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Predator-based selection and the impact of edge sympatry on components of coral snake mimicry

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Abstract

Mimicry is a vivid example of how predator-driven selection can impact phenotypic diversity, which itself can be influenced by the presence (sympatry) or absence (allopatry) of a dangerous model. However, the impact of sympatry and allopatry on predation on mimicry systems at fine spatial scales (e.g., edge sympatry, allopatry) is not well understood. We studied mimicry in a montane tropical site in Honduras with an abrupt elevational gradient where coral snakes and mimics exist in close sympatry and allopatry. Specifically, we used clay replicas to test the impact of edge sympatry on (1) overall attack rates, (2) the fitness benefit of mimetic coloration, and (3) predation on specific mimetic signal components. Unlike previous research, we found that mimetic phenotypes received significantly more attacks than cryptic replicas in edge sympatry, suggesting that mimetic phenotypes might not confer a fitness benefit in areas of edge sympatry. Additionally, we documented temporal variation in predator-based selection, as the impacts of allopatry on predatory attacks varied among years. Our results imply that the effect of sympatry and allopatry on predator-based selection in mimicry systems may be more complex than previously thought for species-rich assemblies of coral snakes and their mimics in the montane tropics.

Keywords Natural selection · Batesian mimicry · Sympatry · Allopatry · Aposematism · Predation · Antipredator traits

Introduction

Our understanding of the origins of phenotypic diversity has been informed by studying the evolutionary drivers of antipredator traits such as warning coloration (e.g. aposematism) and mimicry (Brodie III 1993; Brodie III and Janzen 1995; Ham et al. 2006; Kleisner and Saribay 2018; Kuchta 2005; Pfennig et al. 2001, 2007; Quicke 2017). In aposematic organisms, conspicuous coloration acts as a signal to potential predators that these organisms are inedible or dangerous, thus promoting predator avoidance (Arbuckle and Speed 2015; Kuchta 2005; Leimar et al. 1986; Mappes et al. 2005;

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Ruxton et al. 2004). In turn, mimics honestly (Müllerian) or deceitfully (Batesian) replicate this signal and thereby gain protection (Quicke 2017). Aposematism and mimicry therefore provide a direct link between phenotypic traits and predator-driven selection and can offer strong evidence for how evolution by natural selection operates in nature (Davis Rabosky et al. 2016; Endler 1986; Kleisner and Saribay 2018; Kuchta 2005; Leimar et al. 1986; Pfennig et al. 2007; Stevens and Ruxton 2012). Mimetic phenotypes are known to be subjected to various types of selection, including directional, stabilizing, and frequency-dependent selection (Akcali et al. 2018; Akcali and Pfennig 2014; Cox and Davis Rabosky 2013; Holmes et al. 2017; Lindstedt et al. 2011; Mappes and Alatalo 1997; Ruxton et al. 2004), and these selective forces can themselves be influenced by the spatial co-occurrence (sympatry) or lack thereof (allopatry) of models and mimics (Finkbeiner et al. 2018; Greene and McDiarmid 1981; Kikuchi and Pfennig 2013; Pfennig 2016; Pfennig et al. 2001, 2007; Pfennig and Mullen 2010; Ruxton et al. 2004).

The effectiveness and precision of mimicry vary with presence and abundance of models (Akcali and Pfennig 2017; Finkbeiner et al. 2018; Kikuchi and Pfennig 2013; Lindström et al. 1997; Owen and Owen 1984; Pfennig et al. 2001, 2007; Ruxton et al. 2004; Yamauchi 1993). For example, mimetic precision decreases in areas with denser populations of models and increases where the model is rare (Akcali and Pfennig 2014; Pfennig et al. 2007). Because population densities can decrease in geographic range margins (Hengeveld and Haeck 1982), the relative distance from the sympatry-allopatry border (i.e. edge sympatry vs deep sympatry) can affect mimetic precision. This link between selection and sympatry could be even more important when the model is deadly (Lindström et al. 1997; Pough 1988; Quicke 2017). In coral snake mimicry complexes, for example, some studies suggest elements of color pattern mimicry are precise in edge sympatry, may be relaxed in deep sympatry, and may not convey a fitness advantage at all in allopatry, at least in temperate mimicry systems (Pfennig et al. 2007). Other studies have found that where coral snakes were recently extirpated, their mimics have become more precise, further suggesting that mimicry should be more precise in areas where the model is rare and suggesting that directional selection may favor precise mimicry in a newly allopatric region (Akcali and Pfennig 2014).

Nevertheless, research regarding the evolutionary consequences of sympatry/allopatry on coral snake mimicry has largely been focused on temperate zones, with few studies conducted in diverse tropical ecosystems and even fewer focused on montane tropical environments. In contrast to temperate regions, the enormous taxonomic and phenotypic diversity of tropical systems results in a much wider range of aposematic color patterns of both coral snakes and mimics (Savage and Slowinski 1992). Moreover, this diversity in color patterns of models and mimics persists despite the fact that aposematism generally leads to stabilizing selection on model phenotypes, suggesting that selection may act differently in areas with high biodiversity (Joron and Mallet 1998; Mallet and Turner 1997). The montane tropics not only have higher biodiversity for both coral snakes and mimics than temperate systems, but they also provide areas of allopatry and edge sympatry in close geographic proximity (Townsend and Wilson 2008). Coral snakes are usually limited to lower and intermediate elevations in the tropics so that high elevations are without coral snakes, despite being geographically close to lower elevations with coral snake populations. The changes in elevation in montane environments create a geographic mosaic of sympatry and allopatry that is entirely within the geographic distribution of coral snakes, which is not found in the temperate habitats of previous studies on coral snake mimicry (McCranie 2011). Thus, the poorly-studied montane tropics represent an excellent study system for understanding how mimicry is

influenced by geography at both local (sympatry vs. allopatry) and regional (tropical vs. temperate) scales.

We studied the impact of edge sympatry and allopatry on predation rates on coral snake banding patterns in the montane tropics of Honduras. Highly venomous, elapid coral snakes have evolved aposematism via a brightly colored and banded phenotype, which has subsequently been mimicked by a variety of nonvenomous colubroid snakes in a classic example of Batesian mimicry (Davis Rabosky et al. 2016; Greene and McDiarmid 1981; Hinman et al. 1997; Pfennig et al. 2007; Pough 1988; Quicke 2017). This mimicry system provides an excellent model to study the evolutionary drivers of phenotypic diversity because it involves multiple species of both models and mimics and spans multiple habitats (Quicke 2017; Savage and Slowinski 1992). We know relatively little about the evolution of signal components of coral snake mimicry in the diverse tropics where multiple model and multiple mimic species occur in sympatry and in close allopatry (Davis Rabosky et al. 2016; Pfennig et al. 2001, 2007). By analyzing predation rates on mimicry patterns in edge sympatry and allopatry in the montane tropics, we can achieve a greater understanding of which mimetic phenotypes are most successful in areas with a relatively high diversity of phenotypes.

We conducted a field experiment using mimetic and non-mimetic clay replicas of snakes placed along an elevational gradient in Honduras to study the interaction of coral snake sympatry/allopatry and replica color pattern on predation rate. Empirical research suggests that mimetic phenotypes should convey a fitness advantage in edge sympatry but should suffer a fitness cost in allopatry (Akcali and Pfennig 2017; Pfennig et al. 2007; Ries and Mullen 2008). However, if mimetic phenotypes are attacked less than non-mimetic phenotypes in both habitats, this implies that the fitness advantage of mimetic signals is maintained in allopatry close to the range edge. Conversely, mimetic phenotypes being attacked more than non-mimetic phenotypes in both edge sympatry and allopatry would imply that mimicry is maladaptive in both habitats. First, we tested whether overall attack rates on replicas varied between edge sympatry and allopatry. Second, we tested which color patterns were attacked most in edge sympatry or allopatry. Third, we compared attack rates among mimetic replicas to determine which mimetic signal components may be most important in deterring predation.

Materials and methods

Study site

We conducted our study in Cusuco National Park, Honduras, from June to August of 2018 and 2019. This tropical montane environment is characterized by broad-leaf, pine, and mixed forests and is situated on one mountain at ~ 115 to ~ 2200 m in elevation. Importantly, Cusuco National Park occurs in deep in the geographic range of two species of coral snakes as well as encompassing populations of coral snakes and coral snake mimics in elevational sympatry and allopatry (Alliance 2019; Brown and Arrivillaga 2017; Townsend and Wilson 2008). Changes in elevation also result in changes with other ecological variables such as temperature, vegetation, and diversity of predator and prey species. Potential predators of snakes found throughout both sympatric and allopatric areas of the park include: margays, rats, opossums, weasels, cacomistle, motmots, toucans, and jays (Hoskins et al. 2018; Martin et al. 2021). Over the period of a decade, herpetofaunal

diversity was monitored using opportunistic sampling. Sampling occurred sporadically from May to August. Survey paths through the park were walked by teams of 2–15 people, and each path was walked at least 6 times each year. When a snake was encountered, it was identified and the GPS coordinates noted. Through this extensive herpetofaunal research and monitoring in the park, surveyors have documented the two species of coral snakes (*Micrurus diastema* and *Micrurus nigrocinctus*) and nine species of coral snake mimics (*Geophis nephodrymus*, *Lampropeltis abnorma*, *Ninia sebae*, *Oxyrhopus petolarius*, *Pliocercus elapoides*, *Scaphiodontophis annulatus*, *Scolecophis atrocinctus*, *Sibon dimidiatus*, and *Tropidodipsas sartorii*) that are consistent with local field guides and museum records (Brown and Arrivillaga 2017; Townsend and Wilson 2008). GPS points of each of these species encountered in the surveys were plotted on a map of the park using ArcGIS (ArcGIS version 10.7.1, map projection WGS_1984_UTM_Zone_16N) (Fig. 1). We divided the park into 200 m elevational bands and plotted the number of coral snake and mimic species encountered in each band. This band length results in six bands that are large enough to provide a shift in flora and fauna.

Field experiment

In order to assess predation rates on various mimetic and non-mimetic color patterns, we analyzed the number of attacks on clay replicas. These non-toxic, pre-colored replicas were either cryptic (brown) or mimetic (white-and-black banded, red-and-black banded, or tri-colored with red, white, and black bands) (see electronic supplementary material, Fig. S1a). We chose red, black, and white banding because these colors are pattern components in both coral snakes and their mimics in this area (McCranie 2011). In addition, previous research has found that both red and black banding are important components of mimicry and first appeared after the migration of coral snakes into North, Central, and South America from east and southeast Asia (Brodie III 1993; Brodie III and Janzen 1995; Davis Rabosky et al. 2016). Macroecological analyses have also demonstrated that species richness and abundance of coral snakes predicts a surplus of species richness and abundance of mimics when controlling for total snake diversity in the Western Hemisphere (Davis Rabosky et al. 2016). Finally, work has shown that naïve predators avoid coral snakes in captivity and in the wild (Brodie III 1993; Brodie III and Janzen 1995; Smith 1975, 1977) We elected to use plasticine replicas because they have been widely used as tools to understand predation for decades, including in the context of coral snake and other types of mimicry (Bateman et al. 2017; Brodie III and Janzen 1995; Heninger et al. 2020; Noonan and Comeault 2009; Pfennig et al. 2001). Accordingly, we interpret the results of our study in the context of coral snake mimicry, although we acknowledge that individual predators or predator species might not have an evolved or learned avoidance of coral snake banding patterns.

Clay replicas were positioned in arrays containing one of each of the four replica patterns along transects at different elevations in both sympatric and allopatric habitats (see electronic supplementary material, Table S1 and Fig. S1b). Transects were kept as straight as possible, though due to the steep terrain and dense foliage of the montane tropics, the transects were not always completely straight for the entire length of the transect. We defined sympatric habitats as sites with elevations less than 1800 m, and allopatric habitats as sites with elevations greater than 1800 m. We chose the 1800 m cutoff for three reasons. First, this park has been surveyed extensively for herpetofauna over the last several decades. Because the park is close to the large city of San Pedro Sula, it is easy to access,
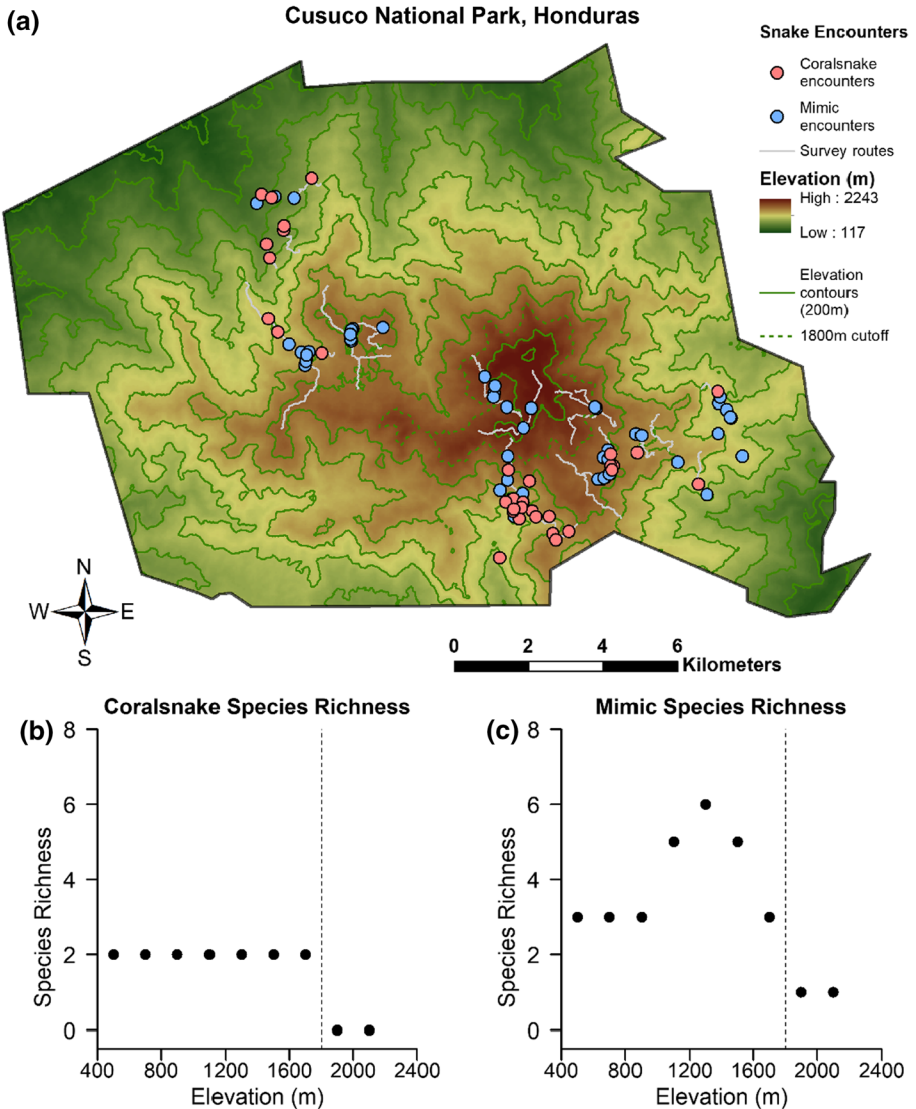
Fig. 1 a Locations of coral snake and coral snake mimic encounters in Cusuco National Park, Honduras from 2007 to 2019. **b**, **c** Species richness of coral snakes and their mimics at differing elevations in Cusuco National Park, Honduras. The dotted line at 1800 m represents the range edge of coral snakes. Note that neither coral snake species in the park is found above 1800 m, but mimics can be found up to the highest elevations

and so relative to other cloud forests in Honduras, it has been very well surveyed, and no coral snake has been recorded at greater than 1684 m. Second, McCranie (2011) list the elevational range of all coral snake species in the park to terminate below the upper limit of 1800 m, which is based upon museum records and field experience of the authors. Finally, our transects were placed adjacent to the normal paths for surveying, so that we know there are no coral snakes above 1800 m where we placed our experimental arrays, and we have

documentation of coral snakes in the park at elevations of our "sympatric" transects. We did not analyze elevation apart from the classifications of sites as sympatric or allopatric because transects were clustered at intermediate and high elevations. Each transect contained seven (in 2018) or ten (in 2019) branches, spaced approximately ten meters apart, with one array per branch (Figure S1a). All transects were located within the surveyed area of the national park. Of the nine transects in 2018, two were allopatric and seven were edge sympatric. Of the 18 transects in 2019, three were allopatric and 15 were edge sympatric. Arrays were positioned on alternate sides of the transect to minimize proximity to other arrays. Replicas were left out for a period of two weeks and checked every three to four days for marks of predation (e.g., beak, teeth, or claw marks). If a replica was attacked more than once during the two weeks, only one attack was counted. While the impressions left on the clay replicas did not permit species level identification of predators because of the diversity of species in the park, each instance of attack was categorized by general predator type (bird, mammal, or unidentifiable).

Statistical analyses

We analyzed the data using (1) contingency analyses of pooled transect data and (2) mixed effect models compared with information theoretic model selection. We used mixed effect models because they allow incorporation of a random effect of transect which accounts for spatial autocorrelation in that clay replicas within a transect are much closer to each other than to any clay replicas in other transects, but the models have many assumptions (homogeneity of variance, correct specification of error distribution, linearity etc.) and parameters, which can increase error. We also used contingency analyses because they are relatively assumption free (only minimum sample size and expected values), but we pooled all samples across transects for these analyses, and so this analysis does not account for spatial autocorrelation. By comparing our results and conclusions from these methods, we gain an understanding of the robustness of our results. Contingency analyses were used to estimate differences in predation rates between clay replica types, habitats, and years, while mixed effects models and model selection were used to test whether coral snake sympatry and color pattern had meaningful effects on attack rates (while accounting for spatial autocorrelation of clay replicas within transects). To avoid missing patterns by discarding ambiguous attack marks, we combined bird and mammal attacks into an overall "attacked" category. We combined data from all transects and performed contingency analyses in JMP v 13.1.0 (SAS Statistical Institute, Cary, NC, USA). We created mixed effect logistic regression models in R (version 3.5.2) and compared them using small sample size-corrected Akaike information criterion (AICc) values to determine which statistical models were most effective in predicting attack rates (Bates et al. 2015; Mazerolle 2019; R Core Team 2020). The response variable for these statistical models was whether a replica was attacked or not attacked at any point during the two-week period. The null models for each year included one term: a random effect for the clay replica's transect. This random effect should account for most spatial autocorrelation because arrays within a transect were closer to each other than to arrays in any other transect. The remaining statistical models included transect as a random effect as well as all potential linear combinations of level of sympatry (edge sympatry or allopatry), one of five color variables, and an interaction between level of sympatry and replica color. The five color variables were individual pattern (the pattern of the replica), the presence of red (two of the replica patterns), the presence of white (two replica patterns), the presence of bands (three replica patterns), or whether it was tricolor (one
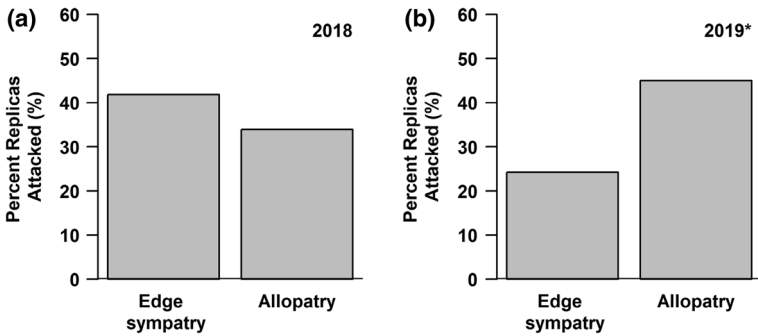
Fig. 2 Attack rates on clay snake replicas in edge sympatric and allopatric habitats in 2018 (**a**) and 2019 (**b**). An asterisk (*) indicates significance from contingency analyses. Attack rates in 2019 were higher in allopatry than in edge sympatry, while attack rates in 2018 did not differ between edge sympatry and allopatry
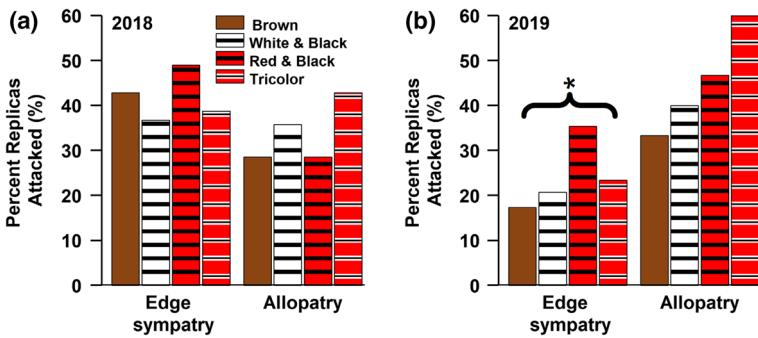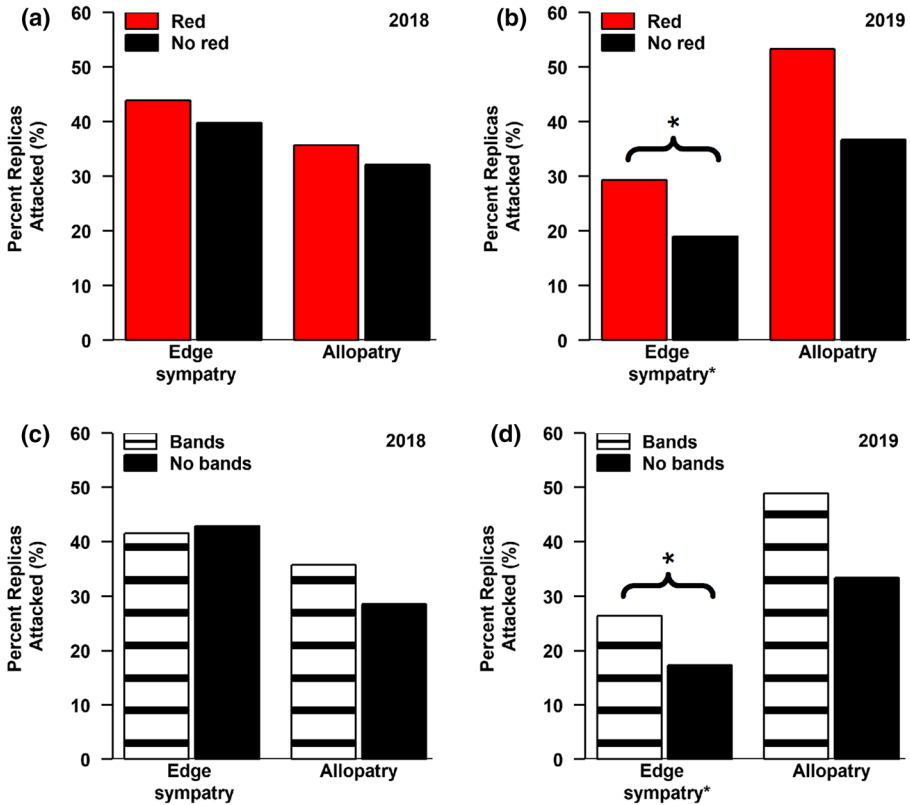

Fig. 3 Attack rates on clay snake replicas with four different color patterns in areas of edge sympatry and allopatry in 2018 (**a**) and 2019 (**b**). An asterisk (*) indicates significance from contingency analyses. Replicas with mimetic patterns (white-and-black-banded, red-and-black banded, or tricolored) were attacked more than brown replicas in almost all scenarios

replica pattern). We report odds ratios (effect sizes) for variables in top models selected by AICc. We analyzed additional models including the array of a replicas as a random effect because replicas within an array were generally closer than replicas in other arrays. However, these models are not able to converge as there is not enough data (especially in 2018) to fit both random effects and the fixed effects that we are interested in. Thus, we only included transect as a random effect in our final analyses.

Results

Coral snakes and mimics have been encountered in most of the same elevational bands throughout the park (Fig. 1a). Both coral snake species have been found from 600 to 1800 m but are notably absent above this threshold (Fig. 1b). Mimic species diversity peaks at 1400 m, but mimics are indeed encountered above 2200 m (Fig. 1c).

We found that both coral snake sympatry (Fig. 2) and elements of replica color pattern (Fig. 3 and Fig. 4) had significant associations with predation rates. Total attack rates on

Fig. 4 a, b Attack rates on clay snake replicas with and without the color red included in their patterns in areas of edge sympatry and allopatry. **c, d** Attack rates on clay snake replicas with and without banded color patterns in areas of edge sympatry and allopatry. An asterisk (*) indicates significance from contingency analyses. Replicas with red or bands were almost always attacked more than replicas without those traits

clay replicas were higher in allopatry than in edge sympatry in 2019 (contingency analysis, $\chi^2 = 21.702$, $p < 0.0001$) but not in 2018 (contingency analysis, $\chi^2 = 1.134$, $p = 0.2869$). The red and black banded replicas were attacked significantly more in edge sympatric habitats in 2019 (contingency analysis, $\chi^2 = 15.088$, $p = 0.0017$), but this was not found in allopatric habitats (contingency analysis, $\chi^2 = 4.714$, $p = 0.1940$). In 2018, color pattern was not associated with attack rate in either habitat (contingency analyses; edge sympatry $\chi^2 = 1.761$, $p = 0.6234$; allopatry $\chi^2 = 0.876$, $p = 0.8312$).

Similar to our contingency analyses, we found that both sympatry and the presence of red were important factors impacting attack rates on clay replicas using mixed effect models. In 2019, clay replicas in areas of sympatry were less likely to be attacked (0.38 times as likely to be attacked as replicas in allopatry), and red replicas were 1.81 times more likely to be attacked compared to other colors (Table 1). The best statistical model in 2019 included transect, sympatry, and the presence of red (no interaction) (Table 2, also see electronic supplementary material Table S2). Two statistical models fell within two AICc units of the best statistical model, and both contained sympatry as a term. These statistical models also included individual color pattern without an interaction, as well as the presence of red with an interaction. Furthermore, we found that in 2019 both the presence

Table 1 Odds ratios for the top three regression models in 2019

Model	Term	Estimate	Odds ratio
Sympatry and red (no interaction)	Sympatry	− 0.9624	0.381975
	Red	0.5949	1.81285
Sympatry and individual pattern	Sympatry	− 0.9677	0.379956
	RB	0.8926	2.441469
	TRI	0.5291	1.697404
	WB	0.2346	1.264403
Sympatry and red (with interaction)	Sympatry	− 0.9044	0.404785
	Red	0.681	1.975853
	Interaction	− 0.1097	0.896103

Table 2 Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc)

K	AICc	ΔAICc	AICc Weight	Log-likeli-hood	Term 1	Term 2	Term 3	Term 4
4	824.6768	0	0.404193	− 408.31	Transect*	Sympatry	Red	–
6	825.3787	0.701893	0.28456	− 406.63	Transect*	Sympatry	Individual pattern	–
5	826.6367	1.959888	0.151707	− 408.276	Transect*	Sympatry**	Red**	interaction

Linear models were created to predict whether a clay replica in 2019 was attacked using the following terms: the transect on which it was located, if it was in sympatry, a color variable (the individual color pattern, the presence of white, the presence of red, the presence of bands, or whether it was mimetic), and an interaction between sympatry and the color variable. *K* is the number of parameters and ΔAICc is the difference between that statistical model and the best model. Only statistical models within 2 ΔAICc units of the top model are included

*Indicates random effect and ** indicates an interaction variable was included between the two variables

of red and the presence of bands increased attack rates in edge sympatric habitats, with a similar pattern in allopatric habitats (Fig. 4, see also electronic supplementary material Table S4). In 2018, the null model was the best model (Table 3, also see electronic supplementary material, Table S3). All of the statistical models that fell within two AICc units of the null model had only one additional term after transect: sympatry or the presence of white or red. The impact of signal components on attack rates did not differ between edge sympatric and allopatric habitats in 2018.

Discussion

Contrary to expectations, we found that coral snake patterns did not confer a protective advantage in either edge sympatry or allopatry in the montane tropics of Honduras. Replicas without mimicry components almost always had lower attack rates than those with mimicry components, regardless of both year and whether they were placed in an edge sympatric habitat or an allopatric habitat. We also found that replicas with red or bands had higher attack rates than those without in 2019 in areas of edge sympatry. These results are in contrast to previous findings, where both brown replicas and replicas with imprecise

Table 3 Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc)

K	AICc	ΔAICc	AICc Weight	Log-likelihood	Term 1	Term 2	Term 3	Term 4
2	341.8013	0	0.223916	− 168.877	Transect*	–	–	–
3	343.1601	1.358776	0.113509	− 168.532	Transect*	Sympatry	–	–
3	343.4256	1.624319	0.099396	− 168.664	Transect*	Red	–	–
3	343.4256	1.624319	0.099396	− 168.664	Transect*	White	–	–

Linear models were created to predict whether a clay replica in 2018 was attacked using the following terms: the transect on which it was located, if it was in sympatry, a color variable (the individual color pattern, the presence of white, the presence of red, the presence of bands, or whether it was mimetic), and an interaction between sympatry and the color variable. *K* is the number of parameters and ΔAICc is the difference between that statistical model and the best model. Only statistical models within 2 ΔAICc units of the top model are included

*Indicates random effect

mimetic patterns were attacked more than precise mimetic replicas in sympatric regions (including edge sympatric) (Brodie III 1993; Brodie III and Janzen 1995; Kikuchi and Pfennig 2010; Pfennig et al. 2001). In addition, we found that patterns of attacks on replicas varied between years, which could be caused by temporal heterogeneity or negative frequency-dependent selection (Akcali et al. 2018; Cox and Davis Rabosky 2013; Holmes et al. 2017). Our study design cannot completely disentangle the effect of elevational gradients in predator assemblages or biophysical variables from the impacts of mimicry on predation rates, and our results may not be generalizable to other locations in the montane tropics. However, the montane tropics do provide the opportunity to minimize the confounding effect of large geographic distances, which often encompass major ecological transitions and gradients, on the role of sympatry and allopatry on mimicry. Regardless, our research supports the idea that mimicry dynamics can differ in the montane tropics compared to temperate habitats.

In temperate regions, mimetic patterns can incur a fitness cost that varies between allopatric regions with different local mimics, implying that even between allopatric populations in similar habitats there can be differences in patterns of selection (Pfennig et al. 2007). In one previous study, predators in the southeastern United States differentially attacked replicas depending on whether they were in deep sympatry or edge sympatry (Pfennig et al. 2007). Those predators avoided both poor and accurate mimetic phenotypes in areas of deep sympatry, but they avoided only accurate mimics in edge sympatry. In studies taking place in the lowland tropics, avian predators attacked brown replicas more often than tricolored or red-and-black banded replicas (Brodie III 1993; Brodie III and Janzen 1995). In our study, we did not find that predators avoided the more accurate mimetic phenotypes, but rather, the replicas with phenotypes most closely resembling those of coral snakes (tricolored and red-and-black banded) were often those attacked most. These results support the idea that in areas where coral snakes are rare or absent (such as the range edge and close allopatry of our study areas), mimetic phenotypes may not confer as much of an advantage as in areas where coral snakes are common (such as the lowland tropics), which is consistent with classic Batesian mimicry theory (Brodie III and Janzen 1995; Pfennig and Mullen 2010; Quicke 2017; Ruxton et al. 2004). Yet why multiple aposematic species of models and mimics may persist in our study area, given the fitness costs that we have demonstrated, is a bit more perplexing. There are three primary, non-mutually exclusive

reasons why mimicry could be maintained in the face of apparent maladaptation: (1) there is an interplay of aposematic coloration and behavior and thus mimetic phenotypes are not actually maladaptive, (2) mimetic phenotypes are indeed maladaptive but may be maintained by gene flow and/or (3) the apparent maladaptation of mimetic phenotypes fluctuates temporally, likely due to negative frequency-dependent selection (Pfennig and Mullen 2010).

First, the behavioral component of coral snake mimicry might reinforce and strengthen the avoidance of mimetic patterns. Coral snakes display stereotyped coiling and thrashing behavior when threatened, and thus behavior is an integrated part of their antipredator display (Brown et al. 2020; Davis Rabosky et al. 2020; Titcomb et al. 2014). The effect of interacting coloration and behavior on predator avoidance has been documented in other systems: for example, moving replicas of brown frogs were attacked significantly more than when stationary, whereas stationary replicas of red aposematic frogs were attacked significantly more than when moving (Paluh et al. 2014). These findings suggest that movement and behavior may play an important role in selection for both cryptic and aposematic individuals (Bateman et al. 2017). Thus, while the use of clay replicas provides a useful tool for studying predation, a limitation of the method is that it is unable to capture the effects of behavior, and it is not known whether a stationary clay replica is recognized as a snake by a bird or mammalian predator (Bateman et al. 2017). In addition, other research has suggested that in range edges where models may be rare, selection for avoidance of aposematic phenotypes may be weaker and thus behavior could play an important role in reinforcing color signals (Charlesworth and Charlesworth 1975).

Second, mimetic phenotypes could indeed be maladaptive in areas of edge sympatry and allopatry, but migration and gene flow from regions where mimicry is adaptive (areas of deep sympatry at lower elevations) maintain the presence of mimetic phenotypes (Ries and Mullen 2008). Indeed, coral snake mimics are known to migrate from areas of sympatry to allopatry in temperate systems (Harper and Pfennig 2008). In and around Cusuco National Park, it is plausible that coral snake mimics could migrate from areas of high coral snake density (e.g., lowlands) to areas where coral snakes are uncommon or absent (e.g., montane regions), thus influencing our study. If high elevations contain more species that have not evolved or learned avoidance of mimetic phenotypes, then this could explain the higher attack rates on mimetic replicas in our study. Similarly, range expansion of mimics may create newer areas of edge sympatry or allopatry where predators have not yet evolved or learned avoidance (Pfennig and Mullen 2010). Thus, immigration and gene flow of mimics between high elevations without coral snakes and low elevations with coral snakes could allow mimicry to persist at high elevations.

Finally, mimicry might be maintained despite a fitness cost through temporally fluctuating selection, such as negative frequency-dependent selection. Many mimicry systems are influenced by frequency-dependent selection, including frogs, snails, butterflies, and snakes (Holmes et al. 2017; Ries and Mullen 2008). Because this type of selection allows rare phenotypes to increase in frequency in the population, the preferred target of predators also changes over time (Holmes et al. 2017; Pfennig et al. 2007). Frequency-dependent selection has been shown to play an important role in Batesian mimicry (Akcali et al. 2018; Cox and Davis Rabosky 2013; Finkbeiner et al. 2018; Holmes et al. 2017; Pfennig et al. 2001; Pfennig and Mullen 2010). In areas where coral snake models are uncommon or absent and relatively harmless mimics are abundant, predators may learn or evolve a preference for conspicuous prey (Pfennig et al. 2007; Pfennig and Mullen 2010). Over time, this may reduce the relative abundance of mimics and thereby decrease the ratio of mimics to models, which eventually leads to selection for the avoidance of mimetic

phenotypes by predators. As the mimic to model ratio then increases once again, predators may re-learn or re-evolve the preference for conspicuous mimetic color patterns. Such a negative frequency-dependent cycle could result in a dynamic relationship between the frequencies of different mimetic phenotypes, causing temporal heterogeneity in the phenotypes most selected against (Cox and Davis Rabosky 2013). Our results are suggestive of temporal variation in predation rates on coral snake color patterns, although we cannot rule out minor variation in experimental implementation between years that might contribute to this perceived temporal variation. Hence, our study may have taken place at the point in the cycle where mimetic phenotypes are maladaptive, yet they are able to persist because the phenotype is favored when rare. In addition, it is important to note that the presence of learned and innate avoidance, as well as the predator assemblages present at a given time, would likely impact the dynamics of frequency-dependent selection (Akcali et al. 2018). For example, naïve juvenile motmots and great kiskadees innately avoid coral snake patterns, yet puffbirds and adult motmots have been documented to consume coral snakes (Smith 1969, 1975, 1977). While predators likely have a combination of innate and learned avoidance, learned avoidance would lead to a shorter period of the negative frequency-dependent cycle than innate avoidance because innate avoidance relies on intergenerational processes.

Although we found that mimetic phenotypes did not confer a fitness advantage and may actually lead to decreased survivorship, some of our results were consistent with previous research on coral snake mimicry. In areas of edge sympatry during 2019, red and black replicas were attacked more often than tricolored replicas. However, we found no significant variation in attack rates between replicas in allopatry in 2019, and in fact the tricolor replicas were attacked more frequently (although non-significantly) than any other replicas in allopatry. This result could indicate that it is beneficial to be a precise mimic in areas where the model is rare (but present), but protection breaks down farther from the model's range, which is consistent with previous findings that predators avoid precise mimics over poor mimics in edge sympatry (Pfennig et al. 2007). Studies using museum specimens have also found differences in mimetic precision in relation to sympatry and allopatry (Akcali and Pfennig 2014, 2017; Pfennig et al. 2007). Within a single species, the most precise mimics to a local model were found at the edge of the model's range rather than in deep sympatry (Pfennig et al. 2007). Nevertheless, other studies have found that mimetic precision differs between species, and in some cases the most precise mimics have been found in areas of allopatry (Akcali and Pfennig 2014, 2017).

Our data suggest that coral snake mimicry may not provide an advantage in areas where coral snakes have low abundance (despite having the high diversity of the tropics), such as in edge sympatry and allopatry. Seemingly maladaptive mimicry might persist because of an interaction between aposematism and defensive behavior that is unable to be captured in a clay replica study, gene flow and immigration of both mimics and predators from areas where mimicry is adaptive, temporal fluctuation in selection such as negative frequency-dependent selection, or a combination of these processes. Our work highlights the importance of the interactions among color patterns, model sympatry, and temporal variation in understanding predation on coral snakes and their mimics. Long-term studies that characterize predation of mimics in locations from deep sympatry to deep allopatry with models would be ideal to further understand the complex nature of how sympatry and allopatry affect selection on mimicry.

Authors' contributions LW participated in the design of the study, collected field data, carried out statistical analyses, and drafted the manuscript; GL participated in the design of the study, aided in field work, and revised the manuscript; JDC participated in the design of the study, collected field data, and revised the manuscript; EH aided in statistical analyses and critically revised the manuscript, CC conceived of the study, designed the study, coordinated the study, and critically revised the manuscript. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

Data availability Data will be deposited at Dryad upon acceptance.

Code availability Software application or custom code.

Declarations

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