Predator-Based Selection And The Impact of Edge Sympatry On Components of Coral Snake Mimicry

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

Running title: Coral snake mimicry in montane tropics

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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 used a clay replica study in a montane tropical site in Honduras to test the impact of edge sympathy on 1) overall attack rates, 2) the fitness benefit of mimetic coloration, 3) predation on specific mimetic signal components, and 4) temporal variation in predator-based selection on mimicry components. Unlike previous research, we found that mimetic phenotypes received significantly more attacks than cryptic replicas in edge sympathy, suggesting that mimetic phenotypes might not confer a fitness benefit in areas of edge sympathy. 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 sympathy 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.
Introduction

Although phenotypic diversity is extremely well-studied in evolutionary biology, the means by which phenotypic patterns occur and are maintained remain unclear in many systems. In order for evolution by natural selection to occur in a population, the population must have variation in a heritable phenotype and a selective force (such as predation) acting upon the population (Endler, 1986; Freeman & Herron, 2004). Studying predation pressure is an effective method to understand phenotypic diversity because the selective agent is known, and much has been learned by analyzing the evolutionary drivers of antipredator traits such as warning coloration (e.g. aposematism) and mimicry (Brodie III, 1993; Brodie III & Janzen, 1995; Ham et al., 2006; Kleisner & Saribay, 2018; Kuchta, 2005; Pfennig et al., 2001; Pfennig et al., 2007; Quicke, 2017). In organisms with aposematism, conspicuous coloration acts as a signal to potential predators that these organisms are inedible or dangerous, thus promoting predator avoidance (Arbuckle & Speed, 2015; Kuchta, 2005; Leimar et al., 1986; Mappes et al., 2005; 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; Harper & Pfennig, 2007; Kleisner & Saribay, 2018; Kuchta, 2005; Leimar et al., 1986; Stevens & 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 & Pfennig, 2014; Cox & Davis Rabosky, 2013; Holmes et al., 2017; Lindstedt et al., 2011; Mappes & 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 & McDiarmid, 1981; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2013; Pfennig, 2016; Pfennig et al., 2001; Pfennig et al., 2007; Pfennig & Mullen, 2010; Ruxton et al., 2004). Nevertheless, the evolutionary effects of sympatry and allopatry are complex and only well studied in some systems (Akcali & Pfennig, 2017; Cox & Davis Rabosky, 2013; Harper & Pfennig, 2007; Holmes et al., 2017; Pfennig et al., 2001; Pfennig et al., 2007; Pfennig & Mullen, 2010).

The effectiveness and precision of mimicry vary with presence and abundance of models (Akcali & Pfennig, 2017; Finkbeiner et al., 2018; Harper & Pfennig, 2007; Kikuchi & Pfennig, 2013; Lindström et al., 1997; Owen & Owen, 1984; Pfennig et al., 2001; 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 & Pfennig, 2014; Harper & Pfennig, 2007). Because population densities often decrease in geographic range margins (Hengeveld & 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 sympathy 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 (Harper & Pfennig, 2007; 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 & 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 & 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 & Mallet, 1998; Mallet & 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 and under a variety of different predator assemblages (Townsend & Wilson, 2008). 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 & 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 & Slowinski, 1992). However, most research on coral snake mimicry has focused on species-poor temperate systems.
that often have only one model and one to three mimics. Furthermore, studies focusing on the
effects of the depth of sympatry, and indirectly model abundance, have also been centered on
temperate systems that lack the species diversity of the tropics (Akcali & Pfennig, 2014; Akcali
& Pfennig, 2017; Harper & Pfennig, 2007; Pfennig et al., 2007). The few studies performed in
the tropics have rarely taken place in montane habitats where elevational gradients exclude coral
snakes in some areas, which creates a mosaic of sympatric and allopatric regions in close
geographic proximity (McCranie & Savage, 2011). Thus, 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; Harper & Pfennig, 2007; Pfennig et al., 2001; Pfennig et al., 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. First, we tested whether overall
attack rates on replicas varied between edge sympatry and allopatry, with higher attack rates
suggesting a greater intensity of predator-mediated selection. Second, we tested which color
patterns were attacked most in edge sympatry or allopatry. Empirical research suggests that
mimetic phenotypes should convey a fitness advantage in edge sympatry but should suffer a
fitness cost in allopatry (Akcali & Pfennig, 2017; Harper & Pfennig, 2007; Ries & 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
Materials & 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 at ~115m to ~2200m in elevation. Importantly, Cusuco National Park encompasses populations of coral snakes and coral snake mimics in both sympatry and allopatry (Alliance, 2019; Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). 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 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*, *Sibon laticinctus*, *Sibon nigrocinctus*, *Sibon prasinus*, *Sibon sulcatus*).
and *Tropidodipsas sartorii* (Brown & Arrivillaga, 2017; Townsend & 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 200m elevational bands and plotted the number of coral snake and mimic species encountered in each band.

**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. We constructed these non-toxic, pre-colored clay replicas to have patterns loosely based on snakes found in the park. Replicas were either cryptic (brown) or mimetic (white-and-black banded, red-and-black banded, or tri-colored with red, white, and bands) (see electronic supplementary material, Fig. S1a). Clay replicas were arranged in tetrads containing each replica pattern along transects at different elevations in both sympatric and allopatric habitats (see electronic supplementary material, Table S1 and Fig. S1b). Tetrads were arranged on alternate sides of the transect to minimize proximity to other tetrads. 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. Each instance of attack was categorized by predator type (bird, mammal, or unidentifiable) and recorded.

**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. Contingency analyses were used to estimate differences in predation rates between clay replica types, habitats, and years,
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 tetrads within a transect were closer to each other than to tetrads 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 replica pattern).

**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 600m to 1800m
but are notably absent above this threshold (Fig. 1b). Mimic species diversity peaks at 1400m, 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 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 $\chi^2 = 0.876$, $p = 0.8312$).

Both sympatry and the presence of red were important factors impacting attack rates on clay replicas. In 2019, the best statistical model included transect, sympatry, and the presence of red (no interaction) (Table 1, 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 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 2, 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 mimetic patterns were attacked more than precise mimetic replicas in sympatric regions (including edge sympatric) (Brodie III, 1993; Brodie III & Janzen, 1995; Kikuchi & 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 & Davis Rabosky, 2013; Holmes et al., 2017). Our research supports the idea that mimicry dynamics might 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 (Harper & Pfennig, 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 & 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 & Janzen, 1995; Pfennig & 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 & 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). Our results might suggest that there may also be variation in how important movement is in relation to prey selection by predators. 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 & 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 sympathy at lower elevations) maintain the presence of mimetic phenotypes (Ries & Mullen, 2008). Indeed, coral snake mimics are known to migrate from areas of sympathy to allopatry in temperate systems (Harper & 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. Similarly, range expansion of mimics may create newer areas of edge sympatry or allopatry where predators have not yet evolved or learned avoidance (Pfennig & 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. We found evidence 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. Many mimicry systems are influenced by frequency-dependent selection, including frogs, snails, butterflies, and snakes (Holmes et al., 2017; Ries & 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 & Davis Rabosky, 2013; Finkbeiner et al., 2018; Holmes et al., 2017; Pfennig et al., 2001; Pfennig & 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 & 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 & Davis Rabosky, 2013). 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; Smith, 1975; Smith,
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, red and black replicas were attacked
more often than tricolored replicas, but the opposite was true in areas of 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
(Harper & Pfennig, 2007). Studies using museum specimens have also found differences in
mimetic precision in relation to sympatry and allopatry (Akcali & Pfennig, 2014; Akcali &
Pfennig, 2017; Harper & Pfennig, 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 (Harper &
Pfennig, 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
&Pfennig, 2014; Akcali & Pfennig, 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
dge 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.

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Code availability: R code used for attack analyses available at
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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.
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Appendices
Extended Methods

Extended study site description

The study location in Cusuco National Park, Honduras, comprises a tropical, montane environment that includes both sympatric and allopatric populations of coral snakes and coral snake mimics (Townsend & Wilson, 2008). The park is a protected area located in the Merendón Mountains of northwest Honduras and is roughly 200 square km in area, with an elevational range of approximately 115 m to just over 2200 m (Alliance, 2019; Brown & Arrivillaga, 2017). Cusuco National Park spans a variety of forest types including cloud forest (distinguished by frequent cloud cover), dwarf forest (distinguished by high elevations, small trees, and increased number of epiphytes), and forest fringes (distinguished by little to no tree cover). These habitats are predominately broad-leaf, pine, or mixed forests (Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). There are two species of coral snakes found in the park: *Micrurus diastema* and *Micrurus nigrocinctus*. Both of these species exhibit tricolor patterns of red, black, and white/yellow, although both have also been found to exhibit bicolor a red and black morph (Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). In addition, there are nine species of colubroid snakes found in the park that are considered coral snake mimics: *Geophis nephodrymus*, *Lampropeltis abnorma*, *Ninia sebae*, *Oxyrhopus petolarius*, *Pliocercus elapoides*, *Scaphiodontophis annulatus*, *Scolecophis atrocinctus*, *Sibon dimidiatus*, and *Tropidodipsas sartorii* (Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). All of these species are considered mimics because at least one morph in each species has banded patterns of black, red, and/or white. They range from tricolor mimics such as *P. elapoides* and *L. abnorma*...
to bicolor red and black (some *G. nephodrymus*) or white/yellow/orange and black (*T. sartorii*)
(Brown & Arrivillaga, 2017; McCranie & Savage, 2011; Townsend & Wilson, 2008).

Extended transect description

In order to assess predation rates on various mimetic and non-mimetic color patterns, we
analyzed the number of attacks on clay replicas. We constructed these non-toxic, pre-colored
clay replicas to have patterns loosely based on snakes found in the park. Replicas were either
cryptic (brown) or mimetic (white-and-black banded, red-and-black banded, or tri-colored with
red, white, and bands) (Figure S1a).

We placed clay replicas in groups of four, hereafter referred to as a tetrad, which included
one of each replica color pattern. Over a span of eight weeks from June to August in 2018 and in
2019, we arranged the tetrads along transects at varying elevations within the park (Table S1).
Transects higher than 1800m in elevation were classified as allopatric, and those lower than
1800m were classified as edge sympatric. Of the nine transects in 2018, three were allopatric and
six were edge sympatric. Of the 18 transects in 2019, three were allopatric and 15 were edge
sympatric. There were fewer allopatric transects because there was much less space to lay out
transects in the higher elevations of the mountaintop. Each transect contained seven (in 2018) or
ten (in 2019) branches, spaced approximately ten meters apart, with one tetrad per branch
(Figure S1a). We placed each replica within a tetrad at least three meters apart from other
replicas in the tetrad. The order of the replicas within each tetrad was randomly determined using
a random number generator. We calculated an ideal sample size for the total number of clay
replicas on transects for 2019 through a power analysis based on the attack data from 2018. We
left replicas out on transects for a period of two weeks and checked them every three to four days
for marks of predation (e.g. distinct beak, bite, or claw marks). Once checked, replicas were
smoothed over and placed in the same spot. If a replica was attacked more than once during the two weeks, only one attack was counted. Each instance of attack was scored for type of predator (bird, mammal, or unidentifiable) and recorded. Different observers checked and scored the replicas from year to year.

Statistical Analyses

We analyzed the data using a combination of mixed effect models compared with model selection and contingency analyses. The mixed effects models and model selection demonstrated whether sympatry and color pattern had meaningful effects on attack rates, and contingency analyses were used to estimate differences in predation rates between clay replica types, habitats, and years. To avoid missing patterns of selection that could occur by discarding ambiguous attack marks, we combined bird and mammal attacks into an overall “attacked” category. We performed contingency analyses in JMP v 13.1.0 (SAS Statistical Institute, Cary, NC, USA) with all samples pooled regardless of transect. We created logistic mixed effect models in R 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 only transect as a random effect. The remaining statistical models included transect as a random effect as well as all potential combinations of: level of sympatry, one of the five color variables, and interaction terms.
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Supplemental Tables

**Table S1.** Data associated with each transect along which clay snake replicas were set out and monitored. Coral snake sympatry or allopatry for each transect was determined by the transect’s elevation.

| Year | Elevation (m) | Coral snake Sympatry/Allopatry |
|------|---------------|---------------------------------|
| 2018 | 1598          | sympatric                       |
| 2018 | 1617          | sympatric                       |
| 2018 | 1617          | sympatric                       |
| 2018 | 2017          | allopatric                      |
| 2018 | 2013          | allopatric                      |
| 2018 | 1766          | sympatric                       |
| 2018 | 1358          | sympatric                       |
| 2018 | 1250          | sympatric                       |
| 2018 | 1244          | sympatric                       |
| 2019 | 1598          | sympatric                       |
| 2019 | 1607          | sympatric                       |
| 2019 | 1618          | sympatric                       |
| 2019 | 1653          | sympatric                       |
| 2019 | 1617          | sympatric                       |
| 2019 | 1624          | sympatric                       |
| 2019 | 1995          | allopatric                      |
| 2019 | 1766          | sympatric                       |
| 2019 | 1998          | allopatric                      |
| 2019 | 1762          | sympatric                       |
| 2019 | 1781          | sympatric                       |
| 2019 | 1826          | allopatric                      |
| 2019 | 1270          | sympatric                       |
| 2019 | 1252          | sympatric                       |
| 2019 | 1244          | sympatric                       |
| 2019 | 1277          | sympatric                       |
| 2019 | 1234          | sympatric                       |
| 2019 | 1354          | sympatric                       |
Table S2. Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc). 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 tricolor), and an interaction between sympatry and the color variable. $K$ is the number of parameters and $\Delta$AICc is the difference between that statistical model and the best model. Statistical models within 2 $\Delta$AICc units of the top model are bolded.

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

| K | AICc     | $\Delta$AICc | AICc Weight | Log-likelihood | term 1       | term 2 | term 3     | term 4     |
|---|----------|--------------|-------------|----------------|--------------|--------|------------|------------|
| 4 | 824.6768 | 0            | 0.404193    | -408.31        | transect*    | sympathy| red        | --         |
| 6 | 825.3787 | 0.701893     | 0.28456     | -406.63        | transect*    | sympathy| individual pattern | --         |
| 5 | 826.6367 | 1.959888     | 0.151707    | -408.276       | transect*    | sympathy** | red**   | interaction |
| 9 | 827.6545 | 2.977695     | 0.091199    | -404.7         | transect*    | sympathy** | individual pattern** | interaction |
| 4 | 829.2339 | 4.557145     | 0.041402    | -410.589       | transect*    | sympathy | bands       | --         |
| 5 | 831.2141 | 6.537345     | 0.015382    | -410.565       | transect*    | sympathy** | bands**   | interaction |
| 3 | 834.7732 | 10.0964      | 0.002595    | -414.37        | transect*    | sympathy |            |            |
| 5 | 835.1136 | 10.43682     | 0.002189    | -412.515       | transect*    | sympathy** | tricolor** | interaction |
| 3 | 835.5943 | 10.91752     | 0.001721    | -414.78        | transect*    | red      |            |            |
| 5 | 836.0688 | 11.39206     | 0.001358    | -412.992       | transect*    | sympathy** | white**   | interaction |
| 5 | 836.2869 | 11.61017     | 0.001218    | -413.101       | transect*    | individual pattern |            |
| 4 | 836.3954 | 11.7186      | 0.001153    | -414.17        | transect*    | sympathy | tricolor   | --         |
| 4 | 836.4445 | 11.76768     | 0.001125    | -414.194       | transect*    | sympathy | white      | --         |
| 3 | 840.1477 | 15.47089     | 0.000177    | -417.057       | transect*    | bands    |            | --         |
| 2 | 845.6788 | 21.00198     | 1.11E-05    | -420.831       | transect*    | --       |            | --         |
| 3 | 847.2958 | 22.61905     | 4.95E-06    | -420.631       | transect*    | tricolor |            | --         |
| 3 | 847.3449 | 22.6681      | 4.83E-06    | -420.656       | transect*    | white    |            | --         |
**Table S3.** Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc). 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 with coral snakes, a color variable (the individual color pattern, the presence of white, the presence of red, the presence of bands, or whether it was tricolor), and an interaction between sympatry and the color variable. $K$ is the number of parameters and $\Delta$AICc is the difference between that statistical model and the best model. Statistical models within 2 $\Delta$AICc units of the top model are bolded.

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

| $K$ | AICc    | $\Delta$AICc | 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    | --     | --       |
| 3   | 343.8442| 2.042923     | 0.080625    | -168.874       | transect*      | tricolor | --     | --       |
| 3   | 343.8442| 2.042923     | 0.080625    | -168.874       | transect*      | bands    | --     | --       |
| 4   | 344.8011| 2.999781     | 0.049968    | -168.32        | transect*      | sympatry | white  | --       |
| 4   | 344.8011| 2.999781     | 0.049968    | -168.32        | transect*      | sympatry | red    | --       |
| 5   | 345.202 | 3.400738     | 0.040891    | -167.479       | transect*      | sympatry | white**| interaction |
| 4   | 345.2196| 3.418288     | 0.040533    | -168.529       | transect*      | sympatry | tricolor| --       |
| 4   | 345.2196| 3.418288     | 0.040533    | -168.529       | transect*      | sympatry**| bands  | --       |
| 5   | 346.3904| 4.589131     | 0.022572    | -168.073       | transect*      | sympatry**| tricolor**| interaction |
| 5   | 346.5182| 5.081478     | 0.017646    | -168.319       | transect*      | sympatry**| red**  | interaction |
| 5   | 346.5318| 5.230468     | 0.01638     | -168.394       | transect*      | sympatry**| bands**| interaction |
| 5   | 347.1333| 5.332028     | 0.015569    | -168.445       | transect*      | --       | --     | --       |
| 6   | 348.5427| 6.741379     | 0.007695    | -168.1         | transect*      | sympatry | individual pattern | -- |
| 9   | 353.1259| 11.32465     | 0.000778    | -167.191       | transect*      | sympatry**| individual pattern** | interaction |
Table S4. Results of contingency analyses to determine the statistical association between elements of replica color pattern and number of predatory attacks ($N =$ number of samples, $df =$ degrees of freedom). * indicates significance

| Color variable | Year | Level of sympatry | N   | $\chi^2$ statistic | df | p-value   |
|----------------|------|-------------------|-----|--------------------|----|-----------|
| Color Pattern  | 2018 | Edge sympatry     | 96  | 1.761              | 3  | 0.6234    |
|                |      | Allopatry         | 56  | 0.876              | 3  | 0.8312    |
|                | 2019 | Edge sympatry     | 600 | 15.088             | 3  | 0.0017*   |
|                |      | Allopatry         | 120 | 4.714              | 3  | 0.1940    |
| Red            | 2018 | Edge sympatry     | 196 | 0.335              | 1  | 0.5625    |
|                |      | Allopatry         | 56  | 0.080              | 1  | 0.7778    |
|                | 2019 | Edge sympatry     | 600 | 8.74               | 1  | 0.0031*   |
|                |      | Allopatry         | 120 | 3.367              | 1  | 0.0665    |
| White          | 2018 | Edge sympatry     | 196 | 1.342              | 1  | 0.2467    |
|                |      | Allopatry         | 56  | 0.717              | 1  | 0.3972    |
|                | 2019 | Edge sympatry     | 600 | 1.537              | 1  | 0.2151    |
|                |      | Allopatry         | 120 | 1.212              | 1  | 0.2709    |
| Bands          | 2018 | Edge sympatry     | 196 | 0.028              | 1  | 0.8672    |
|                |      | Allopatry         | 56  | 0.239              | 1  | 0.6249    |
|                | 2019 | Edge sympatry     | 600 | 5.096              | 1  | 0.0240*   |
|                |      | Allopatry         | 120 | 2.200              | 1  | 0.1380    |
| Tricolored     | 2018 | Edge sympatry     | 196 | 0.252              | 1  | 0.6159    |
|                |      | Allopatry         | 56  | 0.664              | 1  | 0.4152    |
|                | 2019 | Edge sympatry     | 600 | 0.076              | 1  | 0.7831    |
|                |      | Allopatry         | 12  | 3.636              | 1  | 0.0565    |
Figure S1. (a) Clay snake replicas showing four phenotypic color patterns: brown, white-and-black banded, red-and-black banded, and tricolor. Note that the latter three color patterns are considered mimetic, while the brown replicas are considered non-mimetic/cryptic. (b) Diagram showing an example of how clay replicas were arranged along a portion of a transect.
Tables:

**Table 1:** Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc). 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 $\Delta AICc$ is the difference between that statistical model and the best model. Only statistical models within 2 $\Delta AICc$ units of the top model are included.

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

| $K$ | AICc  | $\Delta$AICc | AICc Weight | Log-likelihood | term 1     | term 2     | term 3     | term 4     |
|-----|-------|--------------|-------------|----------------|------------|------------|------------|------------|
| 4   | 824.6768 | 0            | 0.404193    | -408.31       | transect*  | sympathy   | red        | --         |
| 6   | 825.3787 | 0.701893     | 0.28456     | -406.63       | transect*  | sympathy   | individual pattern | --         |
| 5   | 826.6367 | 1.959888     | 0.151707    | -408.276      | transect*  | sympathy** | red**      | interaction |
Table 2. Results of mixed effect model comparison using small sample size-corrected Akaike Information Criterion (AICc). 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 $\Delta$AICc is the difference between that statistical model and the best model. Only statistical models within 2 $\Delta$AICc units of the top model are included.

*indicates random effect

| $K$ | AICc  | $\Delta$AICc | 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* | sympathy  | --       | --       |
| 3   | 343.4256 | 1.624319    | 0.099396    | -168.664       | transect* | red       | --       | --       |
| 3   | 343.4256 | 1.624319    | 0.099396    | -168.664       | transect* | white     | --       | --       |
Figures:

**Figure 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 1800m represents the range edge of coral snakes. Note that neither coral snake species in the park is found above 1800m, but mimics can be found up to the highest elevations.
Figure 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.
**Figure 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.
Figure 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.
Figures

(a) Locations of coral snake and coral snake mimic encounters in Cusuco National Park, Honduras from 2007 to 2019. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal
status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors. (b-c) Species richness of coral snakes and their mimics at differing elevations in Cusuco National Park, Honduras. The dotted line at 1800m represents the range edge of coral snakes. Note that neither coral snake species in the park is found above 1800m, but mimics can be found up to the highest elevations.

![Map of Coral Snake Species and Mimics](image)

**Figure 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.
Figure 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.

Figure 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.
Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- Appendics.pdf
- SupplementryMaterial.pdf