

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

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

2 Running title: Coral snake mimicry in montane tropics

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29

30 **Abstract**

31 Mimicry is a vivid example of how predator-driven selection can impact phenotypic
32 diversity, which itself can be influenced by the presence (sympatry) or absence (allopatry) of a
33 dangerous model. However, the impact of sympatry and allopatry on predation on mimicry
34 systems at fine spatial scales (e.g., edge sympatry, allopatry) is not well understood. We used a
35 clay replica study in a montane tropical site in Honduras to test the impact of edge sympatry on
36 1) overall attack rates, 2) the fitness benefit of mimetic coloration, 3) predation on specific
37 mimetic signal components, and 4) temporal variation in predator-based selection on mimicry
38 components. Unlike previous research, we found that mimetic phenotypes received significantly
39 more attacks than cryptic replicas in edge sympatry, suggesting that mimetic phenotypes might
40 not confer a fitness benefit in areas of edge sympatry. Additionally, we documented temporal
41 variation in predator-based selection, as the impacts of allopatry on predatory attacks varied
42 among years. Our results imply that the effect of sympatry and allopatry on predator-based
43 selection in mimicry systems may be more complex than previously thought for species-rich
44 assemblies of coral snakes and their mimics in the montane tropics.

45 **Introduction**

46 Although phenotypic diversity is extremely well-studied in evolutionary biology, the
47 means by which phenotypic patterns occur and are maintained remain unclear in many systems.
48 In order for evolution by natural selection to occur in a population, the population must have
49 variation in a heritable phenotype and a selective force (such as predation) acting upon the
50 population (Endler, 1986; Freeman & Herron, 2004). Studying predation pressure is an effective
51 method to understand phenotypic diversity because the selective agent is known, and much has
52 been learned by analyzing the evolutionary drivers of antipredator traits such as warning
53 coloration (e.g. aposematism) and mimicry (Brodie III, 1993; Brodie III & Janzen, 1995; Ham et
54 al., 2006; Kleisner & Saribay, 2018; Kuchta, 2005; Pfennig et al., 2001; Pfennig et al., 2007;
55 Quicke, 2017). In organisms with aposematism, conspicuous coloration acts as a signal to
56 potential predators that these organisms are inedible or dangerous, thus promoting predator
57 avoidance (Arbuckle & Speed, 2015; Kuchta, 2005; Leimar et al., 1986; Mappes et al., 2005;
58 Ruxton et al., 2004). In turn, mimics honestly (Müllerian) or deceitfully (Batesian) replicate this
59 signal and thereby gain protection (Quicke, 2017). Aposematism and mimicry therefore provide
60 a direct link between phenotypic traits and predator-driven selection and can offer strong
61 evidence for how evolution by natural selection operates in nature (Davis Rabosky et al., 2016;
62 Endler, 1986; Harper & Pfennig, 2007; Kleisner & Saribay, 2018; Kuchta, 2005; Leimar et al.,
63 1986; Stevens & Ruxton, 2012). Mimetic phenotypes are known to be subjected to various types
64 of selection, including directional, stabilizing, and frequency-dependent selection (Akcali et al.,
65 2018; Akcali & Pfennig, 2014; Cox & Davis Rabosky, 2013; Holmes et al., 2017; Lindstedt et
66 al., 2011; Mappes & Alatalo, 1997; Ruxton et al., 2004), and these selective forces can
67 themselves be influenced by the spatial co-occurrence (sympatry) or lack thereof (allopatry) of

68 models and mimics (Finkbeiner et al., 2018; Greene & McDiarmid, 1981; Harper & Pfennig,
69 2007; Kikuchi & Pfennig, 2013; Pfennig, 2016; Pfennig et al., 2001; Pfennig et al., 2007;
70 Pfennig & Mullen, 2010; Ruxton et al., 2004). Nevertheless, the evolutionary effects of sympatry
71 and allopatry are complex and only well studied in some systems (Akcali & Pfennig, 2017; Cox
72 & Davis Rabosky, 2013; Harper & Pfennig, 2007; Holmes et al., 2017; Pfennig et al., 2001;
73 Pfennig et al., 2007; Pfennig & Mullen, 2010).

74 The effectiveness and precision of mimicry vary with presence and abundance of models
75 (Akcali & Pfennig, 2017; Finkbeiner et al., 2018; Harper & Pfennig, 2007; Kikuchi & Pfennig,
76 2013; Lindström et al., 1997; Owen & Owen, 1984; Pfennig et al., 2001; Ruxton et al., 2004;
77 Yamauchi, 1993). For example, mimetic precision decreases in areas with denser populations of
78 models and increases where the model is rare (Akcali & Pfennig, 2014; Harper & Pfennig,
79 2007). Because population densities often decrease in geographic range margins (Hengeveld &
80 Haeck, 1982), the relative distance from the sympatry-allopatry border (i.e. edge sympatry vs
81 deep sympatry) can affect mimetic precision. This link between selection and sympatry could be
82 even more important when the model is deadly (Lindström et al., 1997; Pough, 1988; Quicke,
83 2017). In coral snake mimicry complexes, for example, some studies suggest elements of color
84 pattern mimicry are precise in edge sympatry, may be relaxed in deep sympatry, and may not
85 convey a fitness advantage at all in allopatry, at least in temperate mimicry systems (Harper &
86 Pfennig, 2007; Pfennig et al., 2007). Other studies have found that where coral snakes were
87 recently extirpated, their mimics have become more precise, further suggesting that mimicry
88 should be more precise in areas where the model is rare and suggesting that directional selection
89 may favor precise mimicry in a newly allopatric region (Akcali & Pfennig, 2014).

90 Nevertheless, research regarding the evolutionary consequences of sympatry/allopatry on
91 coral snake mimicry has largely been focused on temperate zones, with few studies conducted in
92 diverse tropical ecosystems and even fewer focused on montane tropical environments. In
93 contrast to temperate regions, the enormous taxonomic and phenotypic diversity of tropical
94 systems results in a much wider range of aposematic color patterns of both coral snakes and
95 mimics (Savage & Slowinski, 1992). Moreover, this diversity in color patterns of models and
96 mimics persists despite the fact that aposematism generally leads to stabilizing selection on
97 model phenotypes, suggesting that selection may act differently in areas with high biodiversity
98 (Joron & Mallet, 1998; Mallet & Turner, 1997). The montane tropics not only have higher
99 biodiversity for both coral snakes and mimics than temperate systems, but they also provide
100 areas of allopatry and edge sympatry in close geographic proximity and under a variety of
101 different predator assemblages (Townsend & Wilson, 2008). Thus, the poorly-studied montane
102 tropics represent an excellent study system for understanding how mimicry is influenced by
103 geography at both local (sympatry vs. allopatry) and regional (tropical vs. temperate) scales.

104 We studied the impact of edge sympatry and allopatry on predation rates on coral snake
105 banding patterns in the montane tropics of Honduras. Highly venomous, elapid coral snakes have
106 evolved aposematism via a brightly colored and banded phenotype, which has subsequently been
107 mimicked by a variety of nonvenomous colubroid snakes in a classic example of Batesian
108 mimicry (Davis Rabosky et al., 2016; Greene & McDiarmid, 1981; Hinman et al., 1997; Pfennig
109 et al., 2007; Pough, 1988; Quicke, 2017). This mimicry system provides an excellent model to
110 study the evolutionary drivers of phenotypic diversity because it involves multiple species of
111 both models and mimics and spans multiple habitats (Quicke, 2017; Savage & Slowinski, 1992).
112 However, most research on coral snake mimicry has focused on species-poor temperate systems

113 that often have only one model and one to three mimics. Furthermore, studies focusing on the
114 effects of the depth of sympatry, and indirectly model abundance, have also been centered on
115 temperate systems that lack the species diversity of the tropics (Akcali & Pfennig, 2014; Akcali
116 & Pfennig, 2017; Harper & Pfennig, 2007; Pfennig et al., 2007). The few studies performed in
117 the tropics have rarely taken place in montane habitats where elevational gradients exclude coral
118 snakes in some areas, which creates a mosaic of sympatric and allopatric regions in close
119 geographic proximity (McCranie & Savage, 2011). Thus, we know relatively little about the
120 evolution of signal components of coral snake mimicry in the diverse tropics where multiple
121 model and multiple mimic species occur in sympatry and in close allopatry (Davis Rabosky et
122 al., 2016; Harper & Pfennig, 2007; Pfennig et al., 2001; Pfennig et al., 2007). By analyzing
123 predation rates on mimicry patterns in edge sympatry and allopatry in the montane tropics, we
124 can achieve a greater understanding of which mimetic phenotypes are most successful in areas
125 with a relatively high diversity of phenotypes.

126 We conducted a field experiment using mimetic and non-mimetic clay replicas of snakes
127 placed along an elevational gradient in Honduras to study the interaction of coral snake
128 sympatry/allopatry and replica color pattern on predation rate. First, we tested whether overall
129 attack rates on replicas varied between edge sympatry and allopatry, with higher attack rates
130 suggesting a greater intensity of predator-mediated selection. Second, we tested which color
131 patterns were attacked most in edge sympatry or allopatry. Empirical research suggests that
132 mimetic phenotypes should convey a fitness advantage in edge sympatry but should suffer a
133 fitness cost in allopatry (Akcali & Pfennig, 2017; Harper & Pfennig, 2007; Ries & Mullen,
134 2008). However, if mimetic phenotypes are attacked less than non-mimetic phenotypes in both
135 habitats, this implies that the fitness advantage of mimetic signals is maintained in allopatry

136 close to the range edge. Conversely, mimetic phenotypes being attacked more than non-mimetic
137 phenotypes in both edge sympatry and allopatry would imply that mimicry is maladaptive in
138 both habitats. Third, we compared attack rates among mimetic replicas to determine which
139 mimetic signal components may be most important in deterring predation. Finally, we examined
140 whether attack rates varied over time, which could suggest frequency-dependent selection, in
141 which the most common phenotypes are attacked disproportionately more by predators, in turn
142 creating spatial and temporal variation in which color patterns are favored (Holmes et al., 2017).

143

144 **Materials & Methods**

145 *Study site*

146 We conducted our study in Cusuco National Park, Honduras, from June to August of
147 2018 and 2019. This tropical montane environment is characterized by broad-leaf, pine, and
148 mixed forests and is situated at ~115m to ~2200m in elevation. Importantly, Cusuco National
149 Park encompasses populations of coral snakes and coral snake mimics in both sympatry and
150 allopatry (Alliance, 2019; Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). Over the
151 period of a decade, herpetofaunal diversity was monitored using opportunistic sampling.
152 Sampling occurred sporadically from May to August. Survey paths through the park were
153 walked by teams of 2-15 people, and each path was walked at least 6 times each year. When a
154 snake was encountered, it was identified and the GPS coordinates noted. Through this extensive
155 herpetofaunal research and monitoring in the park, surveyors have documented two species of
156 coral snakes (*Micrurus diastema* and *Micrurus nigrocinctus*) and nine species of coral snake
157 mimics (*Geophis nephodrymus*, *Lampropeltis abnorma*, *Ninia sebae*, *Oxyrhopus petolarius*,
158 *Pliocercus elapoides*, *Scaphiodontophis annulatus*, *Scolecophis atrocinctus*, *Sibon dimidiatus*,

159 and *Tropidodipsas sartorii*) (Brown & Arrivillaga, 2017; Townsend & Wilson, 2008). GPS
160 points of each of these species encountered in the surveys were plotted on a map of the park
161 using ArcGIS (ArcGIS version 10.7.1, map projection WGS_1984_UTM_Zone_16N) (Fig. 1).
162 We divided the park into 200m elevational bands and plotted the number of coral snake and
163 mimic species encountered in each band.

164 *Field experiment*

165 In order to assess predation rates on various mimetic and non-mimetic color patterns, we
166 analyzed the number of attacks on clay replicas. We constructed these non-toxic, pre-colored
167 clay replicas to have patterns loosely based on snakes found in the park. Replicas were either
168 cryptic (brown) or mimetic (white-and-black banded, red-and-black banded, or tri-colored with
169 red, white, and bands) (see electronic supplementary material, Fig. S1a). Clay replicas were
170 arranged in tetrads containing each replica pattern along transects at different elevations in both
171 sympatric and allopatric habitats (see electronic supplementary material, Table S1 and Fig. S1b).
172 Tetrads were arranged on alternate sides of the transect to minimize proximity to other tetrads.
173 Replicas were left out for a period of two weeks and checked every three to four days for marks
174 of predation (e.g., beak, teeth, or claw marks). If a replica was attacked more than once during
175 the two weeks, only one attack was counted. Each instance of attack was categorized by predator
176 type (bird, mammal, or unidentifiable) and recorded.

177 *Statistical Analyses*

178 We analyzed the data using 1) contingency analyses of pooled transect data and 2) mixed
179 effect models compared with information theoretic model selection. Contingency analyses were
180 used to estimate differences in predation rates between clay replica types, habitats, and years,

181 while mixed effects models and model selection were used to test whether coral snake sympatry
182 and color pattern had meaningful effects on attack rates (while accounting for spatial
183 autocorrelation of clay replicas within transects). To avoid missing patterns by discarding
184 ambiguous attack marks, we combined bird and mammal attacks into an overall “attacked”
185 category. We combined data from all transects and performed contingency analyses in JMP v
186 13.1.0 (SAS Statistical Institute, Cary, NC, USA). We created mixed effect logistic regression
187 models in R (version 3.5.2) and compared them using small sample size-corrected Akaike
188 information criterion (AICc) values to determine which statistical models were most effective in
189 predicting attack rates (Bates et al., 2015; Mazerolle, 2019; R Core Team, 2020). The response
190 variable for these statistical models was whether a replica was attacked or not attacked at any
191 point during the two-week period. The null models for each year included one term: a random
192 effect for the clay replica’s transect. This random effect should account for most spatial
193 autocorrelation because tetrads within a transect were closer to each other than to tetrads in any
194 other transect. The remaining statistical models included transect as a random effect as well as all
195 potential linear combinations of level of sympatry (edge sympatry or allopatry), one of five color
196 variables, and an interaction between level of sympatry and replica color. The five color
197 variables were individual pattern (the pattern of the replica), the presence of red (two of the
198 replica patterns), the presence of white (two replica patterns), the presence of bands (three replica
199 patterns), or whether it was tricolor (one replica pattern).

200 **Results**

201 Coral snakes and mimics have been encountered in most of the same elevational bands
202 throughout the park (Fig. 1a). Both coral snake species have been found from 600m to 1800m

203 but are notably absent above this threshold (Fig. 1b). Mimic species diversity peaks at 1400m,
204 but mimics are indeed encountered above 2200 m (Fig. 1c).

205 We found that both coral snake sympatry (Fig. 2) and elements of replica color pattern
206 (Fig. 3 and Fig. 4) had significant associations with predation rates. Total attack rates on clay
207 replicas were higher in allopatry than in edge sympatry in 2019 (contingency analysis, $\chi^2 =$
208 21.702, $p < 0.0001$) but not in 2018 (contingency analysis, $\chi^2 = 1.134$, $p = 0.2869$).

209 The red and black banded replicas were attacked significantly more in edge sympatric
210 habitats in 2019 (contingency analysis, $\chi^2 = 15.088$, $p = 0.0017$), but this was not found in
211 allopatric habitats (contingency analysis, $\chi^2 = 4.714$, $p = 0.1940$). In 2018, color pattern was not
212 associated with attack rate in either habitat (contingency analyses; edge sympatry $\chi^2 = 1.761$, $p =$
213 0.6234; allopatry $\chi^2 = 0.876$, $p = 0.8312$).

214 Both sympatry and the presence of red were important factors impacting attack rates on
215 clay replicas. In 2019, the best statistical model included transect, sympatry, and the presence of
216 red (no interaction) (Table 1, also see electronic supplementary material Table S2). Two
217 statistical models fell within two AICc units of the best statistical model, and both contained
218 sympatry as a term. These statistical models also included individual color pattern without an
219 interaction, as well as the presence of red with an interaction. Furthermore, we found that in
220 2019 both the presence of red and the presence of bands increased attack rates in edge sympatric
221 habitats, with a similar pattern in allopatric habitats (Fig. 4, see also electronic supplementary
222 material Table S4). In 2018, the null model was the best model (Table 2, also see electronic
223 supplementary material, Table S3). All of the statistical models that fell within two AICc units of
224 the null model had only one additional term after transect: sympatry or the presence of white or

225 red. The impact of signal components on attack rates did not differ between edge sympatric and
226 allopatric habitats in 2018.

227 **Discussion**

228 Contrary to expectations, we found that coral snake patterns did not confer a protective
229 advantage in either edge sympatry or allopatry in the montane tropics of Honduras. Replicas
230 without mimicry components almost always had lower attack rates than those with mimicry
231 components, regardless of both year and whether they were placed in an edge sympatric habitat
232 or an allopatric habitat. We also found that replicas with red or bands had higher attack rates than
233 those without in 2019 in areas of edge sympatry. These results are in contrast to previous
234 findings, where both brown replicas and replicas with imprecise mimetic patterns were attacked
235 more than precise mimetic replicas in sympatric regions (including edge sympatric) (Brodie III,
236 1993; Brodie III & Janzen, 1995; Kikuchi & Pfennig, 2010; Pfennig et al., 2001). In addition, we
237 found that patterns of attacks on replicas varied between years, which could be caused by
238 temporal heterogeneity or negative frequency-dependent selection (Akcali et al., 2018; Cox &
239 Davis Rabosky, 2013; Holmes et al., 2017). Our research supports the idea that mimicry
240 dynamics might differ in the montane tropics compared to temperate habitats.

241 In temperate regions, mimetic patterns can incur a fitness cost that varies between
242 allopatric regions with different local mimics, implying that even between allopatric populations
243 in similar habitats there can be differences in patterns of selection (Pfennig et al., 2007). In one
244 previous study, predators in the southeastern United States differentially attacked replicas
245 depending on whether they were in deep sympatry or edge sympatry (Harper & Pfennig, 2007).
246 Those predators avoided both poor and accurate mimetic phenotypes in areas of deep sympatry,
247 but they avoided only accurate mimics in edge sympatry. In studies taking place in the lowland

248 tropics, avian predators attacked brown replicas more often than tricolored or red-and-black
249 banded replicas (Brodie III, 1993; Brodie III & Janzen, 1995). In our study, we did not find that
250 predators avoided the more accurate mimetic phenotypes, but rather, the replicas with
251 phenotypes most closely resembling those of coral snakes (tricolored and red-and-black banded)
252 were often those attacked most. These results support the idea that in areas where coral snakes
253 are rare or absent (such as the range edge and close allopatry of our study areas), mimetic
254 phenotypes may not confer as much of an advantage as in areas where coral snakes are common
255 (such as the lowland tropics), which is consistent with classic Batesian mimicry theory (Brodie
256 III & Janzen, 1995; Pfennig & Mullen, 2010; Quicke, 2017; Ruxton et al., 2004). Yet why
257 multiple aposematic species of models and mimics may persist in our study area, given the
258 fitness costs that we have demonstrated, is a bit more perplexing. There are three primary, non-
259 mutually exclusive reasons why mimicry could be maintained in the face of apparent
260 maladaptation: 1) there is an interplay of aposematic coloration and behavior and thus mimetic
261 phenotypes are not actually maladaptive, 2) mimetic phenotypes are indeed maladaptive but may
262 be maintained by gene flow and/or 3) the apparent maladaptation of mimetic phenotypes
263 fluctuates temporally, likely due to negative frequency-dependent selection (Pfennig & Mullen,
264 2010).

265 First, the behavioral component of coral snake mimicry might reinforce and strengthen
266 the avoidance of mimetic patterns. Coral snakes display stereotyped coiling and thrashing
267 behavior when threatened, and thus behavior is an integrated part of their antipredator display
268 (Brown et al., 2020; Davis Rabosky et al., 2020; Titcomb et al., 2014). The effect of interacting
269 coloration and behavior on predator avoidance has been documented in other systems: for
270 example, moving replicas of brown frogs were attacked significantly more than when stationary,

271 whereas stationary replicas of red aposematic frogs were attacked significantly more than when
272 moving (Paluh et al., 2014). These findings suggest that movement and behavior may play an
273 important role in selection for both cryptic and aposematic individuals (Bateman et al., 2017).
274 Thus, while the use of clay replicas provides a useful tool for studying predation, a limitation of
275 the method is that it is unable to capture the effects of behavior, and it is not known whether a
276 stationary clay replica is recognized as a snake by a bird or mammalian predator (Bateman et al.,
277 2017). Our results might suggest that there may also be variation in how important movement is
278 in relation to prey selection by predators. In addition, other research has suggested that in range
279 edges where models may be rare, selection for avoidance of aposematic phenotypes may be
280 weaker and thus behavior could play an important role in reinforcing color signals (Charlesworth
281 & Charlesworth, 1975).

282 Second, mimetic phenotypes could indeed be maladaptive in areas of edge sympatry and
283 allopatry, but migration and gene flow from regions where mimicry is adaptive (areas of deep
284 sympatry at lower elevations) maintain the presence of mimetic phenotypes (Ries & Mullen,
285 2008). Indeed, coral snake mimics are known to migrate from areas of sympatry to allopatry in
286 temperate systems (Harper & Pfennig, 2008). In and around Cusuco National Park, it is plausible
287 that coral snake mimics could migrate from areas of high coral snake density (e.g., lowlands) to
288 areas where coral snakes are uncommon or absent (e.g., montane regions), thus influencing our
289 study. Similarly, range expansion of mimics may create newer areas of edge sympatry or
290 allopatry where predators have not yet evolved or learned avoidance (Pfennig & Mullen, 2010).
291 Thus, immigration and gene flow of mimics between high elevations without coral snakes and
292 low elevations with coral snakes could allow mimicry to persist at high elevations.

293 Finally, mimicry might be maintained despite a fitness cost through temporally fluctuating
294 selection, such as negative frequency-dependent selection. We found evidence of temporal
295 variation in predation rates on coral snake color patterns, although we cannot rule out minor
296 variation in experimental implementation between years that might contribute to this perceived
297 temporal variation. Many mimicry systems are influenced by frequency-dependent selection,
298 including frogs, snails, butterflies, and snakes (Holmes et al., 2017; Ries & Mullen, 2008).
299 Because this type of selection allows rare phenotypes to increase in frequency in the population,
300 the preferred target of predators also changes over time (Holmes et al., 2017; Pfennig et al.,
301 2007). Frequency-dependent selection has been shown to play an important role in Batesian
302 mimicry (Akcali et al., 2018; Cox & Davis Rabosky, 2013; Finkbeiner et al., 2018; Holmes et
303 al., 2017; Pfennig et al., 2001; Pfennig & Mullen, 2010). In areas where coral snake models are
304 uncommon or absent and relatively harmless mimics are abundant, predators may learn or evolve
305 a preference for conspicuous prey (Pfennig et al., 2007; Pfennig & Mullen, 2010). Over time,
306 this may reduce the relative abundance of mimics and thereby decrease the ratio of mimics to
307 models, which eventually leads to selection for the avoidance of mimetic phenotypes by
308 predators. As the mimic to model ratio then increases once again, predators may re-learn or re-
309 evolve the preference for conspicuous mimetic color patterns. Such a negative frequency-
310 dependent cycle could result in a dynamic relationship between the frequencies of different
311 mimetic phenotypes, causing temporal heterogeneity in the phenotypes most selected against
312 (Cox & Davis Rabosky, 2013). Our study may have taken place at the point in the cycle where
313 mimetic phenotypes are maladaptive, yet they are able to persist because the phenotype is
314 favored when rare. In addition, it is important to note that the presence of learned and innate
315 avoidance, as well as the predator assemblages present at a given time, would likely impact the

316 dynamics of frequency-dependent selection (Akcali et al., 2018). For example, naïve juvenile
317 motmots and great kiskadees innately avoid coral snake patterns, yet puffbirds and adult
318 motmots have been documented to consume coral snakes (Smith, 1969; Smith, 1975; Smith,
319 1977). While predators likely have a combination of innate and learned avoidance, learned
320 avoidance would lead to a shorter period of the negative frequency-dependent cycle than innate
321 avoidance because innate avoidance relies on intergenerational processes.

322 Although we found that mimetic phenotypes did not confer a fitness advantage and may
323 actually lead to decreased survivorship, some of our results were consistent with previous
324 research on coral snake mimicry. In areas of edge sympatry, red and black replicas were attacked
325 more often than tricolored replicas, but the opposite was true in areas of allopatry. This result
326 could indicate that it is beneficial to be a precise mimic in areas where the model is rare (but
327 present), but protection breaks down farther from the model's range, which is consistent with
328 previous findings that predators avoid precise mimics over poor mimics in edge sympatry
329 (Harper & Pfennig, 2007). Studies using museum specimens have also found differences in
330 mimetic precision in relation to sympatry and allopatry (Akcali & Pfennig, 2014; Akcali &
331 Pfennig, 2017; Harper & Pfennig, 2007). Within a single species, the most precise mimics to a
332 local model were found at the edge of the model's range rather than in deep sympatry (Harper &
333 Pfennig, 2007). Nevertheless, other studies have found that mimetic precision differs between
334 species, and in some cases the most precise mimics have been found in areas of allopatry (Akcali
335 & Pfennig, 2014; Akcali & Pfennig, 2017).

336 Our data suggest that coral snake mimicry may not provide an advantage in areas where
337 coral snakes have low abundance (despite having the high diversity of the tropics), such as in
338 edge sympatry and allopatry. Seemingly maladaptive mimicry might persist because of an

339 interaction between aposematism and defensive behavior that is unable to be captured in a clay
340 replica study, gene flow and immigration of both mimics and predators from areas where
341 mimicry is adaptive, temporal fluctuation in selection such as negative frequency-dependent
342 selection, or a combination of these processes. Our work highlights the importance of the
343 interactions among color patterns, model sympatry, and temporal variation in understanding
344 predation on coral snakes and their mimics. Long-term studies that characterize predation of
345 mimics in locations from deep sympatry to deep allopatry with models would be ideal to further
346 understand the complex nature of how sympatry and allopatry affect selection on mimicry.

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363 **Authors' contributions:**

364 LW participated in the design of the study, collected field data, carried out statistical analyses,
365 and drafted the manuscript; GL participated in the design of the study, aided in field work, and
366 revised the manuscript; JDC participated in the design of the study, collected field data, and
367 revised the manuscript; EH aided in statistical analyses and critically revised the manuscript, CC
368 conceived of the study, designed the study, coordinated the study, and critically revised the
369 manuscript. All authors gave final approval for publication and agree to be held accountable for
370 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*

530 to bicolor red and black (some *G. nephodrymus*) or white/yellow/orange and black (*T. sartorii*)
531 (Brown & Arrivillaga, 2017; McCranie & Savage, 2011; Townsend & Wilson, 2008).

532 Extended transect description

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

538 We placed clay replicas in groups of four, hereafter referred to as a tetrad, which included
539 one of each replica color pattern. Over a span of eight weeks from June to August in 2018 and in
540 2019, we arranged the tetrads along transects at varying elevations within the park (Table S1).
541 Transects higher than 1800m in elevation were classified as allopatric, and those lower than
542 1800m were classified as edge sympatric. Of the nine transects in 2018, three were allopatric and
543 six were edge sympatric. Of the 18 transects in 2019, three were allopatric and 15 were edge
544 sympatric. There were fewer allopatric transects because there was much less space to lay out
545 transects in the higher elevations of the mountaintop. Each transect contained seven (in 2018) or
546 ten (in 2019) branches, spaced approximately ten meters apart, with one tetrad per branch
547 (Figure S1a). We placed each replica within a tetrad at least three meters apart from other
548 replicas in the tetrad. The order of the replicas within each tetrad was randomly determined using
549 a random number generator. We calculated an ideal sample size for the total number of clay
550 replicas on transects for 2019 through a power analysis based on the attack data from 2018. We
551 left replicas out on transects for a period of two weeks and checked them every three to four days
552 for marks of predation (e.g. distinct beak, bite, or claw marks). Once checked, replicas were

553 smoothed over and placed in the same spot. If a replica was attacked more than once during the
554 two weeks, only one attack was counted. Each instance of attack was scored for type of predator
555 (bird, mammal, or unidentifiable) and recorded. Different observers checked and scored the
556 replicas from year to year.

557 Statistical Analyses

558 We analyzed the data using a combination of mixed effect models compared with model
559 selection and contingency analyses. The mixed effects models and model selection demonstrated
560 whether sympatry and color pattern had meaningful effects on attack rates, and contingency
561 analyses were used to estimate differences in predation rates between clay replica types, habitats,
562 and years. To avoid missing patterns of selection that could occur by discarding ambiguous
563 attack marks, we combined bird and mammal attacks into an overall “attacked” category. We
564 performed contingency analyses in JMP v 13.1.0 (SAS Statistical Institute, Cary, NC, USA) with
565 all samples pooled regardless of transect. We created logistic mixed effect models in R and
566 compared them using small sample size-corrected Akaike information criterion (AICc) values to
567 determine which statistical models were most effective in predicting attack rates (Bates et al.,
568 2015; Mazerolle, 2019; R Core Team, 2020). The response variable for these statistical models
569 was whether a replica was attacked or not attacked at any point during the two week period. The
570 null models for each year included only transect as a random effect. The remaining statistical
571 models included transect as a random effect as well as all potential combinations of: level of
572 sympatry, one of the five color variables, and interaction terms.

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Supplemental References

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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.

<u>Year</u>	<u>Elevation (m)</u>	<u>Coral snake Sympatry/Allopatry</u>
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 Δ AICc is the difference between that statistical model and the best model. Statistical models within 2 Δ AICc units of the top model are bolded

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

<i>K</i>	AICc	Δ AICc	AICc Weight	Log-likelihood	term 1	term 2	term 3	term 4
4	824.6768	0	0.404193	-408.31	transect*	sympatry	red	--
6	825.3787	0.701893	0.28456	-406.63	transect*	sympatry	individual pattern	--
5	826.6367	1.959888	0.151707	-408.276	transect*	sympatry**	red**	interaction
9	827.6545	2.977695	0.091199	-404.7	transect*	sympatry**	individual pattern**	interaction
4	829.2339	4.557145	0.041402	-410.589	transect*	sympatry	bands	--
5	831.2141	6.537345	0.015382	-410.565	transect*	sympatry**	bands**	interaction
3	834.7732	10.0964	0.002595	-414.37	transect*	sympatry		
5	835.1136	10.43682	0.002189	-412.515	transect*	sympatry**	tricolor**	interaction
3	835.5943	10.91752	0.001721	-414.78	transect*	red	--	--
5	836.0688	11.39206	0.001358	-412.992	transect*	sympatry**	white**	interaction
5	836.2869	11.61017	0.001218	-413.101	transect*	individual pattern		--
4	836.3954	11.7186	0.001153	-414.17	transect*	sympatry	tricolor	--
4	836.4445	11.76768	0.001125	-414.194	transect*	sympatry	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 Δ AICc is the difference between that statistical model and the best model. Statistical models within 2 Δ AICc units of the top model are bolded.

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

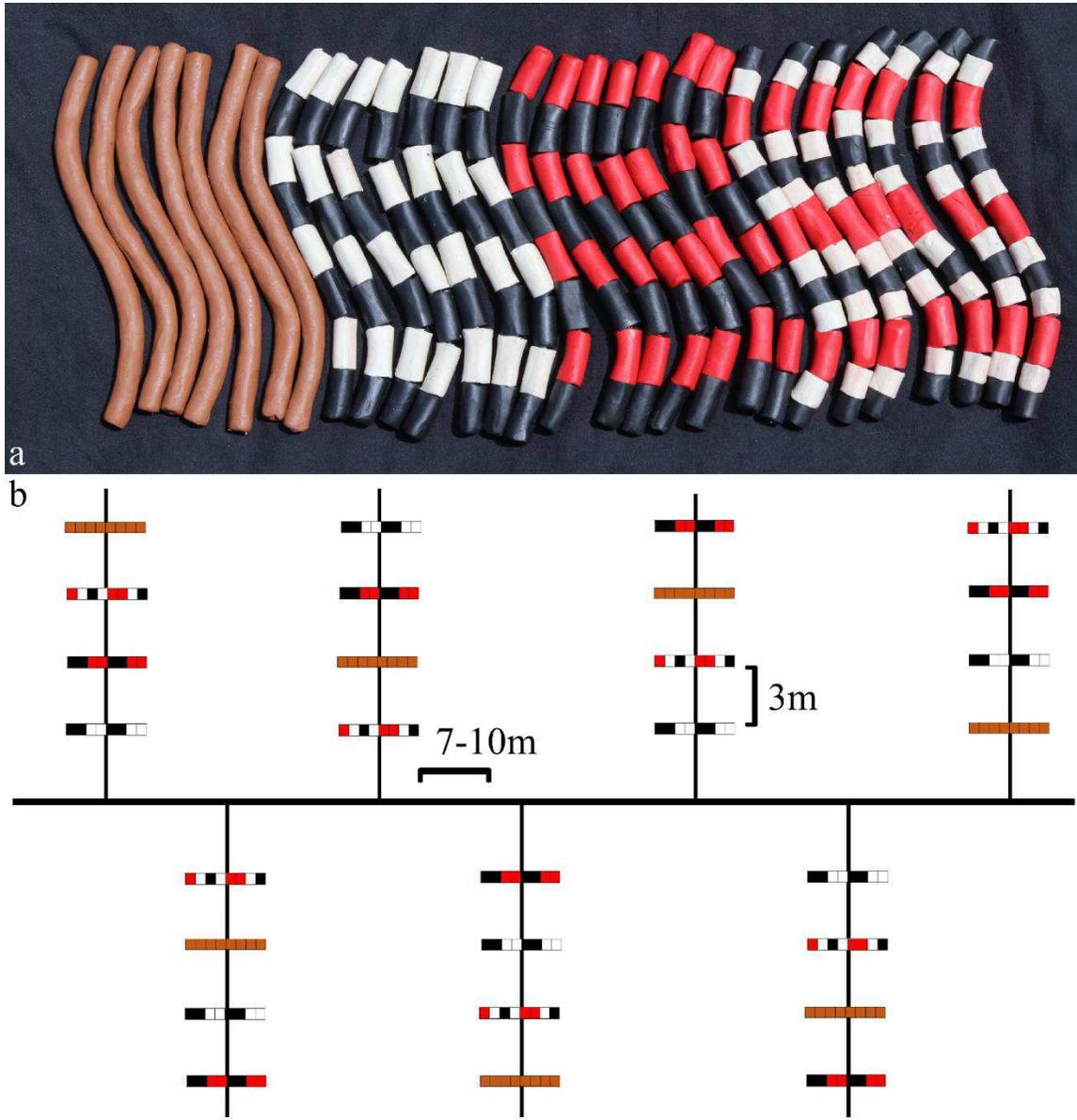
<i>K</i>	AICc	Δ AICc	AICc Weight	Log-likelihood	term 1	term 2	term 3	term 4
2	341.8013	0	0.223916	-168.877	transect*	--	--	--
3	343.1601	1.358776	0.113509	-168.532	transect*	sympatry	--	--
3	343.4256	1.624319	0.099396	-168.664	transect*	red	--	--
3	343.4256	1.624319	0.099396	-168.664	transect*	white	--	--
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	346.8828	5.081478	0.017646	-168.319	transect*	sympatry**	red**	interaction
5	347.0318	5.230468	0.01638	-168.394	transect*	sympatry**	bands**	interaction
5	347.1333	5.332028	0.015569	-168.445	transect*	individual pattern	--	--
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	χ^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

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Supplemental Figure



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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

<i>K</i>	AICc	$\Delta AICc$	AICc Weight	Log-likelihood	term 1	term 2	term 3	term 4
4	824.6768	0	0.404193	-408.31	transect*	sympatry	red	--
6	825.3787	0.701893	0.28456	-406.63	transect*	sympatry	individual pattern	--
5	826.6367	1.959888	0.151707	-408.276	transect*	sympatry**	red**	interaction

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 Δ AICc is the difference between that statistical model and the best model. Only statistical models within 2 Δ AICc units of the top model are included.

*indicates random effect

<i>K</i>	AICc	ΔAICc	AICc Weight	Log-likelihood	term 1	term 2	term 3	term 4
2	341.8013	0	0.223916	-168.877	transect*	--	--	--
3	343.1601	1.358776	0.113509	-168.532	transect*	sympatry	--	--
3	343.4256	1.624319	0.099396	-168.664	transect*	red	--	--
3	343.4256	1.624319	0.099396	-168.664	transect*	white	--	--

Figures:

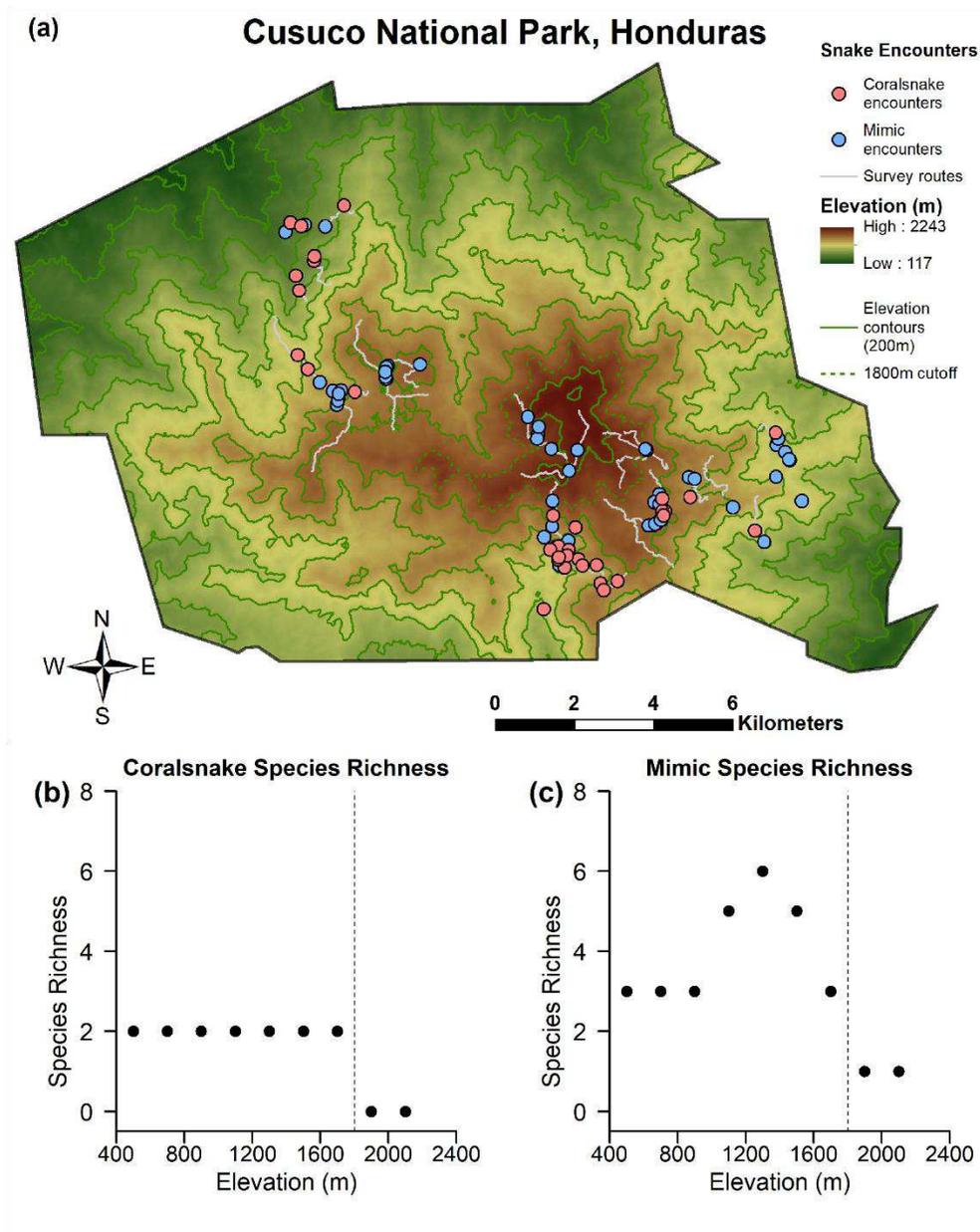


Figure 1. (a) Locations of coral snake and coral snake mimic encounters in Cusuco National Park, Honduras from 2007 to 2019. (b-c) Species richness of coral snakes and their mimics at differing elevations in Cusuco National Park, Honduras. The dotted line at 1800m represents the range edge of coral snakes. Note that neither coral snake species in the park is found above 1800m, but mimics can be found up to the highest elevations.

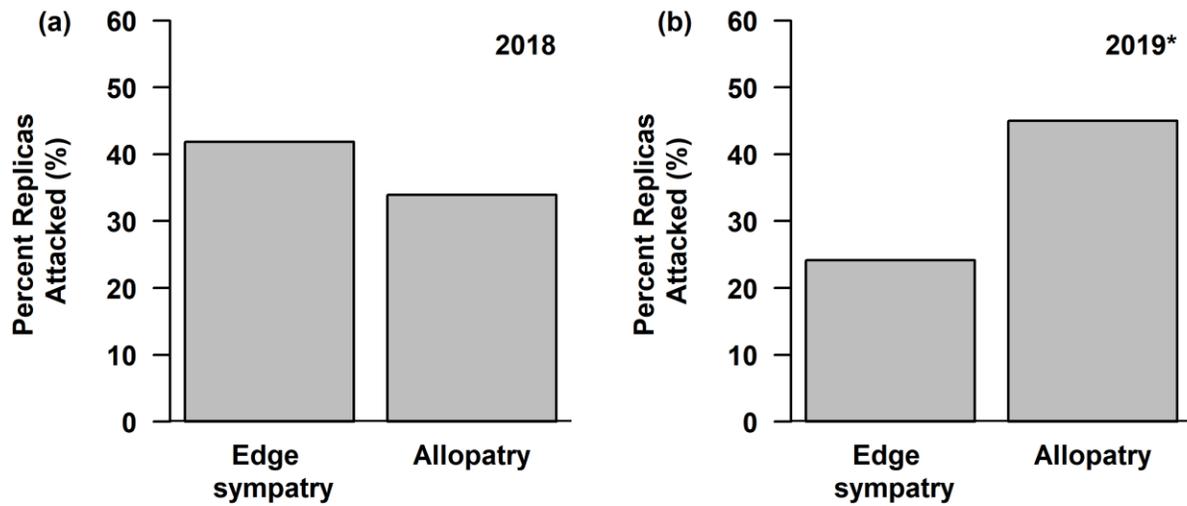


Figure 2. Attack rates on clay snake replicas in edge sympatric and allopatric habitats in 2018 (a) and 2019 (b). An asterisk (*) indicates significance from contingency analyses. Attack rates in 2019 were higher in allopatry than in edge sympatry, while attack rates in 2018 did not differ between edge sympatry and allopatry.

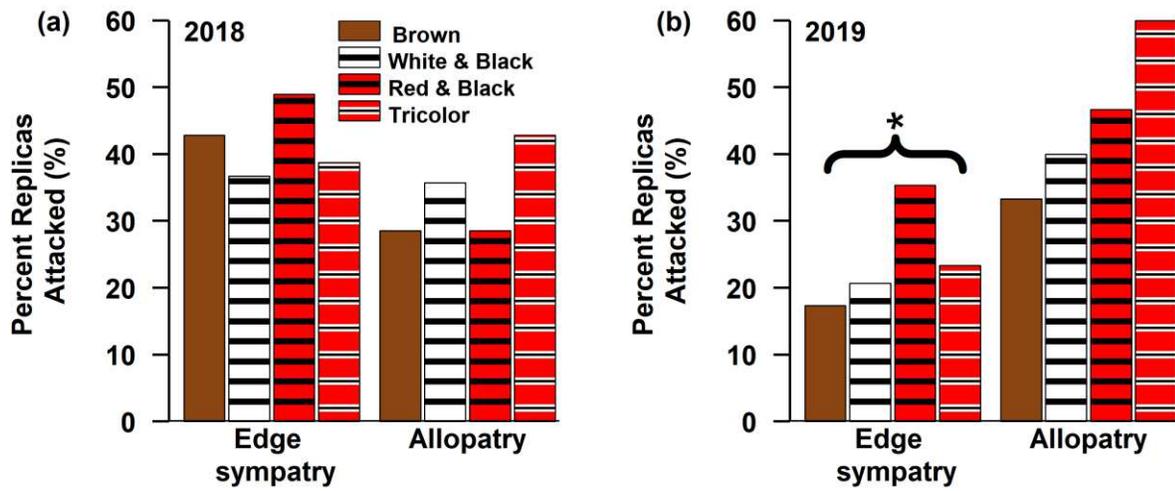


Figure 3. Attack rates on clay snake replicas with four different color patterns in areas of edge sympatry and allopatry in 2018 (a) and 2019 (b). An asterisk (*) indicates significance from contingency analyses. Replicas with mimetic patterns (white-and-black-banded, red-and-black banded, or tricolored)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

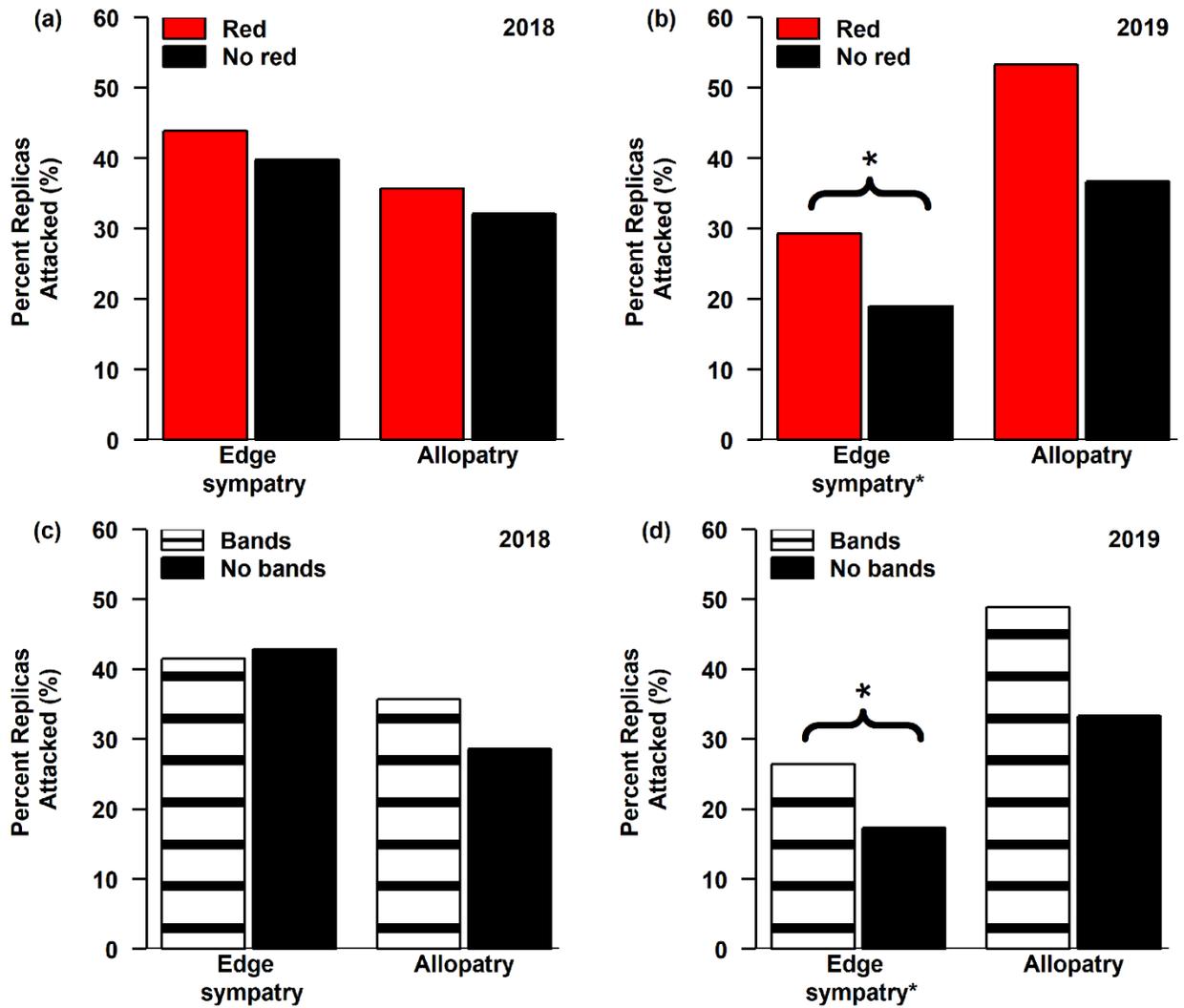


Figure 4. (a-b) Attack rates on clay snake replicas with and without the color red included in their patterns in areas of edge sympatry and allopatry. (c-d) Attack rates on clay snake replicas with and without banded color patterns in areas of edge sympatry and allopatry. An asterisk (*) indicates significance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

Figures

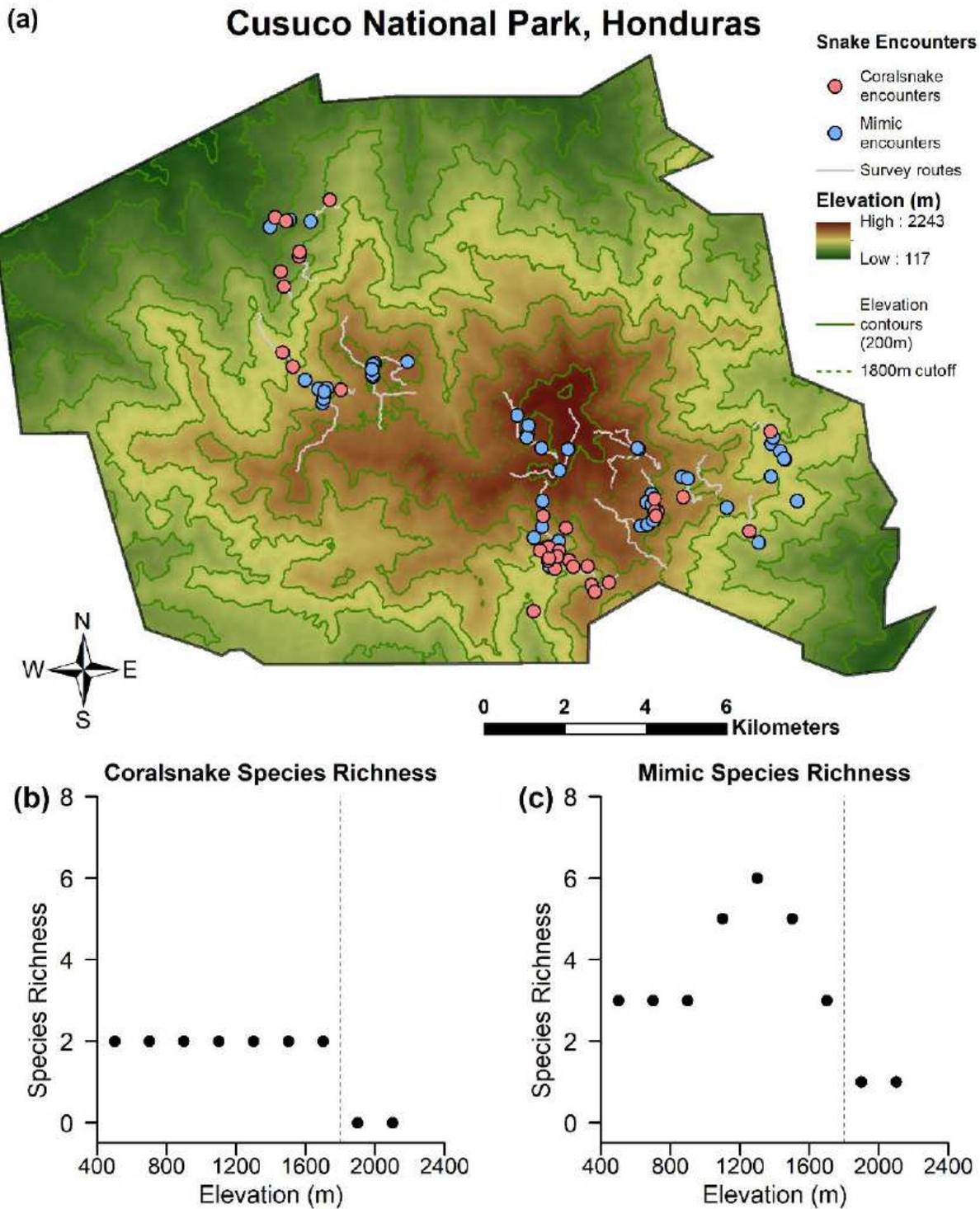


Figure 1

(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.

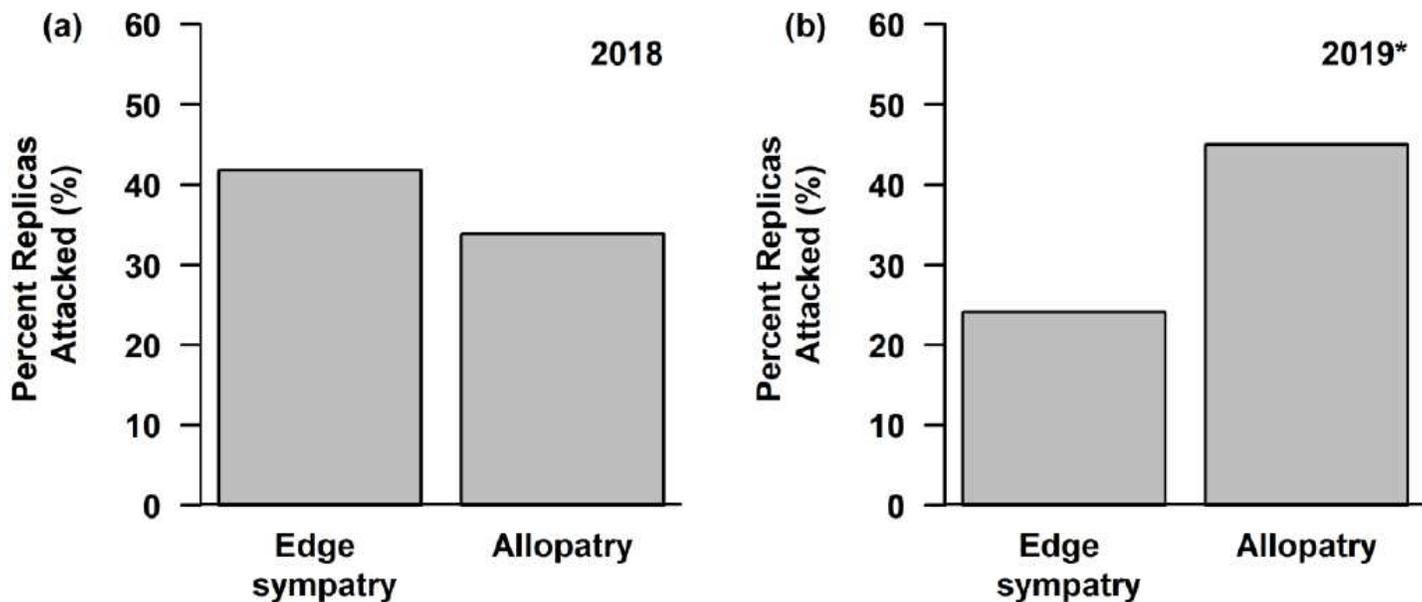


Figure 2

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.

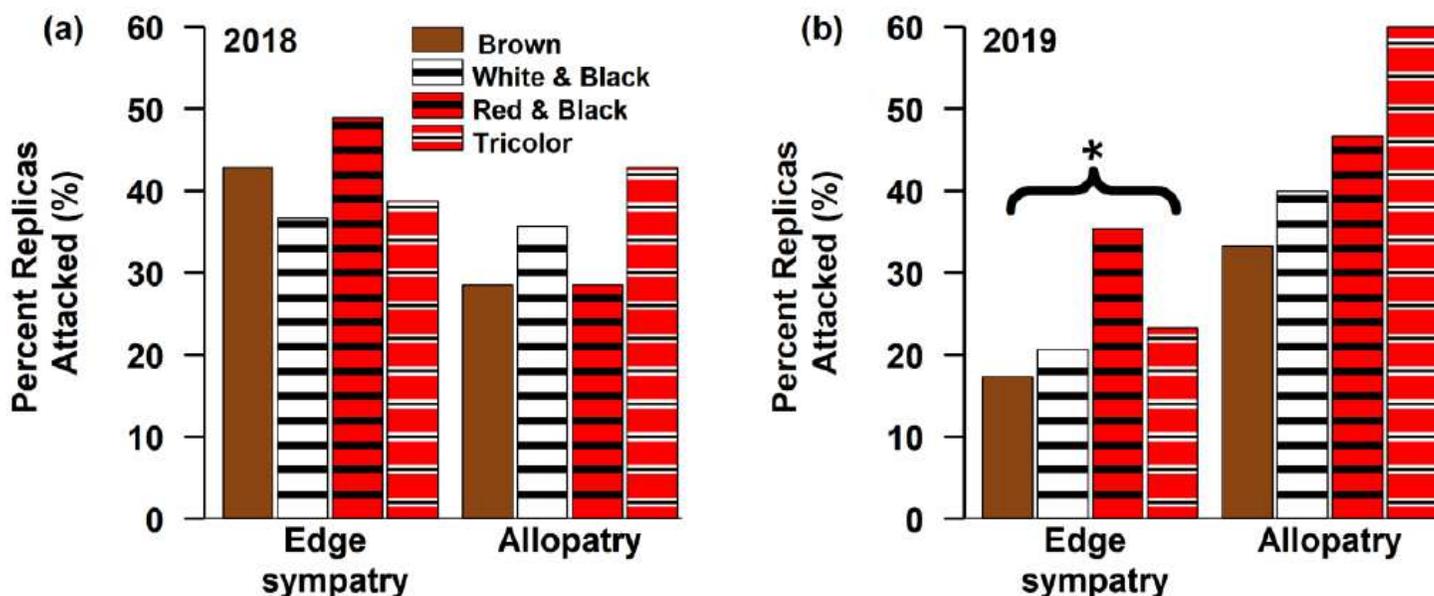


Figure 3

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.

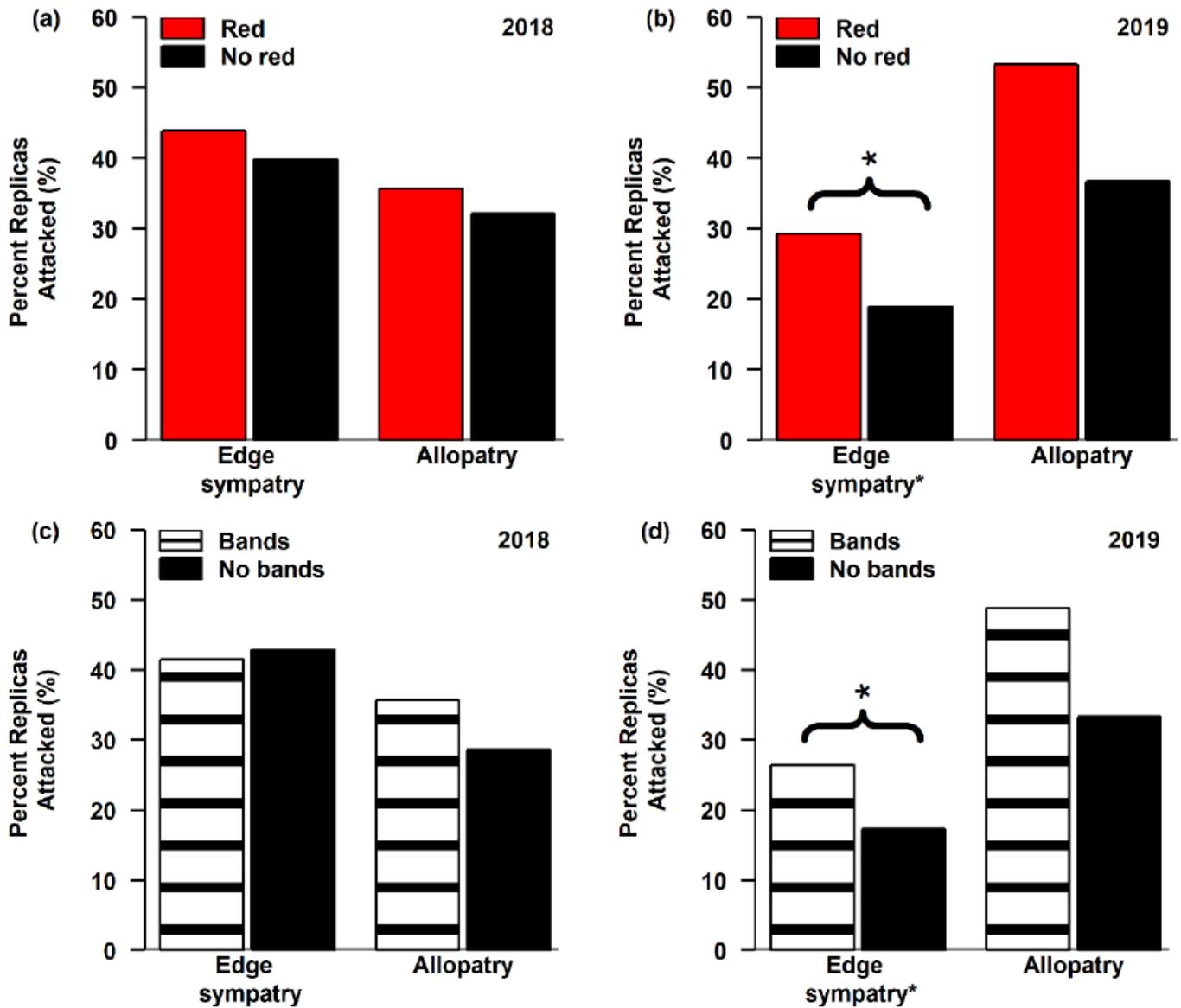


Figure 4

(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

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- [Appendics.pdf](#)
- [SupplementaryMaterial.pdf](#)