

Summer 2020

Predator-based Selection and the Impact of Edge Sympatry on Components of Coralsnake Mimicry

Lauren E. Wilson

Follow this and additional works at: <https://digitalcommons.georgiasouthern.edu/etd>



Part of the [Biology Commons](#), [Evolution Commons](#), and the [Other Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Wilson, Lauren E., "Predator-based Selection and the Impact of Edge Sympatry on Components of Coralsnake Mimicry" (2020). *Electronic Theses and Dissertations*. 2139. <https://digitalcommons.georgiasouthern.edu/etd/2139>

This thesis (open access) is brought to you for free and open access by the Graduate Studies, Jack N. Averitt College of at Digital Commons@Georgia Southern. It has been accepted for inclusion in Electronic Theses and Dissertations by an authorized administrator of Digital Commons@Georgia Southern. For more information, please contact digitalcommons@georgiasouthern.edu.

PREDATOR-BASED SELECTION AND THE IMPACT OF EDGE SYMPATRY ON
COMPONENTS OF CORALSNAKE MIMICRY

by

LAUREN E. WILSON

(Under the Direction of Christian L. Cox)

ABSTRACT

Studying warning coloration and mimicry is an effective way to understand predator-driven selection and phenotypic diversity. The presence (sympatry) or absence (allopatry) of a toxic model plays a role in shaping mimetic phenotypes. However, the impact of edge sympatry and allopatry on predation of mimetic phenotypes is not well understood. We studied coralsnake mimicry to test how edge sympatry and allopatry affect predation on mimetic phenotypes. Specifically, we tested 1) if overall attack rates varied with edge sympatry of coralsnakes 2) which color patterns conferred a fitness advantage 3) which specific mimetic signal components are important in driving predatory attacks and 4) whether selection patterns varied temporally. We deployed clay replicas that utilized a cryptic pattern, two different signal components (red and white), and a tricolor pattern that included both signal components. We found that overall attacks did differ between edge sympatry and allopatry, with higher attack rates in allopatry. All mimetic phenotypes in 2019 had higher attack rates than cryptic phenotypes in edge sympatry, with a similar but nonspecific pattern in allopatry. Replicas with red and banded patterns received more predatory attacks in edge sympatry than those without, once again with a similar pattern in allopatry. There was also a difference in attack rates and patterns between years,

indicating temporally variable selection such as frequency-dependent selection. These results suggest that mimetic phenotypes may not have a fitness advantage in areas of edge sympatry or allopatry. This suggests the role of sympatry and allopatry may be more complex than previously thought, particularly in how sympatry may interact with extraneous factors such as behavior and frequency of phenotypes.

INDEX WORDS: Coralsnake, Batesian mimicry, Selection, Predation

PREDATOR-BASED SELECTION AND THE IMPACT OF EDGE SYMPATRY ON
COMPONENTS OF CORALSNAKE MIMICRY

by

LAUREN E. WILSON

B.A., Maryville College, 2017

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

© 2020

LAUREN E. WILSON

All Rights Reserved

PREDATOR-BASED SELECTION AND THE IMPACT OF EDGE SYMPATRY ON
COMPONENTS OF CORALSNAKE MIMICRY

by

LAUREN E. WILSON

Major Professor: Christian L. Cox
Committee: Elizabeth A. Hunter
Lance D. McBrayer

Electronic Version Approved
July 2020

TABLE OF CONTENTS

	Page
LIST OF TABLES.....	3
LIST OF FIGURES.....	4
CHAPTER	
1 INTRODUCTION.....	5
Purpose of the Study.....	5
2 METHODOLOGY.....	11
Study System.....	11
Field Experiment.....	12
Statistical Analyses.....	13
3 RESULTS.....	15
Model Comparison.....	15
Contingency Analyses.....	15
4 DISCUSSION.....	23
REFERENCES.....	29
APPENDIX	
A SUPPLEMENTAL METHODS FOR MAXENT CORALSNAKE DISTRIBUTION MODEL	35

LIST OF TABLES

	Page
Table 3.1: Results of mixed effect model comparison using Akaike Information Criterion (AIC) (2018).....	17
Table 3.2: Results of mixed effect model comparison using Akaike Information Criterion (AIC) (2019).....	18
Table 3.3: Results of contingency analyses to determine which color variables are independent of a clay snake replica getting attacked.....	19

LIST OF FIGURES

	Page
Figure 1.1: (a) Coralsnake and mimic encounters in Cusuco National Park, Honduras from 2007-2019.....	10
Figure 2.1. (a) Example placement of clay snake replicas showing one of four color variations throughout a portion of a transect.....	14
Figure 3.1: Attack rates on clay snake replicas in both edge sympatric and allopatric habitats...	20
Figure 3.2: Attack rates on clay snake replicas with 4 different color patterns within edge sympatric and allopatric habitats.....	21
Figure 3.3: (a, b) Attack rates on clay snake replicas with and without the color red included in their patterns within edge sympatric and allopatric habitats.....	22

CHAPTER 1

INTRODUCTION

Purpose of the study

A fundamental goal of biology is understanding the forces that drive the evolution of phenotypic diversity. In order for evolution by natural selection to occur in a population, the population must have both variation in phenotype and a selective force (such as predation) acting upon the population (Endler 1986; Freeman and Herron 2004). Studying predator-driven selection 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 and Janzen 1995; Ham et al. 2006; Kleisner and Saribay 2018; Kuchta 2005; Pfennig et al. 2001; Pfennig et al. 2007; Quicke 2017). For aposematism, conspicuous coloration acts as a signal to predators that the prey is unpalatable and thus promotes avoidance of inedible or dangerous prey (Arbuckle and Speed 2015; Kuchta 2005; Leimar et al. 1986; Mappes et al. 2005; Ruxton et al. 2004). Mimics then honestly (Müllerian) or deceitfully (Batesian) replicate this signal to deter predators (Quicke 2017). Therefore, aposematism and mimicry provide a direct link between phenotype 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 and Pfennig 2007; Kleisner and Saribay 2018; Kuchta 2005; Leimar et al. 1986; Stevens and Ruxton 2012). For example, the abundant literature on mimicry has revealed that mimetic phenotypes can be subject to multiple 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). One factor that

can influence the form of selection on mimetic phenotypes is the presence (occurring in sympatry) or absence (occurring in allopatry) of the toxic model species in the habitats of the mimetic species (Finkbeiner et al. 2018; Greene and McDiarmid 1981; Harper and Pfennig 2007; Kikuchi and Pfennig 2013; Pfennig 2016; Pfennig et al. 2001; Pfennig et al. 2007; Pfennig and Mullen 2010; Ruxton et al. 2004). However, the effect of this co-occurrence, or lack thereof, is complex and is only well studied in some well characterized systems (Akcali and Pfennig 2017; Cox and Davis Rabosky 2013; Harper and Pfennig 2007; Holmes et al. 2017; Pfennig et al. 2001; Pfennig et al. 2007; Pfennig and Mullen 2010).

The effectiveness and precision of mimicry varies with presence and abundance of models (Akcali and Pfennig 2017; Finkbeiner et al. 2018; Harper and Pfennig 2007; Kikuchi and Pfennig 2013; Lindström et al. 1997; Owen and 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 and Pfennig 2014; Harper and Pfennig 2007). Because population densities often 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). For example, in the harmless snakes that mimic deadly coralsnakes (family Elapidae, which also includes mambas and cobras), components of color mimicry patterns are precise in edge sympatry, may be relaxed in deep sympatry, and may not convey a fitness advantage at all in allopatry in a temperate mimicry system (Harper and Pfennig 2007; Pfennig et al. 2007). In addition, in areas of allopatry where coralsnakes only recently went extinct, their mimics became more precise, supporting the idea that mimicry must be more precise in areas

where the model is rare (Akcali and Pfennig 2014). These results imply directional selection towards precise mimicry in a newly allopatric region. However, this research has largely been focused on temperate zones, with few studies conducted in diverse tropical ecosystems and even fewer focused on montane tropical environments. The diversity in these systems yields a vast range of aposematic patterns on both coralsnakes and mimics (Savage and Slowinski 1992). Because aposematic coloration generally leads to stabilizing selection on models, this may indicate that selection acts differently in areas with high biodiversity (Joron and Mallet 1998; Mallet and Turner 1997). The montane tropics not only have higher biodiversity for both coralsnakes and mimics than temperate systems, but also provide habitats both in allopatry and edge sympatry of coralsnakes and their mimics in close geographic range as well as under a variety of different predator assemblages (Figure 1.1) (Townsend and Wilson 2008). Thus, more research is needed to determine how selection on mimetic phenotypes in the montane tropics might act differently than in temperate habitats. Research that focuses on mimicry dynamics in the poorly studied montane tropics would allow us to see how selection on mimicry could change with habitat.

We studied the impact of edge sympatry and allopatry on predation rates on coralsnake banding patterns in the montane tropics of Honduras. Highly venomous, elapid coralsnakes 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).

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. In these systems, there are few local phenotypes, and so it may be more difficult to determine which aspects of these phenotypes are important in deterring predation. In systems with many mimics, we can tease out precisely which signal components are most effective because there may be more local mimics showing these phenotypes. Furthermore, studies focusing on the effects of the level of sympatry, and indirectly model abundance, have been centered on temperate systems that lack the species diversity of the tropics (Akcali and Pfennig 2014; Akcali and Pfennig 2017; Harper and 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 to create a mosaic of sympatric and allopatric regions in close geographic proximity (Figure 1.1) (McCranie and 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 and 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 clay replicas of snakes along an elevational gradient to determine how attack rates on aposematic snakes change with edge sympatry or allopatry with coral snakes in the montane tropics of northwestern Honduras. Specifically, we studied whether predation rates differ with level of sympatry (edge sympatry or allopatry) and mimetic signal components (i.e. presence of red, white, or bands) within the color pattern. First, we tested whether overall attack rates on models varied between edge sympatry and allopatry.

Greater intensity of predation in one habitat over the other could suggest selection is stronger there. Second, we tested which mimetic color patterns conferred a fitness advantage in edge sympatry or allopatry. Empirical research suggests that mimetic phenotypes should convey a fitness advantage in edge sympatry but should have a fitness cost in allopatry (Akcali and Pfennig 2017; Harper and Pfennig 2007; Ries and Mullen 2008). However, if mimetic phenotypes convey a fitness advantage in both habitats, this implies that the fitness advantage of mimetic signals is maintained allopatry close to the range edge. Conversely, if mimetic phenotypes impose a fitness cost in both edge sympatry and allopatry, then this implies that the mimetic signals could be maladaptive in range edges and allopatry. Third, we tested which mimetic signal components would be important in driving predatory attacks. Previous research has suggested that both the presence of red and banding are critical signal components of coralsnake mimicry (Akcali and Pfennig 2014; Pfennig and Mullen 2010). Finally, we examined whether attack rates varied temporally, which could suggest negative frequency dependent selection. Negative frequency-dependent selection occurs when the most common phenotypes in a population are attacked disproportionately more by predators. Over time, this allows rarer phenotypes to become more prominent in the population, thus creating temporal variation (Holmes et al. 2017). Our results will contribute to understanding the effect edge sympatry and allopatry have on predation rates on coralsnakes and their mimics in the tropics and so will provide insight into the broader evolutionary processes that drive the evolution of phenotypic diversity.

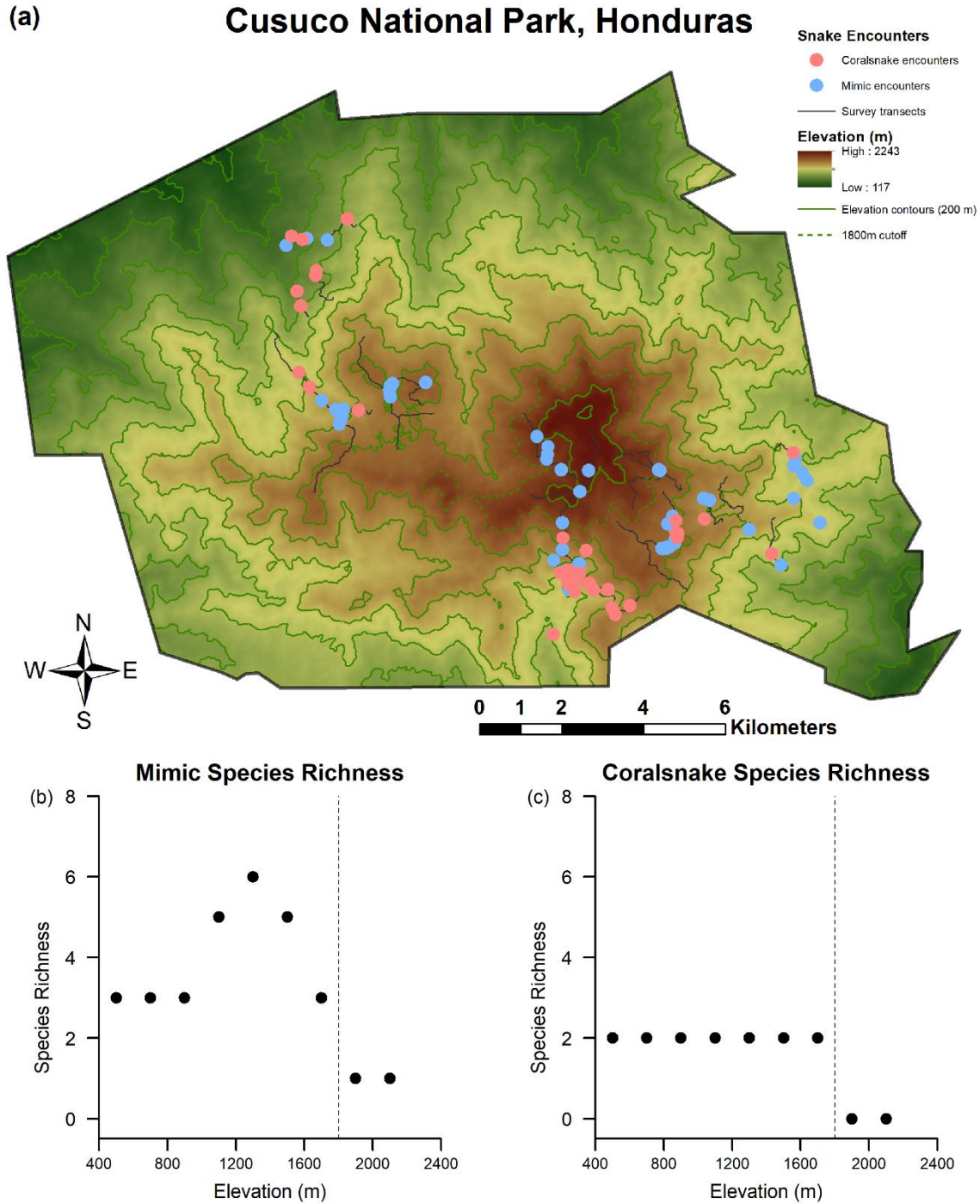


Figure 1.1 (a) Coralsnake and mimic encounters in Cusuco National Park, Honduras from 2007-2019
 (b) Species richness of coralsnakes and their mimics at differing elevations in Cusuco National Park, Honduras. Dotted line at 1800m represents range edge of coralsnakes. Neither coralsnake species in the park is found above 1800m, but mimics can be found up to the highest elevations in the park.

CHAPTER 2

METHODOLOGY

Study site

The study location in Cusuco National Park, Honduras, houses a tropical, montane environment that includes both sympatric and allopatric populations of coral snakes and coral snake mimics (Townsend and Wilson 2008). The park is a protected area located in the Merendón Mountains of northwest Honduras and is around 200km², with an elevation range of just around sea level to just over 2200m (Amphibian Survival Alliance 2019; Brown and Arrivillaga 2017). There are two species of coralsnakes found in the park: *Micrurus diastema* and *Micrurus nigrocinctus*. Both of these species exhibit tricolor red, yellow, and black patterns, though *M. nigrocinctus*, aptly named the “variable coralsnake,” also has a red and black morph (Brown and Arrivillaga 2017; Townsend and Wilson 2008). The nine species of colubrid snakes found in the park that are considered coralsnake mimics are *Geophis nephodrymus*, *Lampropeltis triangulum*, *Ninia sebae*, *Oxyrhopus petolarius*, *Pliocercus elapoides*, *Scaphiodontophis annulatus*, *Scolecophis atrocinctus*, *Sibon dimidiatus*, and *Tropidodipsas sartorii* (Brown and Arrivillaga 2017; Townsend and Wilson 2008). These species are considered mimics because they have banded patterns with black, red, and/or white. They range from tricolor mimics such as *P. elapoides* and *L. triangulum* to bicolor red and black (some *G. nephodrymus*) or whitish yellow and black (*T. sartorii*) (Brown and Arrivillaga 2017; McCranie and Savage 2011; Townsend and Wilson 2008) The park spans a variety of forest types including cloud forest (distinguished by frequent cloud cover), dwarf forest (distinguished by higher elevations, small trees, and increased number of epiphytes), and forest fringes (distinguished by little to no tree

cover). These forests are predominately broad-leaf, pine, or mixed forests (Brown and Arrivillaga 2017; Townsend and Wilson 2008).

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 the replicas using non-toxic, pre-colored clay, and they displayed one of four color patterns. These patterns are based on native models and mimics: fully mimetic (tri-color), black and red banded, black and white banded, or brown (Figure 2.1).

We placed replicas in groups of 4, hereafter referred to as a tetrad, which included one of each replica type. Over a span of 8 weeks from June to August in 2018 and 2019, we arranged the tetrads along 9 or 18 transects, respectively, at varying elevations within the park. Transects over 1800m in elevation we classified as allopatric, and those under 1800m we classified as edge sympatric. These classifications were confirmed with a Maxent analysis (for methods, see electronic supplementary material). Of the 9 transects in 2018, 3 were allopatric and 6 were edge sympatric. Of the 18 transects in 2019, 3 were allopatric and 16 were edge sympatric. There are less allopatric transects because there was much less area in the higher elevations at the top of the mountain. Each transect contained 7 (in 2018) or 10 (in 2019) branches, spaced approximately 10 meters apart, with one tetrad per branch (see electronic supplementary material, figure S1a). We placed each replica within a tetrad at least 3 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 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 3-4 days for marks of predation (for example, 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 model comparison of mixed effect models and contingency analyses. 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. For analysis, replicas were classified according to five color variables. These variables included one categorical variable of replica color pattern (brown, white & black, red & black, or fully mimetic; hereafter referred to as individual pattern), and four binary variables: the presence of red, presence of white, presence of bands, and whether it is a mimetic color pattern. We created logistic mixed effect models in R and compared them using Akaike information criterion (AIC) values to determine which models were most effective in predicting attack rates (Bates et al. 2015). The response variable for these models was whether a replica was attacked or not attacked during the two week period. The null models for each year included only transect as a random effect. The remaining models included transect as a random effect as well as all combinations of: level of sympatry, one of the five color variables, and interaction terms. We performed contingency analyses in JMP.

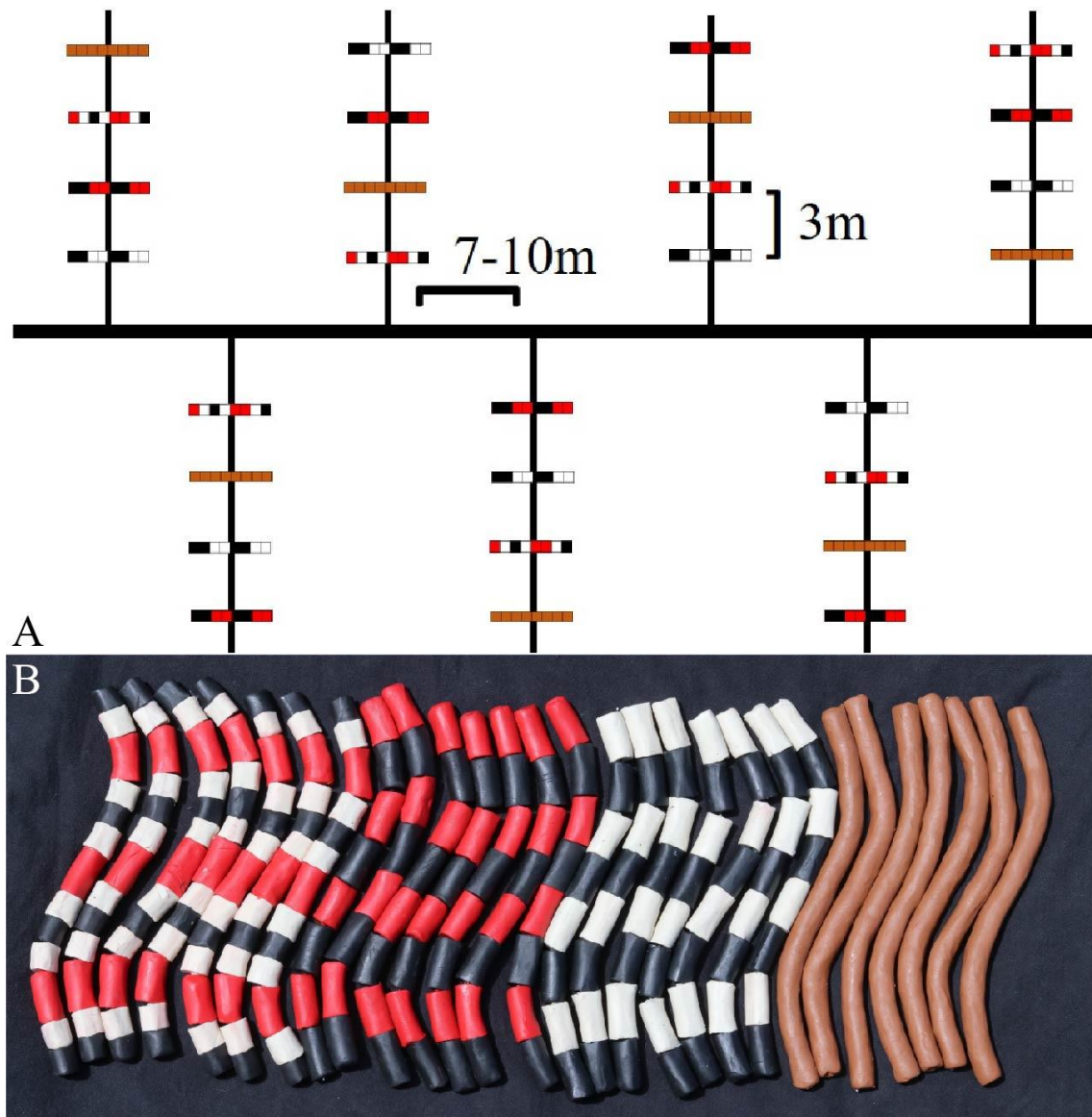


Figure 2.1. (a) Example placement of clay snake replicas showing one of four color variations throughout a portion of a transect. (b) Clay snake replicas showing four phenotypic color patterns: brown, white & black, red & black, and tricolor

CHAPTER 3

RESULTS

Model comparison

Sympatry and presence of red were the most important factors impacting attack rates on models. In 2018, the null model had the lowest AIC score (Table 3.1). All of the models that fell within 2 AIC units of the best model had only one additional term after transect: sympatry, the presence of white, red, or bands, or whether it was mimetic. In 2019, the best model included transect, sympatry, and the presence of red (no interaction) (Table 3.2). Three models fell within 2 AIC units of the best of model, and they all contained sympatry as a term in the model. Those models also included individual color pattern both with and without an interaction, and the presence of red with an interaction.

Contingency analyses

The level of sympatry impacted attack rates: we found a difference in attack rates on all replica colors combined in allopatric and edge sympatric habitats with a contingency analysis in data from 2019 ($p < .0001$) but not 2018 ($p = 0.2869$) (Figure 3.1).

When taking color pattern of replicas into account, we found differences between edge sympatric and allopatric habitats in the specific patterns and signal components that were important in affecting attack rates (Figure 3.2). Specifically, we found that in 2019 individual pattern of the replica was not independent of getting attacked in edge sympatric habitats, but this was not found to be significant in allopatric habitats (Table 3.3). Additionally, we did not find this pattern in 2018 in either edge sympatric or allopatric habitats.

When analyzing within allopatric and edge sympatric habitats, the presence of red and bands had an impact on attack rates. We did not find any differences between edge sympatric and allopatric habitats in 2018 (Table 3.3). However, in 2019 we found that in edge sympatric habitats both replicas with both red and bands were attacked more (Table 3.3, Figure 3.3). In allopatric habitats, only the presence of red affected attack rates (Table 3.3, Figure 3.3).

Table 3.1 Results of mixed effect model comparison using Akaike Information Criterion (AIC). 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 pattern, presence of white, presence of red, presence of bands, or whether it is mimetic), and an interaction between sympatry and the color variable. K is the number of parameters and Δ AIC is the difference between that model and the best model.

Model Name	K	AIC	Δ AIC	AIC Weight	Log-likelihood	term 1	term 2	term 3	term 4
null	3	360.0262	0	0.216424	-177.013	transect*	--	--	--
sym	4	361.3376	1.311461	0.112338	-176.669	transect*	sympatry	--	--
white	4	361.6016	1.575368	0.098451	-176.801	transect*	white	--	--
red	4	361.6016	1.575368	0.098451	-176.801	transect*	red	--	--
bands	4	362.0205	1.994343	0.079843	-177.01	transect*	bands	--	--
mimetic	4	362.0205	1.994343	0.079843	-177.01	transect*	mimetic	--	--
symRedB	5	362.913	2.886828	0.051102	-176.457	transect*	sympatry	red	--
symWhiteB	5	362.913	2.886828	0.051102	-176.457	transect*	sympatry	white	--
symWhiteA	6	363.2449	3.218745	0.043288	-175.622	transect*	sympatry**	white**	interaction
symMimB	5	363.332	3.305804	0.041444	-176.666	transect*	sympatry	mimetic	--
symBandsB	5	363.332	3.305804	0.041444	-176.666	transect*	sympatry	bands	--
symMimA	6	364.4378	4.411574	0.023842	-176.219	transect*	sympatry**	mimetic**	interaction
symRedA	6	364.9118	4.885614	0.018811	-176.456	transect*	sympatry**	red**	interaction
symBandsA	6	365.0793	5.05313	0.017299	-176.54	transect*	sympatry**	bands**	interaction
pattern	6	365.1591	5.132962	0.016623	-176.58	transect*	individual pattern	--	--
symPattB	7	366.4706	6.444422	0.008628	-176.235	transect*	sympatry	individual pattern	--
symPattA	10	370.65	10.6238	0.001068	-175.325	transect*	sympatry**	individual color pattern**	interaction

Table 3.2: Results of mixed effect model comparison using Akaike Information Criterion (AIC). 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 pattern, presence of white, presence of red, presence of bands, or whether it is mimetic), and an interaction between sympatry and the color variable. K is the number of parameters and Δ AIC is the difference between that model and the best model.

Model Name	K	AIC	Δ AIC	AIC Weight	Log-likelihood	term 1	term 2	term 3	term 4
symRedB	5	860.2784	0	0.344672	-425.139	transect*	sympatry	red	--
symPattB	7	860.6971	0.418658	0.279573	-423.349	transect*	sympatry	individual pattern	--
symRedA	6	861.7519	1.473447	0.164988	-424.876	transect*	sympatry**	red**	interaction
symPattA	10	861.8456	1.567224	0.15743	-420.923	transect*	sympatry**	individual pattern**	interaction
symBandsB	5	865.1653	4.886859	0.029939	-427.583	transect*	sympatry	bands	--
symBandsA	6	866.7593	6.480837	0.013493	-427.38	transect*	sympatry**	bands**	interaction
symMimA	6	869.697	9.418588	0.003106	-428.849	transect*	sympatry**	mimetic**	interaction
sym	4	870.4276	10.14917	0.002155	-431.214	transect*	sympatry	--	--
symWhiteA	6	871.4204	11.14197	0.001312	-429.71	transect*	sympatry**	white**	interaction
symMimB	5	872.0238	11.74542	0.00097	-431.012	transect*	sympatry	mimetic	--
symWhiteB	5	872.0764	11.79799	0.000945	-431.038	transect*	sympatry	white	--
red	4	872.5624	12.28396	0.000741	-432.281	transect*	red	--	--
pattern	6	872.981	12.70262	0.000601	-430.491	transect*	individual pattern	--	--
bands	4	877.4492	17.17082	6.44E-05	-434.725	transect*	bands	--	--
null	3	882.7115	22.43314	4.64E-06	-438.356	transect*	--	--	--
mimetic	4	884.3078	24.02938	2.09E-06	-438.154	transect*	mimetic	--	--
white	4	884.3604	24.08195	2.03E-06	-438.18	transect*	white	--	--

Table 3.3. Results of contingency analyses to determine which color variables are independent of a clay snake replica getting attacked (n = number of samples, df = degrees of freedom)

Color variable	Year	Level sympatry	n	df	Chi-squared	p-value
Individual pattern	2018	Edge sympatry	96	3	1.761	.6234
		Allopatry	56	3	.876	.8312
	2019	Edge sympatry	600	3	15.088	.0017
		Allopatry	120	3	4.714	.194
Red	2018	Edge sympatry	196	1	.335	.5625
		Allopatry	56	1	.08	.7778
	2019	Edge sympatry	600	1	8.74	.0031
		Allopatry	120	1	3.367	.0665
White	2018	Edge sympatry	196	1	1.342	.2467
		Allopatry	56	1	.717	.3972
	2019	Edge sympatry	600	1	1.537	.2151
		Allopatry	120	1	1.212	.2709
Bands	2018	Edge sympatry	196	1	.028	.8672
		Allopatry	56	1	.239	.6249
	2019	Edge sympatry	600	1	5.096	.024
		Allopatry	120	1	2.2	.138
Mimetic	2018	Edge sympatry	196	1	.252	.6159
		Allopatry	56	1	.664	.4152
	2019	Edge sympatry	600	1	.076	.7831
		Allopatry	12	1	3.636	.0565

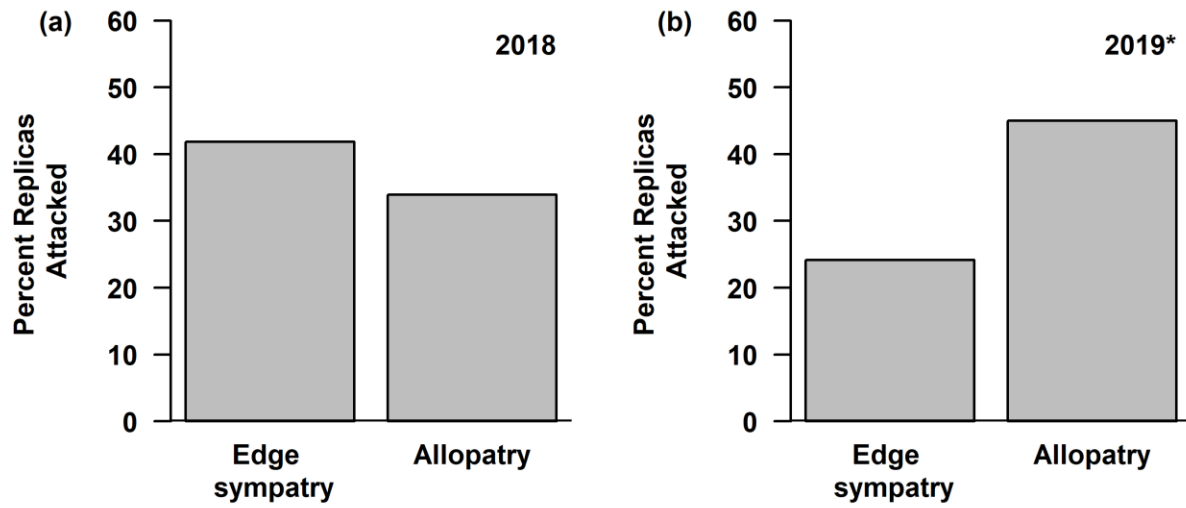


Figure 3.1. Attack rates on clay snake replicas in edge sympatric and allopatric habitats in 2018 (a) and 2019 (b). An asterisk (*) indicates significance from contingency analyses. Attack rates in 2019 were higher in allopatry, while attack rates in 2018 were about the same in edge sympatry and allopatry.

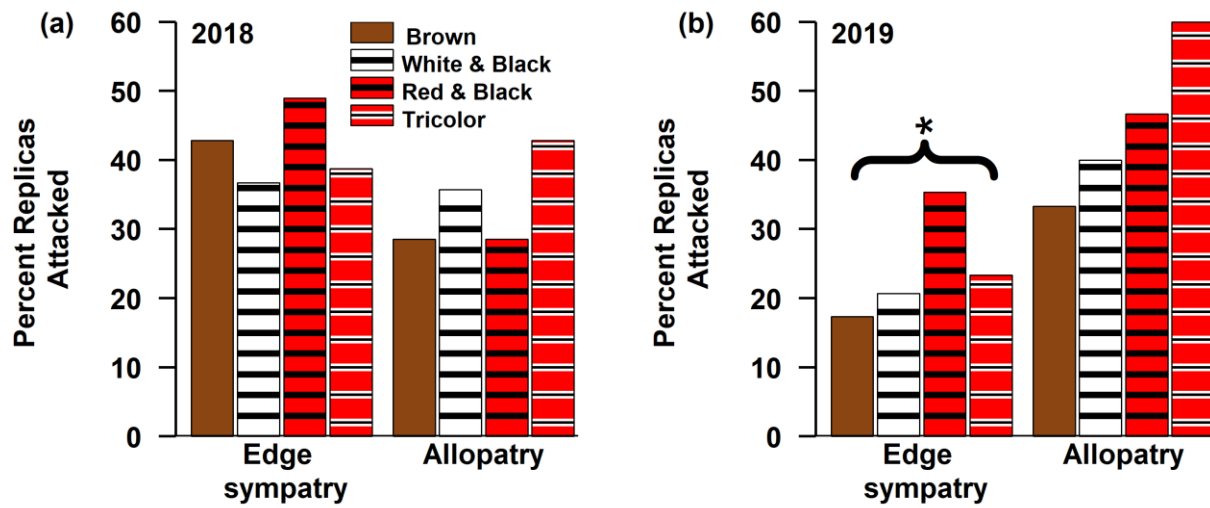


Figure 3.2 Attack rates on clay snake replicas with 4 different color patterns within edge sympatric and allopatric habitats in 2018 (a) and 2019 (b). An asterisk (*) indicates significance from contingency analyses. Replicas with mimetic patterns were attacked more than brown replicas in almost all scenarios.

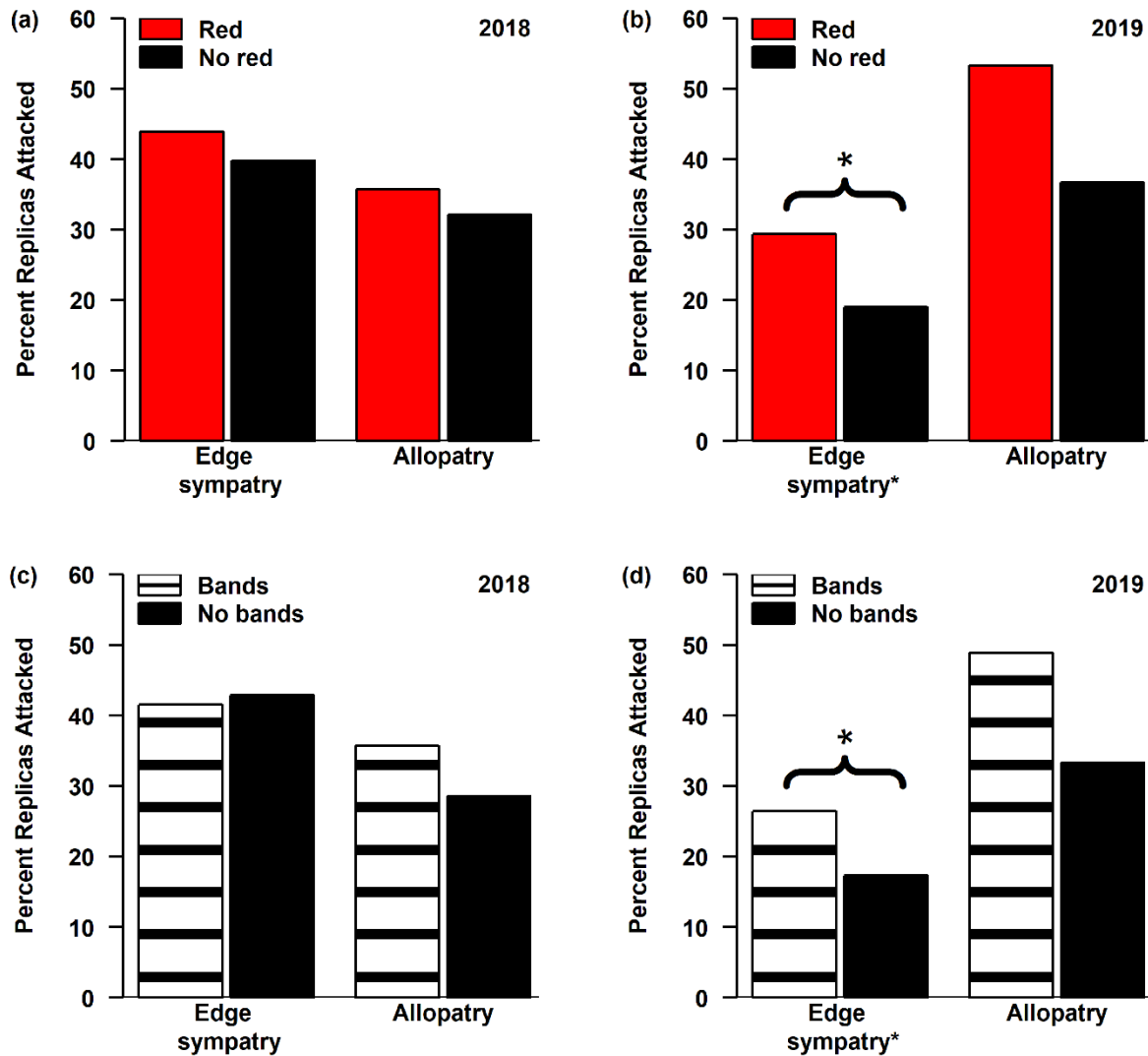


Figure 3.3 Attack rates on clay snake replicas with and without the color red included in their patterns in both edge sympatric and allopatric habitats (a, b). Attack rates on clay snake replicas with and without banded color patterns within edge sympatric and allopatric habitats (c, d). An asterisk (*) indicates significance from contingency analyses. Replicas with red or bands were almost always attacked more than replicas without.

CHAPTER 4

DISCUSSION

Contrary to expectations, we found that while sympatry does impact predation, coral snake patterns do not have a fitness advantage in either edge sympatry or allopatry. Specifically, replicas without mimicry components almost always had lower attack rates than replicas with the three mimetic patterns, regardless of both year and whether they were placed in an edge sympatric habitat or an allopatric habitat. We also found that the presence of red and bands were particularly important regarding attack rates in 2019 in areas of edge sympatry—replicas with red or bands had higher attack rates than those without. Attack rates in allopatry showed similar patterns but likely do not have enough statistical power due to a lower sample size. This is in contrast to what has previously been found, where both brown replicas and replicas with imprecise mimetic patterns were attacked more than accurate 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 patterns of attacks on models varied temporally, which in a stable, tropical system, could be caused by negative frequency-dependent selection (Akcali et al. 2018; Cox and Davis Rabosky 2013; Holmes et al. 2017). Our research implies that mimicry could operate differently in the montane tropics than in temperate habitats and may not be entirely advantageous.

We found that mimetic traits do not convey a fitness advantage of protection from predators and might even confer a fitness cost in both edge sympatry and allopatry in the montane tropics. In temperate regions, mimetic patterns can incur a fitness cost that varies between allopatric regions with different local mimics, which implies that even between allopatric populations in similar habitats there can be differences in patterns of selection (Pfennig

et al. 2007). Predators in the southeast United States differentially attacked replicas depending on whether they were in deep sympatry or edge sympatry (Harper and Pfennig 2007). Those predators avoided both poor and accurate mimetic phenotypes in areas of deep sympatry, whereas they avoided only accurate mimics in edge sympatry. Furthermore, avian predators in the lowland tropics attacked brown replicas more than tricolor or red & black banded replicas (Brodie III 1993; Brodie III and Janzen 1995). However, while we did find overall attack rates were lower in areas of edge sympatry, we did not find that predators avoided the more accurate mimetic phenotypes. Indeed, the replicas with phenotypes most closely resembling those of coralsnakes (tricolor and red & black banded) were often those attacked most both in areas of edge sympatry and allopatry. These results support the idea that in areas where coralsnakes are rare or absent, mimetic phenotypes may not confer as much an advantage as in areas where coralsnakes 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). Given the fitness cost of mimetic phenotypes in the montane tropics, what permits the persistence of multiple species of models and mimics in these areas? There are three primary reasons that 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 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 coralsnake mimicry might reinforce and strengthen the avoidance of mimetic patterns. For example, brown replicas of frogs were attacked significantly more when moving than when stationary, whereas red replicas of aposematic frogs were attacked

significantly more when stationary than when moving (Paluh et al. 2014). Coralsnakes display stereotyped coiling and thrashing behavior when threatened, and thus behavior is an integrated part of their antipredator coloration (Davis Rabosky et al. 2020). These findings suggest that movement and behavior may play an important role in selection for both cryptic and aposematic individuals (Bateman et al. 2017). Hence, 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 (Bateman et al. 2017). Our results suggest that there may also be variation in how important movement is in relation to selection behavior. In tropical, sympatric regions where coralsnakes are relatively common, stationary mimetic replicas were avoided as predicted by mimicry theory (Brodie III 1993; Brodie III and Janzen 1995). However, in range edges where the 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). Whether mimetic color signals coupled with behavior would confer a fitness advantage in the montane tropics would be a fruitful area for future research.

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) maintains the presence of mimetic phenotypes (Ries and Mullen 2008). Coralsnake mimics in temperate systems migrate from areas of sympatry to allopatry based upon indirect DNA evidence (Harper and Pfennig 2008). Because our study was conducted on a limited geographic scale, high-elevation allopatric sites were within a few kilometers of low elevation areas, so immigration from higher coralsnake density in lower elevations to higher elevations with lower coralsnake density is plausible. 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), although this is less common in the climatically stable tropics. Thus, there could be enough immigration and gene flow of mimics between high elevations without coralsnakes and low elevations with coralsnakes that 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. Indeed, we found evidence of temporal variation in predation rates on coral snake color patterns, yet we cannot rule out variation in experimental design between years that could contribute to temporal variation. Many mimicry systems are influenced by frequency-dependent selection, including frogs, snails, butterflies, and snakes (Holmes et al. 2017; Ries and Mullen 2008). When this selection allows rarer phenotypes to increase in population, over time this could change the ratio of which patterns are most common, thus altering the pattern that is targeted by predators (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 the context of the coralsnake mimicry system, in areas where models are uncommon or absent and mimics are abundant, the high abundance of harmless mimics might override predator avoidance, thus leading to predators learning or evolving a preference for conspicuous prey (Pfennig et al. 2007; Pfennig and Mullen 2010). This in turn reduces the population of mimics and potentially induces polymorphic mimics to shift morph frequencies to non-mimetic morphs. The decrease in mimics then increases the ratio of models to mimics, which exerts stronger selection on predators to avoid mimetic phenotypes. Mimics then have a fitness advantage in survivorship. Therefore, negative frequency-dependent selection 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 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. The presence of both learned and innate avoidance would likely impact the dynamics of frequency dependent cycles (Akcali et al. 2018). For example, naïve juveniles of motmots and great kiskadees innately avoid coralsnake patterns, despite no experience with snakes (Smith 1975; Smith 1977). However, tropical birds such as puffbirds and adult motmots have been documented to consume coralsnakes (Smith 1969). While predators likely have a combination of innate and learned avoidance, learned avoidance would lead to shorter periods of negative frequency-dependent cycles than innate avoidance because innate avoidance relies on intergenerational processes.

While we found that the mimetic phenotype did not confer a fitness advantage, and may impose a fitness cost of decreased survivorship, our results were consistent with previous research on coralsnake mimicry. Replicas that included red as a signal component were attacked more than those without. In addition, replicas with just red and black bands were attacked more than the tricolor replicas in areas of edge sympatry during both years. In allopatric habitats, however, tricolor replicas were attacked more than red and black replicas. This could indicate that it is beneficial to be a precise mimic in areas where the model is rare but present, but that protection breaks down farther from the model's range. These results are consistent with previous findings where predators avoided good mimics over poor mimics in edge (Harper and Pfennig 2007). Observational studies using museum specimen have also found differences in mimetic precision in relation to sympatry and allopatry (Akcali and Pfennig 2014; Akcali and Pfennig 2017; Harper and 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 and Pfennig 2007). However, 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; Akcali and Pfennig 2017). A potential future study could use museum specimen from the tropics to link our findings on selection with patterns of mimetic precision to determine if these patterns are similar between temperate and tropical habitats.

Our data suggest that coralsnake mimicry may not provide an advantage in areas where coralsnakes are rare or absent, such as in edge sympatry and allopatry. Despite this, mimicry persists. This may be because of gene flow and immigration of both mimics and predators, frequency-dependent selection, or a combination. Frequency-dependent selection may also play a role in the temporal heterogeneity seen in our results. In addition, behavior is an important aspect of antipredator defenses in coralsnakes that is unable to be captured using stationary clay replicas yet may play an integral role in selection. Mimicry may even operate differently between temperate and tropical habitats. To further understand the complex nature of how sympatry and allopatry effect selection on coralsnake mimics, studies comprising multiple years and locations ranging from deep sympatry to deep allopatry would be ideal.

REFERENCES

- Akcali, C., D. Kikuchi, and D. Pfennig. 2018. Coevolutionary arms races in Batesian mimicry? A test of the chase-away hypothesis. *Biological Journal of the Linnean Society* 124:668-676.
- Akcali, C. K., and D. W. Pfennig. 2014. Rapid evolution of mimicry following local model extinction. *Biol Lett* 10.
- . 2017. Geographic variation in mimetic precision among different species of coral snake mimics. *J Evol Biol* 30:1420-1428.
- Amphibian Survival Alliance. 2019. Spike-thumb Frog, *Plectrohyla dasypus*. Amphibian Survival Alliance.
- Arbuckle, K., and M. P. Speed. 2015. Antipredator defenses predict diversification rates. *Proc Natl Acad Sci U S A* 112:13597-13602.
- Bateman, P. W., P. A. Fleming, and A. K. Wolfe. 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.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67:1-48.
- Brodie III, E. 1993. Differential Avoidance of Coral Snake Banded Patterns by Free-Ranging Avian Predators in Costa Rica. *Evolution* 47:227-235.
- Brodie III, E., and F. J. Janzen. 1995. Experimental Studies of Coral Snake Mimicry: Generalized Avoidance of Ringed Snake Patterns by Free-Ranging Avian Predators. *Functional Ecology* 9.

- Brown, T., and C. Arrivillaga. 2017. Herpetofauna of Cusuco National Park, Honduras, Operation Wallacea.
- Charlesworth, D., and B. Charlesworth. 1975. Theoretical genetics of batesian mimicry I. Single-locus models. *Journal of Theoretical Biology* 55:283-303.
- Cox, C. L., and A. R. Davis Rabosky. 2013. Spatial and temporal drivers of phenotypic diversity in polymorphic snakes. *Am Nat* 182:E40-57.
- Davis Rabosky, A. R., C. L. Cox, D. L. Rabosky, P. O. Title, I. A. Holmes, A. Feldman, and J. A. McGuire. 2016. Coral snakes predict the evolution of mimicry across New World snakes. *Nat Commun* 7:11484.
- Davis Rabosky, A. R., J. G. Larson, S. M. Danforth, and T. Y. Moore. 2020. A Quantitative Analysis of *Micrurus* Coral Snakes Reveals Unexpected Variation in Stereotyped Anti-Predator Displays Within a Mimicry System. *Integrative Organismal Biology* 2.
- Endler, J. A. 1986, *Natural Selection in the Wild*. Princeton, New Jersey, USA, Princeton University Press.
- Finkbeiner, S. D., P. A. Salazar, S. Nogales, C. E. Rush, A. D. Briscoe, R. I. Hill, M. R. Kronforst et al. 2018. Frequency dependence shapes the adaptive landscape of imperfect Batesian mimicry. *Proc Biol Sci* 285.
- Freeman, S., and J. C. Herron. 2004. Ch 3: Darwinian Natural Selection Evolutionary Analysis.
- Greene, H. W., and R. W. McDiarmid. 1981. Coral snake mimicry: does it occur? *Science* 213:1207-1212.
- Ham, A. D., E. Ihalainen, L. Lindström, and J. Mappes. 2006. Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behavioral Ecology and Sociobiology* 60:482-491.

- Harper, G. R., Jr., and D. W. Pfennig. 2008. Selection overrides gene flow to break down maladaptive mimicry. *Nature* 451:1103-1106.
- Harper, G. R., and D. W. Pfennig. 2007. Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proc Biol Sci* 274:1955-1961.
- Hengeveld, R., and J. Haeck. 1982. The Distribution of Abundance. I. Measurements. *Journal of biogeography* 9:303-316.
- Hinman, K. E., H. Throop, K. L Adams, A. J Dake, K. McLauchlan, and M. J McKone. 1997, Predation by free-ranging birds on partial coral snake mimics: the importance of ring width and color, v. 51.
- Holmes, I. A., M. R. Grundler, and A. R. Davis Rabosky. 2017. Predator Perspective Drives Geographic Variation in Frequency-Dependent Polymorphism. *Am Nat* 190:E78-E93.
- Joron, M., and J. L. B. Mallet. 1998. Diversity in mimicry: paradox or paradigm? *Trends in Ecology & Evolution* 13:461-466.
- Kikuchi, D. W., and D. W. Pfennig. 2010. Predator cognition permits imperfect coral snake mimicry. *Am Nat* 176:830-834.
- . 2013. Imperfect mimicry and the limits of natural selection. *The Quarterly review of biology* 88:297.
- Kleisner, K., and S. A. Saribay. 2018. The Dual Nature of Mimicry: Organismal Form and Beholder's Eye. *Biosemitotics*.
- Kuchta, S. R. 2005. Experimental Support for Aposematic Coloration in the Salamander *Ensatina eschscholtzii xanthoptica*: Implications for Mimicry of Pacific Newts. *Copeia* 2005:265-271.

- Leimar, O., M. Enquist, and B. Sillen-Tullberg. 1986. Evolutionary Stability of Aposematic Coloration and Prey Unprofitability: A Theoretical Analysis. *The American Naturalist* 128:469-490.
- Lindstedt, C., H. Eager, E. Ihalainen, A. Kahilainen, M. Stevens, and J. Mappes. 2011. Direction and strength of selection by predators for the color of the aposematic wood tiger moth. *Behavioral Ecology* 22:580-587.
- Lindström, L., R. V. Alatalo, and J. Mappes. 1997. Imperfect Batesian mimicry—the effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society B: Biological Sciences* 264:149-153.
- Mallet, J., and J. Turner. 1997. Biotic drift or the shifting balance — Did forest islands drive the diversity of warningly coloured butterflies?, Pages 262–280.
- Mappes, J., and R. V. Alatalo. 1997. Batesian Mimicry and Signal Accuracy. *Evolution* 51:2050-2053.
- Mappes, J., N. Marples, and J. A. Endler. 2005. The complex business of survival by aposematism. *Trends Ecol Evol* 20:598-603.
- McCranie, J. R., and J. M. Savage. 2011, *The Snakes of Honduras: Systematics, Distribution, and Conservation*, Society for the Study Of Amphibians.
- Owen, R. E., and A. R. G. Owen. 1984. Mathematical paradigms for mimicry: Recurrent sampling. *Journal of Theoretical Biology* 109:217-247.
- Paluh, D. J., M. M. Hantak, and R. A. Saporito. 2014. A Test of Aposematism in the Dendrobatid Poison Frog *Oophaga pumilio*: The Importance of Movement in Clay Model Experiments. *Journal of Herpetology* 48:249-254.
- Pfennig, D. W. 2016. Evolutionary biology: To mimicry and back again. *Nature* 534:184-185.

- Pfennig, D. W., W. R. Harcombe, and K. S. Pfennig. 2001. Frequency-dependent Batesian mimicry. *Nature* 410:323.
- Pfennig, D. W., G. R. Harper, A. F. Brumo, W. R. Harcombe, and K. S. Pfennig. 2007. Population differences in predation on Batesian mimics in allopatry with their model: selection against mimics is strongest when they are common. *Behavioral Ecology and Sociobiology* 61:505-511.
- Pfennig, D. W., and S. P. Mullen. 2010. Mimics without models: causes and consequences of allopatry in Batesian mimicry complexes. *Proc Biol Sci* 277:2577-2585.
- Pough, F. H. 1988. Mimicry of Vertebrates: Are the Rules Different? *The American Naturalist* 131:S67-S102.
- Quicke, D. L. J. 2017, *Mimicry, crypsis, masquerade and other adaptive resemblances*, Hoboken, NJ : Wiley Blackwell, 2017.
- Ries, L., and S. P. Mullen. 2008. A rare model limits the distribution of its more common mimic: a twist on frequency-dependent Batesian mimicry. *Evolution* 62:1798-1803.
- Ruxton, G., W. Allen, T. N. Sherratt, and M. Speed. 2004, *Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry*. New York, Oxford University Press.
- Savage, J. M., and J. B. Slowinski. 1992. The colouration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae) 45:235-254.
- Smith, N. G. 1969. Avian Predation of Coral Snakes. *Copeia* 1969:402-404.
- Smith, S. M. 1975. Innate Recognition of Coral Snake Pattern by a Possible Avian Predator. *Science* 187:759.
- . 1977. Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* 265:535-536.

Stevens, M., and G. D. Ruxton. 2012. Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society B: Biological Sciences* 279:417-426.

Townsend, J. H., and L. D. Wilson. 2008, *The Amphibians & Reptiles of Cusuco National Park, Honduras*. Salt Lake City, Utah, Bibliomania!

Yamauchi, A. 1993. A population dynamic model of Batesian mimicry 35:295-315.

APPENDIX

A Supplemental Methods for MaxEnt Coralsnake Distribution Model

Occurrence Point Collection

Occurrence points have been collected by researchers at Operation Wallacea. The earliest records are from 2007 and the most recent are from 2019, and all records occurred from June to August. 32 occurrence points were utilized, with 26 points used for training the model and 6 used to test the model.

Occurrence points were collected using two methods: transect surveys and opportunistic encounters. Operation Wallacea utilizes a variety of campsites within the park, and near each camp there are 4-5 terrestrial transects and 1-2 river transects. During the field season of June to August, terrestrial transects are each surveyed during the day once a week and river transects are surveyed at night at least twice a week. Snakes encountered on these surveys are recorded as transect occurrence points. Any snake encountered outside of a transect—for example, in the camp or on a non-herpetological survey—is recorded as an opportunistic occurrence point. For the purposes of this study, transect and opportunistic points were combined.

MaxEnt Distribution Model

A coralsnake distribution model was created in Maxent with the following variables: elevation, percent sand composition on the surface, and percent tree cover. The extent of this distribution model is Cusuco National Park, and the grain size is 228 m². Map layers with smaller grain sizes were resampled using the nearest neighbor technique to match the grain size of 228 m².