 1975.** Batesian mimicry and signal detection theory. *Bulletin of Mathematical Biology* **37**: 367–387.
- Ohsaki N. 1995.** Preferential predation of female butterflies and the evolution of Batesian mimicry. *Nature* **378**: 173–175.
- Palmer WM, Braswell AL. 1995.** *Reptiles of North Carolina*. Chapel Hill: University of North Carolina Press.
- Penney HD, Hassall C, Skevington JH, Abbott KR, Sherratt TN. 2012.** A comparative analysis of the evolution of imperfect mimicry. *Nature* **483**: 461–464.



- Pfennig DW, Akcali CK, Kikuchi DW. 2015.** Batesian mimicry promotes pre- and post-mating isolation in a snake mimicry complex. *Evolution* **69**: 1085–1090.
- Pfennig DW, Harcombe WR, Pfennig KS. 2001.** Frequency-dependent Batesian mimicry. *Nature* **410**: 323.
- Pfennig DW, Harper GR, Brumo AF, Harcombe WR, Pfennig KS. 2007.** Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. *Behavioural Ecology and Sociobiology* **61**: 505–511.
- Pough FH. 1988.** Mimicry of vertebrates: are the rules different? *The American Naturalist* **131**: 67–102.
- Poulton EB. 1890.** *The colours of animals: their meaning and use especially considered in the case of insects*. New York: D. Appleton and Company.
- Powell R, Conant R, Collins JT. 2016.** *Peterson field guide to reptiles and amphibians of Eastern and Central North America, 4th edn*. Boston: Houghton Mifflin Harcourt.
- R Core Team. 2016.** R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available at: <http://www.R-project.org/>
- Rowland HM, Mappes J, Ruxton GD, Speed MP. 2010.** Mimicry between unequally defended prey can be parasitic: evidence for quasi-Batesian mimicry. *Ecology Letters* **13**: 1494–1502.
- Ruxton GD, Sherratt TN, Speed MP. 2004.** *Avoiding attack: the evolutionary ecology of crypsis, warning signals, and mimicry*. Oxford: Oxford University Press.
- Sherratt TN, Franks DW. 2005.** Do unprofitable prey evolve traits that profitable prey find difficult to exploit? *Proceedings of the Royal Society B: Biological Sciences* **272**: 2441–2447.
- Sherratt TN, Peet-Paré CA. 2017.** The perfection of mimicry: an information approach. *Proceedings of the Royal Society B: Biological Sciences* **372**: 20160340.
- Smith SM. 1975.** Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**: 759–760.
- Smith SM. 1977.** Coral-snake pattern recognition and stimulus generalization by naïve great kiskadees (Aves: Tyrannidae). *Nature* **265**: 535–536.
- Spottiswoode CN, Stevens M. 2012.** Host-parasite arms races and rapid changes in bird egg appearance. *The American Naturalist* **179**: 633–648.
- Thompson JN. 1994.** *The coevolutionary process*. Chicago: University of Chicago Press.
- Van Valen L. 1973.** A new evolutionary law. *Evolutionary Theory* **1**: 1–30.