Received: 21 October 2019 | Revised: 25 April 2020 | Accepted: 17 May 2020

DOI: 10.1111/btp.12831

ORIGINAL ARTICLE

bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

Being a bright snake: Testing aposematism and mimicry in a neotropical forest

Karina R. S. Banci[1] | **André Eterovic**[2] | **Patrícia S. Marinho**[1] | **Otavio A. V. Marques**[1]

[1]Laboratório de Ecologia e Evolução, Instituto Butantan, São Paulo, Brazil

[2]Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Santo André, Brazil

Correspondence
Karina R. S. Banci, Laboratório de Ecologia e Evolução, Instituto Butantan, Avenida Vital Brazil, 1500, CEP 05503-900, São Paulo, Brazil.
Email: karina.banci@butantan.gov.br

Funding information
Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: #2012/07334-9

Associate Editor: Jennifer Powers

Handling Editor: Steven Whitfield

Abstract

Based on color patterns and behavioral similarities, venomous coral snake *Micrurus corallinus* (Elapidae) may act as a model for two polymorphic species, *Erythrolamprus aesculapii* (Dipsadidae) and *Micrurus decoratus* (Elapidae). Plasticine replicas were used to investigate the aposematism of these coloration patterns and whether these species may be part of mimetic complexes in two Atlantic Forest localities in Southeast Brazil. Coral replicas were more avoided when set upon a white background, evincing that the pattern may act aposematically in contrast with light substrates. Birds attacked all four patterns equally during the mimicry experiments. Birds of prey, known to be effective in predating snakes, are quite abundant in the study areas, which may have led to this lack of avoidance. Accordingly, they predated more adult-sized replicas, which could be more dangerous. Interestingly, opossum avoided the *Micrurus corallinus* and *Erythrolamprus aesculapii* replicas that resembled the model. This suggests that opportunistic predators, as the opossum may be important selective agents in mimicry complexes.

Abstract in Portuguese is available with online material.

KEYWORDS

atlantic forest, color pattern, defense, defensive behavior, *Erythrolamprus aesculapii*, *Micrurus corallinus*, *Micrurus decoratus*

1 | INTRODUCTION

Some species have evolved conspicuous coloration that acts as a warning signal to predators. This defense mechanism is known as aposematism (Poulton, 1890). Because predators avoid attacking aposematic organisms, other palatable or harmless species are sometimes observed to mimic aposematic noxious organisms. This tactic is called Batesian mimicry (Bates, 1862). Additionally, some warning signals of different aposematic noxious species converge (Müller, 1879), which is classified as Müllerian mimicry. Müllerian mimics benefit from sharing the same (or similar) warning signal because they share the "cost" of educating predators to avoid the signal (Huheey, 1961; Wickler, 1968). These are only two mimicry categories among many others that have been proposed according to the noxiousness of both models and mimics (Balogh, Gamberale-Stille, & Leimar, 2008; Greene & McDiarmid, 1981; Mertens, 1946, 1956; Speed, 1999; Wickler, 1968).

The existence of mimicry among coral snakes has long been debated in the literature (Dunn, 1954; Gelbach, 1972; Greene & McDiarmid, 1981; Hecht & Marien, 1956; Savage & Slowinsky, 1992; Smith, 1975, 1977; Wickler, 1968). However, the increase in evidence in favor of mimicry among coral snakes is undeniable (Rabosky et al., 2016; Rabosky, Cox & Rabosky, 2016; Ruxton, Allen, Sherratt, & Speed, 2018). Fieldwork for assessing predation pressure upon specific coral snake patterns has also provided valuable data on aposematism, in addition to supporting the existence of some mimetic complexes (*e.g.*, Brodie III, 1993; Brodie III & Janzen, 1995; Pfennig, Harper, Brumo, Harcombe & Pfennig, 2007; Kikuchi

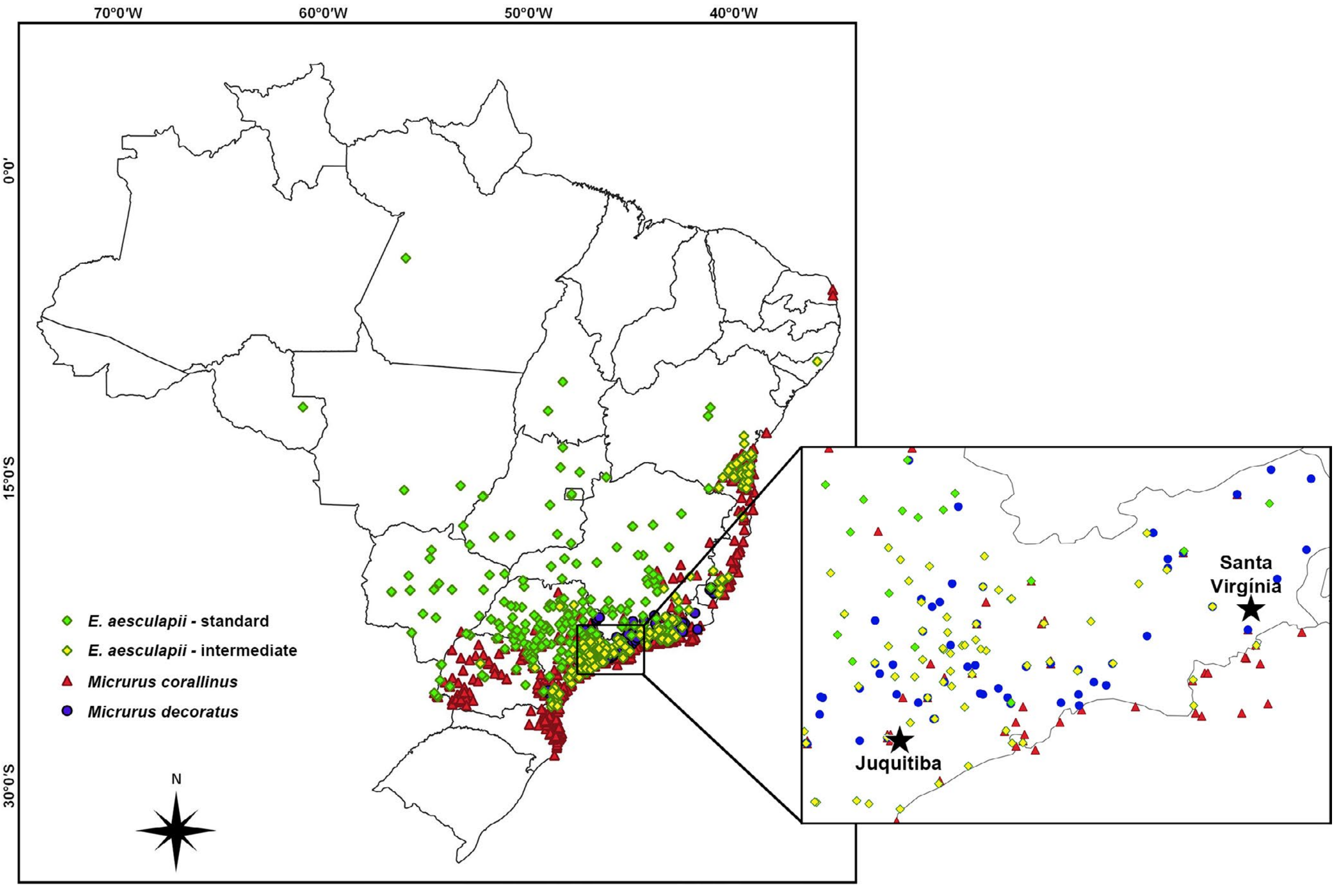


FIGURE 1 Map showing the study sites and the distributions of *Micrurus corallinus*, *Micrurus decoratus*, and *Erythrolamprus aesculapii* with standard and intermediate patterns

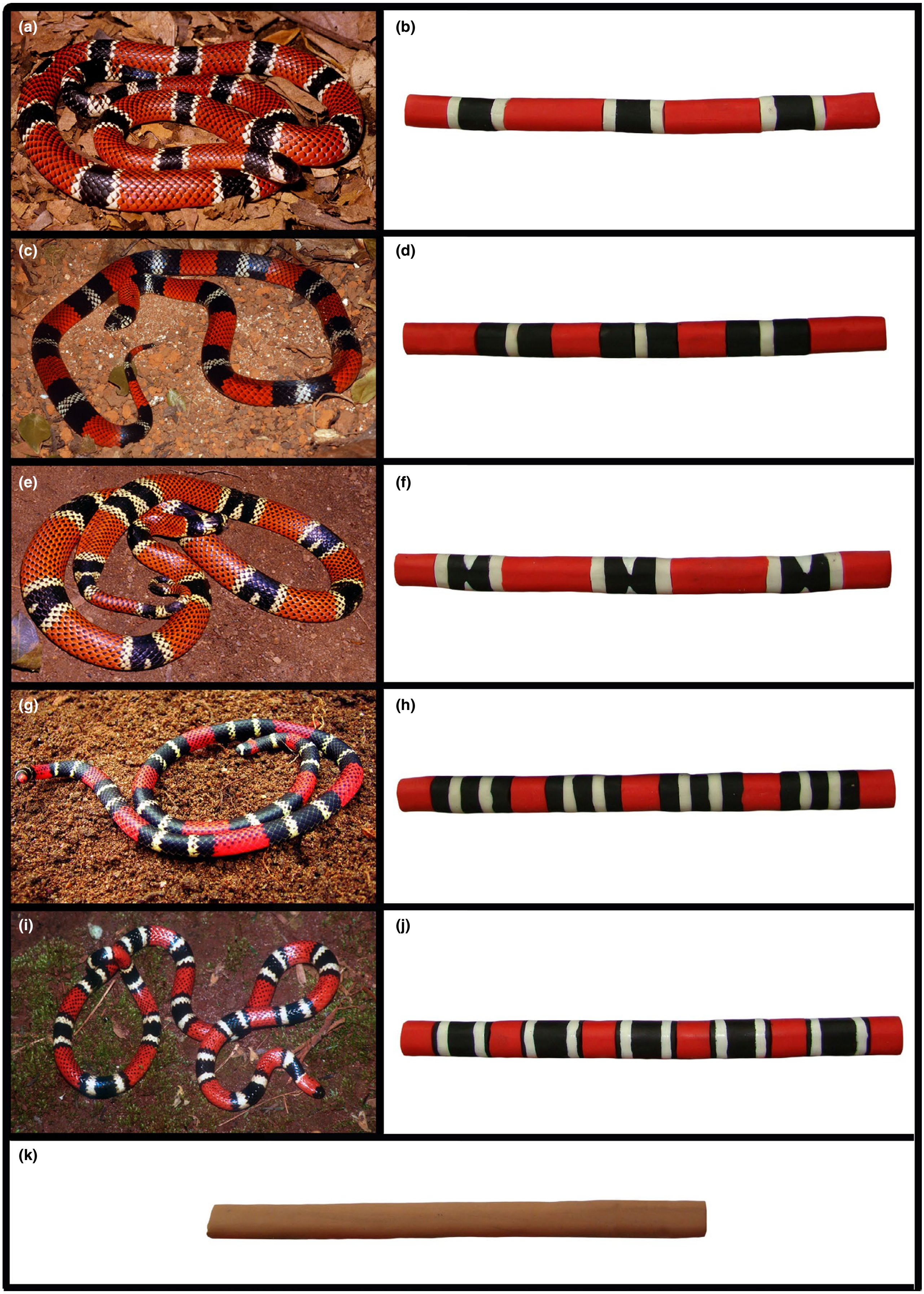
& Pfennig, 2010). Even without displaying snake movements, the use of plasticine replicas is beneficial for studying predation on aposematic species because a large number of replicas can be used, predator attacks leave identifiable marks on the models, and one can study different traits, such as the influence of the microhabitat, body size, or type of predators (Madsen, 1987; Brodie III, 1993; Bateman, Fleming, & Wolfe, 2017).

Based on similarities in coloration patterns, behavior, and geographic overlap, two putative mimetic complexes have been described in the Atlantic Forest of Southeast Brazil. In these complexes, the true coral snake *Micrurus corallinus* would act as a model for *Erythrolamprus aesculapii* in coastal areas (Marques & Puorto, 1991) and for *Micrurus decoratus* in highland areas of the Atlantic Forest (Marques, 1992, 2002). However, the protective role of their color patterns has never been tested.

Although predation rates on reptiles appear to be size-dependent, only a few studies have addressed this issue (Ferguson & Fox, 1984; Forsman, 1993; Taylor & Cox, 2019). It has been shown that replicas of juvenile snakes seem to be more susceptible (Bittner, 2003; Mitrovich & Cotroneo, 2006). Despite both juveniles and adults being aposematic (Madsen, 1987), the intensity of the warning signals emitted by them is different, because of their body sizes. The aposematic signal transmitted by juveniles may not be as strong as that transmitted by the adults, resulting in higher mortality of the former (Niskanen & Map pes, 2005). Predation pressure upon coral snakes of different sizes, however, remains unknown.

The present study aims to address the following questions. Does the *M. corallinus* pattern act as a warning signal for predators? Do *E. aesculapii* and *M. decoratus* gain any protection against predation by bearing a coloration pattern similar to *M. corallinus*? Is this protection similar for both juveniles and adults? Snake replicas made of plasticine were used to test the hypotheses that the coral pattern is aposematic and that a higher resemblance to the model is more protective for both adults and juveniles.

FIGURE 2 Snake species used in the present study and their respective replicas: *Micrurus corallinus* (a, b), *Erythrolamplus aesculapii* with a standard (c, d) and an intermediate pattern (e, f), *Micrurus decoratus* with a standard (g, h) and an intermediate pattern (i, j), and the brown control (k). Replicas b, d, f, and K were used in mimicry experiments in Juquitiba. b, h, j, and K were used in mimicry experiments in Santa Virgínia. Replicas B and K were used in aposematism experiments in both localities. Photographs by Otavio A.V. Marques (a, c, e, and i), Karina R.S. Banci (b, d, f, h, j, and k), and Thiago Marcial de Castro (g)


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
(j)
(k)

2 | METHODS

2.1 | Study system

Micrurus corallinus is endemic to the Brazilian Atlantic Forest, being widely distributed throughout this biome (Figure 1) and abundant throughout the Serra do Mar (Hartmann, Hartmann, & Martins, 2009; Marques, 1992; Marques, Eterovic, & Sazima, 2019). This species has a monad pattern, with one black ring surrounded by white rings and separated from one another by red rings (i.e., red-white-black-white-red; Figure 2a).

Erythrolamprus aesculapii is a polymorphic species and includes specimens with distinct color patterns occurring in the same area (Figure 1). Some of these snakes have a dyad pattern of two black rings separated by a white ring and surrounded by red rings (i.e., red-black-white-black-red; Figure 2c). Individuals with such a color pattern have a more inland distribution but also reach eastern regions of South America (even though they are rare in coastal regions; Marques & Puorto, 1991). On the other hand, in the coastal region, *E. aesculapii* individuals usually have additional narrow white rings between black and red rings (i.e., red-white-black-white-black-white-red) and usually present a partial or complete fusion of the dyads, resembling the monad pattern of *M. corallinus* (*cf*. Marques & Puorto, 1991; Figure 2e). *Erythrolamprus aesculapii* is a rear-fanged and mildly venomous snake, and it may be considered a quasi-Batesian mimic of the highly venomous elapid *M. corallinus*, gaining protection from the high toxicity of the model (Marques & Puorto, 1991).

Micrurus decoratus and *M. corallinus* are endemic to the Atlantic Forest and are considered to be Müllerian mimics. Nevertheless, they are relatively very small species; consequently, they may be less efficient at biting predators (Marques, 2002). *Micrurus decoratus* occurs exclusively in the Atlantic Forest of the Serra do Mar, between 20° and 30°S, in highland areas from approximately 400 to 1,600 m a.s.l. (Campbell & Lamar, 2004; Gonzalez, Silva-Soares, De Castro, & Bérnils, 2014; Marques, 2002; Figure 1). This coral snake shows a tricolored triad pattern with three black rings separated from one another by white rings and externally in contact with red rings (i.e., red-black-white-black-white-black-red; Figure 2g). However, this species is polymorphic, and some individuals show narrowing of the two external black rings, acquiring an aspect similar to a monad pattern, such as that of *M. corallinus* (*cf*. Marques, 2002; Figure 2i).

2.2 | Study site

The studies were conducted in two localities in the Serra do Mar, a mountain range in the Atlantic Forest of Southeast Brazil, chosen for being areas of sympatry of the highly venomous elapid *M. corallinus* and its supposed mimics *E. aesculapii* and *M. decoratus* (Hartmann et al., 2009; personal observation). Experiments focusing on the mimicry of *E. aesculapii* were performed at the Lymington Foundation, a conservation area located in Juquitiba, São Paulo state (23°57′S, 47°00′W; Figure 1), with an elevation range of 709 to 772 m a. s. l. Experiments focusing on the mimicry of *M. decoratus* were conducted at Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, São Paulo state (23°20′S; 45°06′W; Figure 1), with an elevation range of 905 to 1,120 m a. s. l. Experiments focusing on the aposematism of *M. corallinus* were performed at both sites.

2.3 | General experimental setup

Snake replicas were manufactured following the coloration patterns of the supposed model, *M. corallinus*, and the putative mimics, *E. aesculapii* and *M. decoratus*, utilizing non-toxic, pre-colored red, white, black, and brown plasticine (Acrilex # 507, 519, 520, and 531, respectively). The replicas were 20 cm long and had a diameter of either 1 cm (similar to adult coral snakes) or 0.5 cm (similar to juvenile coral snakes). They had non-differentiated ends (head and tail) and were threaded onto 26-cm-long iron wires, which allowed us to anchor them to the ground, preventing them from being taken away by potential predators. Each replica was placed in an S-shaped posture to mimic a real snake moving through the leaf litter (*cf*. Brodie III, 1993).

Ten 400-m transects were established in each locality, with a minimum distance of 500 m between them. Two experiments labeled "aposematism" and "mimicry" were performed every other month in each locality from September 2012 to August 2013. In both cases, the replicas were left in the field for 48 hr, and after this period, they were checked and removed, and every predation mark was photographed and subsequently analyzed to identify the supposed agent.

Bird pecks were defined by "U"- or "V"-shaped marks imprinted on the replicas. Mammal bites were defined by tooth imprints, usually with two deeper marks made by the incisors. Marks made by insects or rodents were not considered predation attempts. Similarly, the marks made by a tegu lizard (only one record) were discarded. Replicas with multiple marks made by only one type of predator (bird or mammal) were recorded as a single attack. Marks on two neighboring replicas were considered distinct predation attempts only if it was evident that they had been made by different predator species. Otherwise, the target was sorted among the pair to confer independence of events (i.e., multiple attacks made by the same individual).

2.4 | Aposematism experiment

To test for a possible effect of aposematism on predation attempts, the snake replicas were exposed to the following binary factors (with two levels each):

- Locality—Replicas were distributed between Juquitiba and Santa Virginia, separated by 10 meters in ten transects in each locality.

- Color pattern—Replicas of two color patterns were employed: brown (control; Figure 2k) and *M. corallinus* (coral, the aposematic pattern; Figure 2b).
- Season—Replicas were exposed to potential predation during the dry (April to September) and wet seasons (October to March).
- Substrate—Replicas were set upon the natural substrate or upon a 22x30 cm white card to show their color pattern on a contrasting background.
- Size—Replicas were small (simulating juveniles as a control for size) or large (simulating adults).

This "aposematism" experiment used a total of 2,400 replicas equally distributed among the 32 treatments that emerge from the combination of the levels of these five binary factors. The relative position of the replicas in the transects at each sampling location was randomly chosen.

2.5 | Mimicry experiment

To investigate whether there is a selective advantage for *E. aesculapii* due to its higher resemblance to the supposed (Batesian) mimetic model *M. corallinus*, replicas of four color patterns were used in Juquitiba: brown (control; Figure 2k), *M. corallinus* (Figure 2b), *E. aesculapii* with the common dyads (henceforth, the "standard" pattern; Figure 2d), and the "intermediate" pattern (a fusion of the dyads, plus white edges; Figure 2f).

To investigate the possible selective advantage of *M. decoratus* being more similar to the supposed (Müllerian) mimetic model *M. corallinus*, replicas of another set of four color patterns were used in Santa Virginia: brown (control; Figure 2k), *M. corallinus* pattern (Figure 2b), *M. decoratus* with the common triads (henceforth, the "standard" pattern; Figure 2h), and the "intermediate" pattern (triads but with two narrower external black rings; Figure 2j).

All the snake replicas were set upon natural ground in their respective locality, varying in the other factors (season and size) as described for the previous experiment. This "mimicry" experiment used a total of 4,800 replicas specified for each locality and equally distributed among 16 treatments that emerge from the combination of the levels of the two binary factors (season and size) and the pattern variable (four levels). The relative position of the replicas in the transects at each sampling opportunity was randomly chosen.

2.6 | Data analyses

In the dataset, for each replica (arranged in lines), we had one column for predation attempts by birds and another for mammals, filled with either 0 (no attack) or 1 (attack). Therefore, there were four mutually exclusive categories in which a replica was classified: 00 (no attack), 10 (bird only), 01 (mammal only), and 11 (both bird and mammal). Data were analyzed using binary logistic regression, considering all attacks by birds or mammals as binomial response variables independently and without discarding any data. Previous multinomial logistic regression using "no attack," "attack by bird," and "attack by mammal" as three possible states of the outcomes presented virtually the same results.

The additive models included pattern, locality, season, size, and substrate (only for the "aposematism" experiment) as factors to predict the outcome for the two kinds of predators (or the absence of attack). The β-coefficients and standard errors of these models allowed a direct comparison of the selected factors. A significant, positive β-coefficient indicates the amount of increase (or amount of decrease for negative coefficients) in the log odds of being attacked by a given kind of predator when the replica condition differs (treatment) from the reference level (control) for a specific factor. Therefore, the exponential of such indexes (the odds ratio) indicates a proportional change in the chance of being attacked when the condition of a replica departs from the reference level of a given factor. "Brown" was considered the reference level for pattern, "Juquitiba" for locality, "dry season" for season, "small" for size, and "natural substrate" for substrate. In the "mimicry" experiments, the pattern variable consisted of four states (the reference level "brown" control, "*Micrurus corallinus*", and, exclusively for each locality, the respective "standard" and "intermediate" patterns).

The alternative models included only second-order interactions among pattern (the main variable of interest), with the remaining factors used to evaluate their relative combined effect on the same outcomes (predation attempt by birds or mammals or the absence of attacks). The β-coefficients of these models allowed a direct comparison of the selected interactions in the same manner used for single factors. In these cases, the exponentials of the indexes (the odds ratio) indicate a proportional change in the chance of being attacked when the condition of a replica departs from the reference level of a given factor and the paired factor remains fixed at a chosen level. Higher-order interactions were not assessed.

Factors and the interactions among them were considered significant when $p < .05$, that is, when the confidence interval of the odds ratio does not indicate unity. When necessary, we indicated a correction for the critical P-values. The confidence limits of the odds ratio estimates were obtained from the standard errors of the β-coefficient estimates. The analyses were performed using the R package base (Venables & Ripley, 2002).

3 | RESULTS

3.1 | Aposematism

Aposematism— Of the 2,400 total replicas used in the "aposematism" experiment, 90 (3.75% ± 0.39%; percentage ± standard error) were attacked by birds and 50 (2.08% ± 0.39%) by mammals.

Predation attempts by birds occurred at the same rate for both color patterns, localities, and seasons, but not for different replica sizes or when the replicas were placed on different substrates (Table 1; Figure 3). Birds attacked the large replicas significantly more (1.60 times as often as the small replicas) and avoided the replicas on the white substrates (0.59 times the chance of the attempts being directed to the replicas on the natural substrate, as indicated by the odds ratio in Table 1).

Among the attacks by birds, only on the replicas with the *Micrurus corallinus* pattern (*n* = 42), it is evident that, in addition to the effect caused by the white substrate alone, the coral replicas set on the white substrate were attacked significantly less by birds (0.37 times the chance of attacks compared with those on natural substrates, as indicated by the odds ratio of the pattern-substrate interaction in Table 1; Figure 3). No interaction effects between the color pattern and the remaining factors were detected (Figure 3).

Predation attempts by mammals occurred at the same rate for both color patterns, seasons, and substrates, but not in different localities (Figure 3 and Table 1). Mammals attacked significantly fewer replicas in Santa Virginia (0.47 times the chance of replicas being attacked in Juquitiba; Figure 3 and Table 1). Predation attempts by mammals on the *Micrurus corallinus* pattern (*n* = 20) did not differ significantly by locality, season, replica size, or substrate (pattern interactions in Figure 3; Table 1).

The effects of the size factor for birds and the locality factor for mammals did not remain significant after setting the critical P-values to 0.025 in a Bonferroni correction (two binomial logistic regression tests; additive models for birds and mammals).

3.2 | Mimicry

Mimicry—Of the 4,800 total replicas used in the "mimicry" experiment, 154 (3.21 ± 0.25%) were attacked by birds and 90 (1.88 ± 0.20%) by mammals. There were significantly more predation attempts by birds in Santa Virginia (1.57 times the chance of the replicas being attacked in Juquitiba; Figure 4 and Table 2). No significant differences were detected between the distinct levels of season, size, and color pattern (Figure 4 and Table 2).

Significant interactions among some levels of color pattern and locality were detected, with both *Micrurus corallinus* and the standard patterns being more prone to attack by birds in Santa Virginia (approximately two times their respective chances in Juquitiba; Figure 4 and Table 2). The remaining factors (season and size) did not significantly interact with the color pattern (Figure 4 and Table 2.

There were significantly fewer predation attempts by mammals in Santa Virginia (0.36 the chance of predation in Juquitiba; Figure 4 and Table 2) and more attacks in the wet season (1.87 times the chance of predation in the dry season). No significant differences

TABLE 1 Binomial logistic models for the "aposematism" experiment

Predator	Model	Factors	β (SE)	OR (CL95%)	*p*
Birds	Additive	Pattern	−0.137 (0.216)	0.87 (0.57–1.33)	.5252
		Locality	0.281 (0.217)	1.32 (0.86–2.03)	.1962
		Season	0.323 (0.218)	1.38 (0.90–2.12)	.1384
		Size	0.468 (0.221)	1.60 (1.04–2.46)	*.0340
		Substrate	−0.537 (0.222)	0.58 (0.38–0.90)	*.0155
	Interaction with pattern	Locality	0.365 (0.269)	1.44 (0.85–2.44)	.1750
		Season	0.164 (0.272)	1.18 (0.69–2.01)	.5470
		Size	0.313 (0.273)	1.37 (0.80–2.33)	.2510
		Substrate	−1.003 (0.325)	0.37 (0.19–0.69)	*.0020
Mammals	Additive	Pattern	−0.417 (0.292)	0.66 (0.37–1.17)	.1532
		Locality	−0.590 (0.298)	0.55 (0.31–0.99)	*.0477
		Season	0.503 (0.295)	1.65 (0.93–2.95)	.0880
		Size	0.074 (0.287)	1.08 (0.61–1.89)	.7954
		Substrate	0.402 (0.292)	1.50 (0.84–2.65)	.1685
	Interaction with pattern	Locality	−0.693 (0.418)	0.50 (0.22–1.13)	.0973
		Season	0.015 (0.376)	1.02 (0.49–2.12)	.9679
		Size	0.173 (0.376)	1.19 (0.57–2.48)	.6448
		Substrate	0.176 (0.375)	1.19 (0.57–2.49)	.6400

Note: The additive effects of five factors on the predation attempts on 2,400 plastic snake replicas were modeled separately for birds and mammals. The factors assumed two states, and the first is the reference level (see Figure 3). The interaction effects of the color pattern paired with the remaining factors were also modeled separately for both kinds of potential predators. β-coefficients and standard errors (SE) were used to compute the odds ratios (OR) and respective confidence limits (CL95%). OR indicate the chance of being attacked when a replica condition departs from the reference level of a given factor. In the interaction models, OR indicate the chance of being attacked when a replica with a given color pattern departs from the combined reference levels of the two interacting factors. The asterisks indicate significant factor or interaction effects ($p < .05$), that is, when the unity is outside the confidence intervals of OR estimates.

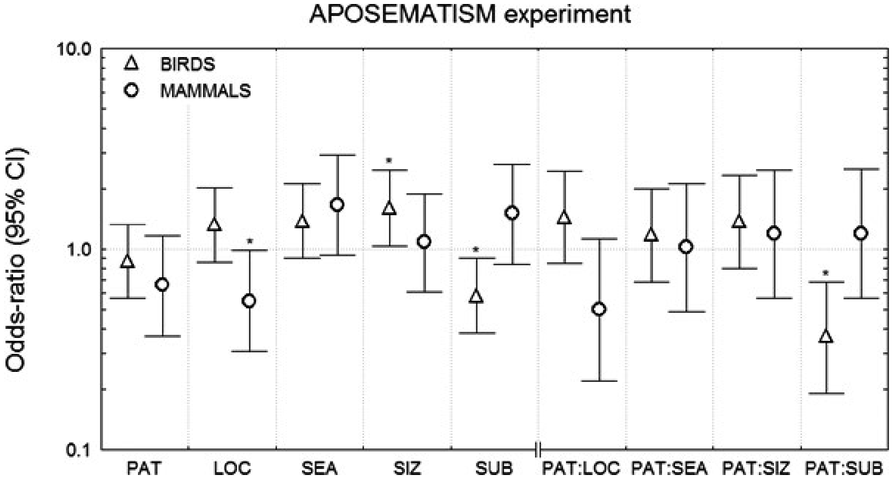


FIGURE 3 "Aposematism" experiment. Percentage of replicas (total $n = 2,400$) attacked by birds or mammals according to each level for each of five binary factors (upper panel) or combining levels of color pattern with the remaining factors (lower panel). The replicas were allocated equally at each level of all factors. The first level of a given factor was considered a control. SE are standard errors. The asterisks indicate significant differences ($p < .05$) detected by posterior tests among the levels of a given factor or interactions among levels of color pattern with the remaining factors (Table 1)

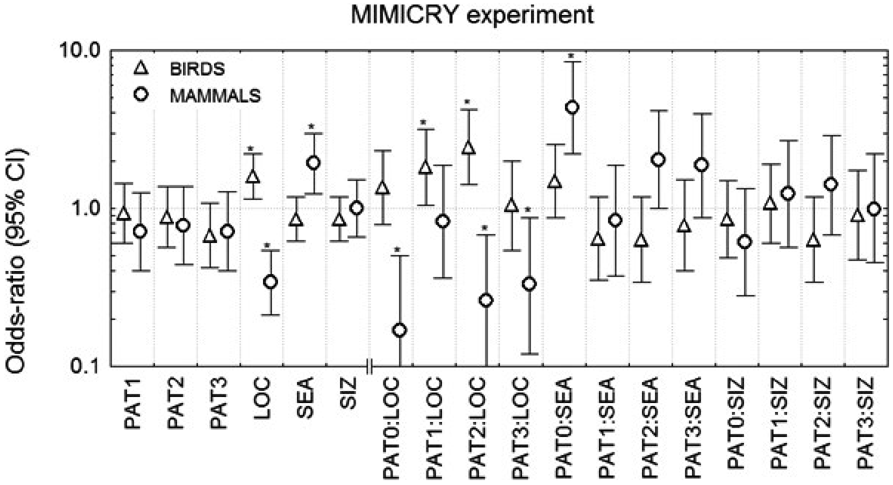


FIGURE 4 "Mimicry" experiment. Percentage of replicas (total $n = 4,800$) attacked by birds or mammals according to each level of color pattern and three binary factors (upper panel) or combining the four levels of color pattern with the remaining factors (lower panel). The replicas were allocated equally at each level of the four factors. The first level of a given factor was considered a control. SE are standard errors. The asterisks indicate significant differences ($p < .05$) detected by posterior tests among the levels of a given factor or interactions among levels of color pattern with the remaining factors (Table 2)

were detected between the distinct levels of size or color pattern (Figure 4 and Table 2).

Considering predation attempts by mammals, we found significant interactions among the color patterns—except for the *Micrurus corallinus* pattern—and locality (Figure 4 and Table 2). There was a reduction in predation attempts by mammals in Santa Virginia compared with those in Juquitiba (the chance of being attacked by mammals was 0.19, 0.27, and 0.36% for the brown control and the standard and intermediate pattern, respectively; Figure 4 and Table 2). For the brown control, the predation rate by mammals during the rainy season was 4.3 times higher than the predation rate by mammals during the dry season (Figure 4 and Table 2).

The interaction effect between the *Micrurus corallinus* pattern and locality for mammals did not remain significant after correcting the critical P-values to 0.025 (two binomial logistic regression tests; interaction models for birds and mammals).

4 | DISCUSSION

The aposematism experiments demonstrated that the coral snake replicas received fewer attacks by avian predators. However, this finding occurred only when the replicas were set upon white backgrounds. The strategy of using a white background to reduce crypticism with the forest substrate has been successfully employed

TABLE 2 Binomial logistic models for the "mimicry" experiment

Predator	Model	Factors	Level	β (SE)	OR (CL95%)	*P*
Birds	Additive	Pattern	coral	−0.077 (0.221)	0.93 (0.60–1.43)	.7264
			Standard	−0.128 (0.224)	0.88 (0.57–1.36)	.5670
			Intermediate	−0.397 (0.241)	0.67 (0.42–1.08)	.0991
		Locality		0.464 (0.168)	1.59 (1.14–2.21)	*.0057
		Season		−0.162 (0.165)	0.85 (0.62–1.17)	.3261
		Size		−0.163 (0.165)	0.85 (0.62–1.17)	.3205
	Interaction with pattern	Locality	Brown	0.302 (0.272)	1.35 (0.79–2.31)	.2675
			Coral	0.596 (0.281)	1.81 (1.05–3.15)	*.0337
			Standard	0.889 (0.283)	2.43 (1.40–4.23)	*.0017
			Intermediate	0.035 (0.331)	1.04 (0.54–1.98)	.9155
		Season	Brown	0.389 (0.271)	1.48 (0.87–2.51)	.1509
			Coral	−0.440 (0.309)	0.64 (0.35–1.18)	.1539
			Standard	−0.461 (0.318)	0.63 (0.34–1.18)	.1481
			Intermediate	−0.247 (0.343)	0.78 (0.40–1.53)	.4710
		Size	Brown	−0.158 (0.282)	0.85 (0.49–1.49)	.5771
			Coral	0.065 (0.291)	1.07 (0.60–1.89)	.8234
			Standard	−0.468 (0.318)	0.63 (0.34–1.17)	.1421
			Intermediate	−0.104 (0.336)	0.90 (0.47–1.74)	.7575

(Continues)

TABLE 2 (Continued)

Predator	Model	Factors	Level	β (SE)	OR (CL95%)	*P*
Mammals	Additive	Pattern	Coral	−0.347 (0.297)	0.71 (0.40–1.26)	.2423
			Standard	−0.249 (0.289)	0.78 (0.44–1.37)	.3888
			Intermediate	−0.346 (0.297)	0.71 (0.40–1.27)	.2435
		Locality		−1.090 (0.244)	0.34 (0.21–0.54)	*.0001
		Season		0.659 (0.224)	1.93 (1.24–3.00)	*.0033
		Size		−0.002 (0.214)	1.00 (0.66–1.52)	.9924
	Interaction with pattern	Locality	Brown	−1.751 (0.542)	0.17 (0.06–0.50)	*.0012
			Coral	−0.197 (0.417)	0.82 (0.36–1.86)	.6376
			Standard	−1.364 (0.496)	0.26 (0.10–0.68)	*.0059
			Intermediate	−1.120 (0.504)	0.33 (0.12–0.88)	*.0262
		Season	Brown	1.468 (0.344)	4.34 (2.21–8.52)	*.0001
			Coral	−0.189 (0.417)	0.83 (0.37–1.87)	.6501
			Standard	0.709 (0.363)	2.03 (1.00–4.14)	.0510
			Intermediate	0.623 (0.387)	1.86 (0.87–3.98)	.1074
		Size	Brown	−0.494 (0.394)	0.61 (0.28–1.32)	.2101
			Coral	0.212 (0.399)	1.24 (0.57–2.70)	.5940
			Standard	0.337 (0.371)	1.40 (0.68–2.90)	.3636
			Intermediate	−0.005 (0.409)	0.99 (0.45–2.22)	.9898

Note: The additive effects of four factors on the predation attempts on 4,800 plastic snake replicas were modeled separately for birds and mammals. Color pattern assumed four states, and the remaining are binary factors. The first is always the reference level (see Figure 4). The interaction effects of the color pattern paired with the remaining factors were also modeled separately for both kinds of potential predators. β-coefficients and standard errors (SE) were used to compute the odds ratios (OR) and respective confidence limits (CL95%). OR indicate the chance of being attacked when a replica condition departs from the reference level of a given factor. In the interaction models, OR indicate the chance of being attacked when a replica with a given color pattern departs from the combined reference levels of the two interacting factors. The asterisks indicate significant factor or interaction effects ($p < .05$), that is, when the unity is outside the confidence intervals of OR estimates.

by previous studies (*e.g.*, Brodie III, 1993, Buasso, Leynaud, & Cruz, 2006). However, it has been hypothesized that the white background may seem suspicious and artificial to birds, causing neophobia (Niskanen & Map pes, 2005), which would lead to a lower predation rate of the replicas placed upon it. This may explain the effect we detected herein. In particular, not only the coral replicas but also the brown replicas were predated less when set on the white backgrounds.

Not all the effects, however, may be attributed to neophobia. Interestingly, only the coral replicas placed on a white background were attacked less often than those on the natural substrate, indicating that the contrast created may evidence its warning signal. Some authors have alleged that the coral pattern may operate differently according to the circumstances under which the snake is encountered by a predator (Mochida, Zhang, & Toda, 2015). For instance, aside from acting as a warning signal, this pattern may also act cryptically or play an important role when the animal is moving through the litter. During flight, this pattern generates a visual blending illusion because the rings pass through the observer's plane faster than the critical flicker frequency (CFF), merging to form a uniform pattern that confuses the predator (Allen, Baddeley, Scott-Samuel, & Cuthill, 2013; Brattstrom, 1955; Titcomb, Kikuchi, & Pfennig, 2014). Our results show that, when contrasted against a light background (such as rocks), the warning signal of the coral pattern may deter visually oriented predators, such as birds. It seems plausible, then, to believe that the coral pattern does have multiple functions, being protective for the snakes under different circumstances, whether moving through the litter or lying on a uniform light substrate. Despite being still objects that do not move like snakes, plasticine replicas are satisfactory models for assessing predation rates on specific color patterns of snakes. In this sense, experiments employing plasticine replicas have been performed to study both aposematism and mimicry, considering predation by birds and/or mammals (Madsen, 1987; Brodie III, 1993; Brodie III & Janzen, 1995; Wüster et al., 2004; Niskanen & Map pes, 2005; Buasso et al., 2006; Kikuchi & Pfennig, 2010). However, some authors have questioned the validity of considering attacks by mammalian predators (Brattstrom, 1955; Brodie III, 1993). Unlike birds, which have tetrachromatic color vision and are well known for having very accurate vision, most eutherian mammals have dichromatic vision (Bowmaker, 2008). Therefore, the colors of the coral pattern may not influence their choice. This might explain, for instance, why only birds attacked the coral replicas set on the white backgrounds significantly less; the conspicuousness of the pattern, and consequently, its role as a warning signal, was evidenced. Even though mammals may not see colors, the coral pattern may be easily recognized by the presence of contrasting rings (Hecht & Marien, 1956). Like ours, several studies have accounted for predation attempts by mammals and have also shown that mammals do avoid the coral pattern (*e.g.*, Buasso et al., 2006; Harper Jr. & Pfennig, 2007; Kikuchi & Pfennig, 2010).

In contrast to previous studies, which found higher avoidance of coral patterns by birds (*e.g.*, Brodie III, 1993), in our study avian predators attacked all four patterns equally in the mimicry complexes tested. Interestingly, however, mammals did avoid the replicas of the model (*M. corallinus*) and those of the mimic that better resembled it (*E. aesculapii* with the intermediate pattern), regardless of their sizes. This was observed only during the wet season, when the predation rate by such predators was higher.

A considerable number of mammalian attacks, especially in Juquitiba, were made by opossum, which are known to opportunistically feed on snakes (Cáceres & Monteiro-Filho, 2001; Oliveira & Santori, 1999). Studies conducted at the Atlantic Forest show that *Didelphis aurita* are more abundant during the wet season, as this is the reproductive time of the species (Bergallo & Bossi, 2004). During this period, the females are more territorial, and the males increase their home range size (Cáceres & Monteiro-Filho, 2001). An increase in the consumption of ectothermic vertebrates (such as snakes) during the wet season coincides with recruitment (Cáceres, 2002). In this sense, an increase in the predation rate during the wet season was expected. It is possible that the lower number of attacks during the dry season impaired the power of the analyses, impeding us from detecting the avoidance of specific color patterns. Furthermore, during the wet season, when food resources are abundant, opossum may act more selectively, leading to the avoidance of *M. corallinus* and the replicas that better resemble them.

It is noteworthy that birds were the primary predators in Santa Virgínia, while mammals were the main predators in Juquitiba. This might be associated with the differential abundances of these groups of predators in each area. Due to its proximity to urban centers, Juquitiba experiences effects from predatory hunting, activities related to charcoal production, and native palmetto (*Euterpe edulis*) exploitation, so the remaining forest areas with advanced regeneration statuses are rare (Polisel & Franco, 2010). On the other hand, Santa Virgínia is part of the Parque Estadual da Serra do Mar, a state park created in 1977 (São Paulo, 1977), which has more than 315,000 ha and constitutes the largest conservation unit in the Atlantic Forest. The Santa Virgínia Nucleus alone comprises 17,500 ha. Generally, the abundance and diversity of birds is directly connected to the conservation status of an area (Andren, 1994), which may explain our results.

However, birds' species richness alone cannot explain why they attacked equally all the patterns of the replicas. Raptors are well known for their ability to subdue snakes, and feed on them, either with or without coral patterns (Brugger, 1989; DuVal, Greene, & Manno, 2006; Jackson & Franz, 1981; Knight & Erickson, 1976; Smith, 1969). Raptors are commonly seen in both Juquitiba and Santa Virgínia. Previous studies have confirmed that raptor species richness is directly linked to the conservation status of the area (Carrete, Tella, Blanco, & Bertellotti, 2009), concurring with higher number of predation attempts by birds in Santa Virgínia. Therefore, raptor species richness might partially explain why the coral pattern would not cause avoidance by these birds. The birds consistently attacked more adult-sized than juvenile-sized replicas. Adult individuals of the snake *Haldea striatula* are also attacked more often than the juveniles of this species (Taylor & Cox, 2019).

It is also possible that prey encounters would be optimized when the replicas represented adults and thus larger individuals, especially because birds usually seek prey when flying. Opossum, on the other hand, forage while moving through the forest, so the likelihood of such predators encountering the replicas was not influenced by the replica size.

In Santa Virgínia, none of the patterns was more protective against any of the predators. Previous studies have shown that the success of the mimetic complex is dependent on the abundance of the model (*e.g.*, Pfennig, Harcombe, & Pfennig, 2001). Despite being less abundant than *M. corallinus* throughout most of its range (Marques, 2002), *M. decoratus* is more abundant in localities above 700 m a.s.l., while *M. corallinus* is less frequent at higher elevations (Gonzalez et al., 2014; Marques, 1992). The study areas in Santa Virgínia were above 900 m a.s.l., and accordingly, *M. decoratus* was recorded more frequently than *M. corallinus* (Hartmann et al., 2009; pers. obs.).

In summary, we show that the coral pattern may act as an aposematic warning signal when set on a contrasting background. We also demonstrate that opossum, the most common predators in Juquitiba, predate coral snakes bearing the pattern of the model and the mimics that better resemble the model less often, supporting the existence of a mimetic complex in which *M. corallinus* poses as a model for *E. aesculapii* (as suggested by Marques & Puorto, 1991). Accordingly, it can be inferred that opportunistic, rather than specialist snake predators, may play an important role as selection agents. Although our results do not support the existence of a mimetic complex in which *M. corallinus* serves as a model for *M. decoratus*, the resemblance between the intermediate pattern of the latter and that of the former is still intriguing. Although it is not possible to evaluate historical predation pressure, which may have led to the selection of patterns, additional studies on this mimetic complex in areas with higher sympatry of the species could contribute to the elucidation of this issue.

ACKNOWLEDGMENTS

We would like to thank Bill and Linda Wittkoff (*in memorian*) from Lymington Foundation (Juquitiba/SP), and the staff from Parque Estadual da Serra do Mar—Núcleo Santa Virgínia, especially João Paulo Villani, Will Briet, and Cristiano Silva. We would also like to thank all of those who helped perform the experiments: Natália F. Torello-Viera, Lucas H.C. Siqueira, Thiago Cinco, Daniela P. Araújo, Cristian A. Gomes, Paulo R. Machado Filho, Maísa A. Matuoka, Marina B. Carandina, Michael S. Santana, Daniel Z. La Laina, Daniela Gennari, Fernanda Magno, Thiago A. Pires, Kalena B. Silva, Mayriele S. Machado, Fernando A. J. Silva, Raúl P. Fernández, Karina M. Pereira, and Pedro O. Calixto. We thank the reviewers of the manuscript for providing valuable suggestions. This work was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP #2012/07334-9).

CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets of the present study are openly available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.s1rn8pk4z (Banci, Eterovic, Marinho, & Marques, 2020).

ORCID

Karina R. S. Banci https://orcid.org/0000-0003-4891-3768

REFERENCES

Allen, W. L., Baddeley, R., Scott-Samuel, N. E., & Cuthill, I. C. (2013). The evolution and function of pattern diversity in snakes. *Behavioral Ecology*, *24*, 1237–1250. https://doi.org/10.1093/beheco/art058

Andren, H. (1994). Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat : A review. *Oikos*, *71*, 355–366.

Balogh, A. C. V., Gamberale-Stille, G., & Leimar, O. (2008). Learning and the mimicry spectrum: From quasi-Bates to super-Müller. *Animal Behavior*, *76*, 1591–1599. https://doi.org/10.1016/j.anbehav.2008.07.017

Banci, K. R. S., Eterovic, A., Marinho, P. S., & Marques, O. A. V. (2020). Data from: Being a bright snake: Testing aposematism and mimicry in a Neotropical forest. Dryad Digital Repository,https://doi.org/10.5061/dryad.s1rn8pk4z

Bateman, P. W., Fleming, P. A., & Wolfe, A. K. (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. https://doi.org/10.1111/jzo.12415

Bates, H. W. (1862). Contributions to an insect fauna of the Amazon Valley: Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London*, *23*, 495–566.

Bergallo, H. G., & Bossi, D. E. P. (2004). Os roedores e os marsupiais da Juréia: Ecologia e parasitismo na comunidade de pequenos mamíferos terrestres. In O. A. V. Marques & W. Duleba (Eds.), *Estação Ecológica Juréia-Itatins. Ambiente físico, flora e fauna* (pp. 296–303). Ribeirão Preto: Holos Editora.

Bittner, T. D. (2003). Polymorphic clay models of *Thamnophis sirtalis* suggest patterns of avian predation. *Ohio Journal of Science*, *103*, 62–66.

Bowmaker, J. K. (2008). Evolution of vertebrate visual pigments. *Vision Research*, *48*, 2022–2041. https://doi.org/10.1016/j.visres.2008.03.025

Brattstrom, B. H. (1955). The coral snake "mimic" problem and protective coloration. *Evolution*, *973*, 217–219.

Brodie, E. D. III (1993). Differential avoidance of coral snake banded patterns by free-ranging avian predators in Costa Rica. *Evolution*, *47*, 227–235. https://doi.org/10.1111/j.1558-5646.1993.tb01212.x

Brodie, E. D. III, & Janzen, F. J. (1995). Experimental studies of coral snake mimicry: Generalized avoidance of ringed patterns by free-ranging avian predators. *Functional Ecology*, *9*, 186–190.

Brugger, K. E. (1989). Red-tailed hawk dies with coral snake in Talons. *Copeia*, *1989*, 508–510. https://doi.org/10.2307/1445456

Buasso, C. M., Leynaud, G. C., & Cruz, F. B. (2006). Predation on snakes of Argentina: Effects of coloration and ring pattern on coral and false coral snakes. *Studies on Neotropical Fauna and Environment*, *41*, 183–188. https://doi.org/10.1080/01650520600630725

Cáceres, N. C. (2002). Food habits and seed dispersal by the white-eared opossum, *Didelphis albiventris*, in southern Brazil. *Studies on Neotropical Fauna and Environment*, *37*, 97–104. https://doi.org/10.1076/snfe.37.2.97.8582

Cáceres, N. C., & Monteiro-Filho, E. L. A. (2001). Food habits, home range and activity of *Didelphis aurita* (Mammalia, Marsupialia) in a forest fragment of southern Brazil. *Studies on Neotropical Fauna and Environment*, *36*, 85–92. https://doi.org/10.1076/snfe.36.2.85.2138

Campbell, J. A., & Lamar, W. W. (2004). *The venomous reptiles of the western hemisphere*. New York, NY: Cornell University Press.

Carrete, M., Tella, J. L., Blanco, G., & Bertellotti, M. (2009). Effects of habitat degradation on the abundance, richness and diversity of raptors across Neotropical biomes. *Biological Conservation*, *142*, 2002–2011. https://doi.org/10.1016/j.biocon.2009.02.012

Dunn, E. R. (1954). The coral snake "mimic" problem in Panama. *Evolution*, *8*, 97–102.

DuVal, E. H., Greene, H. W., & Manno, K. L. (2006). Laughing falcon (*Herpetotheres cachinnans*) predation on coral snakes (*Micrurus nigrocinctus*). *Biotropica*, *38*, 566–568.

Ferguson, G. W., & Fox, S. F. (1984). Annual variation of survival advantage of large juvenile side-blotched lizards, *Uta stansburiana*: Its causes and evolutionary significance. *Evolution*, *38*, 342–349.

Forsman, A. (1993). Survival in relation to body size and growth rate in the adder, *Vipera berus*. *The Journal of Animal Ecology*, *62*, 647–655. https://doi.org/10.2307/5385

Gelbach, F. R. (1972). Coral snake mimicry reconsidered: The strategy of self-mimicry. *Forma Et Functio*, *5*, 311–320.

Gonzalez, R. C., Silva-Soares, T., De Castro, T. M., & Bérnils, R. S. (2014). Review of the geographic distribution of *Micrurus decoratus* (Jan, 1858) (Serpentes: Elapidae). *Phyllomedusa*, *13*, 29–39. https://doi.org/10.11606/issn.2316-9079.v13i1p29-39

Greene, H. W., & McDiarmid, R. W. (1981). Coral snake mimicry: Does it occur? *Science*, *213*, 1207–1212. https://doi.org/10.1126/science.213.4513.1207

Harper, G. R., & Pfennig, D. W. (2007). Mimicry on the edge: Why do mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1955–1961. https://doi.org/10.1098/rspb.2007.0558

Hartmann, P. A., Hartmann, M. T., & Martins, M. (2009). Ecologia e história natural de uma taxocenose de serpentes no Núcleo Santa Virgínia do Parque Estadual da Serra do Mar, no sudeste do Brasil. *Biota Neotropica*, *9*, 173–184. https://doi.org/10.1590/S1676-06032009000300018

Hecht, M. K., & Marien, D. (1956). The coral snake mimic problem: A reinterpretation. *Journal of Morphology*, *98*, 335–365. https://doi.org/10.1002/jmor.1050980207

Huheey, J. E. (1961). Studies in warning coloration and mimicry. III. Evolution of müllerian mimicry. *Evolution*, *15*, 567–568.

Jackson, D. R., & Franz, R. (1981). Ecology of the Eastern Coral Snake (*Micrurus fulvius*) in Northern Peninsular Florida. *Herpetologica*, *37*, 213–228.

Kikuchi, D. W., & Pfennig, D. W. (2010). Predator cognition permits imperfect coral snake mimicry. *American Naturalist*, *176*, 830–834. https://doi.org/10.1086/657041

Knight, R. L., & Erickson, A. W. (1976). High incidence of snakes in the diet of nesting red-tailed hawks. *Raptor Research*, *10*, 108–111.

Madsen, T. (1987). Are Juvenile Grass Snakes, *Natrix natrix*, Aposematically Colored? *Oikos*, *48*, 265–267.

Marques, O. A. V. (1992). História natural de *Micrurus corallinus* (Master's Thesis). Universidade de São Paulo.

Marques, O. A. V. (2002). Natural history of the coral snake *Micrurus decoratus* (Elapidae) from the Atlantic Forest in southeast Brazil, with comments on possible mimicry. *Amphibia Reptilia*, *23*, 228–232.

Marques, O. A. V., Eterovic, A., & Sazima, I. (2019). *Serpentes da Mata Atlântica*. Ponto A, Cotia: Guia ilustrado para as Florestas Costeiras do Brasil.

Marques, O. A. V., & Puorto, G. (1991). Padrões cromáticos, distribuição e possível mimetismo em *Erythrolamprus aesculapii* (Serpentes, Colubridae). *Memórias do Instituto Butantan*, *53*, 127–134.

Mertens, R. (1946). Die Warn- und Droh-Reaktionen der Reptilien. *Abhandlungen Der Senckenbergischen Naturforschenden Gesellschaft Abhandlung*, *471*, 1–108.

Mertens, R. (1956). Das problem der Mimikry bei Korallenschlangen. Zoologische Jahrbücher. *Abteilung Für Systematik, Ökologie, Und Geographie Der Tiere*, *84*, 541–576.

Mitrovich, M. J., & Cotroneo, R. A. (2006). Use of Plasticine Replica Snakes To Elicit Antipredator Behavior in the California Ground Squirrel (*Spermophilus beecheyi*). *The Southwestern Naturalist*, *51*, 263–267. https://doi.org/10.1894/0038-4909(2006)51[263:UOPRST]2.0.CO;2

Mochida, K., Zhang, W. Y., & Toda, M. (2015). The function of body coloration of the hai coral snake *Sinomicrurus japonicus boettgeri*. *Zoological Studies*, *54*, 33. https://doi.org/10.1186/s40555-015-0110-2

Müller, F. (1879). Ituna and Thyridia, a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London*.

Niskanen, M., & Mappes, J. (2005). Significance of the dorsal zigzag pattern of *Vipera latastei gaditana* against avian predators. *Journal of Animal Ecology*, *74*, 1091–1101. https://doi.org/10.1111/j.1365-2656.2005.01008.x

Oliveira, M. E., & Santori, R. T. (1999). Studies on Neotropical Fauna and Environment Predatory Behavior of the Opossum *Didelphis albiventris* on the Pitviper *Bothrops jararaca*. *Studies on Neotropical Fauna & Environment*, *34*, 72–75. https://doi.org/10.1076/snfe.34.2.72.2105

São Paulo (1977). Decreto no 10.251, de 30 de Agosto de 1977. Diário Oficial do Estado, Brazil.

Pfennig, D. W., Harcombe, W. R., & Pfennig, K. S. (2001). Frequency-dependent Batesian mimicry. *Nature*, *410*, 323. https://doi.org/10.1038/35066628

Pfennig, D. W., Harper, G. R., Brumo, A. F., Harcombe, W. R., & Pfennig, K. S. (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. https://doi.org/10.1007/s00265-006-0278-x

Polisel, R. T., & Franco, G. A. D. C. (2010). Comparação florística e estrutural entre dois trechos de Floresta Ombrófila Densa em diferentes estádios sucessionais, Juquitiba, SP, Brasil. *Hoehnea*, *37*, 691–718. https://doi.org/10.1590/S2236-89062010000400002

Poulton, E. B. (1890). *The colors of the animals: their meaning and use. Especially considered in the case of insects*, 2nd ed. New York, NY: Kegan Paul, Trench, Trübner & Co.

Rabosky, A. R. D., Cox, C. L., & Rabosky, D. L. (2016). Unlinked Mendelian inheritance of red and black pigmentation in snakes: Implications for Batesian mimicry. *Evolution*, *70*, 944–953. https://doi.org/10.1111/evo.12902

Rabosky, A. R. D., Cox, C. L., Rabosky, D. L., Title, P. O., Holmes, I. A., Feldman, A., & McGuire, J. A. (2016). Coral snakes predict the evolution of mimicry across New World snakes. *Nature Communications*, *7*, 1–9.

Ruxton, G., Allen, W. L., Sherratt, T. N., & Speed, M. P. (2018). *Avoiding attack: The evolutionary ecology of crypsis, aposematism, and mimicry*, 2nd ed. Oxford, UK: Oxford University Press.

Savage, J. M., & Slowinsky, J. B. (1992). The coloration of the venomous coral snakes (family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biological Journal of the Linnean Society*, *45*, 235–254.

Smith, N. G. (1969). Avian predation of coral snakes. *Copeia*, *1969*, 402–404. https://doi.org/10.2307/1442098

Smith, S. M. (1975). Innate recognition of coral snake pattern by a possible avian predator. *Science*, *187*, 759–760. https://doi.org/10.1126/science.187.4178.759

Smith, S. M. (1977). Coral-snake pattern recognition and stimulus generalization by naive great kiskadees (Aves: Tyrannidea). *Nature*, *265*, 535–536.

Speed, M. P. (1999). Batesian, quasi-Batesian or Müllerian mimicry? Theory and data in mimicry research. *Evolutionary Ecology*, *13*, 755–776. https://doi.org/10.1023/A:1010871106763

Taylor, Q., & Cox, C. L. (2019). Evidence of predation risk increases with body size in a diminutive snake. *Journal of Zoology*, *307*, 141–148. https://doi.org/10.1111/jzo.12627

Titcomb, G. C., Kikuchi, D. W., & Pfennig, D. W. (2014). More than mimicry? Evaluating scope for flicker-fusion as a defense strategy in coral snake mimics. *Current Zoology*, *60*, 123–130.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S*. 4th ed. Springer.

Wickler, W. (1968). *Mimicry in plants and animals*. New York, NY: McGraw-Hill.

Wüster, W., Allum, C. S. E., Bjargardóttir, I. B., Bailey, K. L., Dawson, K. J., Guenioui, J., ... Pollard, C. P. (2004). Do aposematism and Batesian mimicry require bright colors? A test, using European viper markings. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 2495–2499.

How to cite this article: Banci KRS, Eterovic A, Marinho PS, Marques OAV. Being a bright snake: Testing aposematism and mimicry in a neotropical forest. *Biotropica*. 2020;52:1229–1241. https://doi.org/10.1111/btp.12831