Müllerian mimicry and the coloration patterns of sympatric coral snakes

RENAN JANKE BOSQUE[1],[*],[●], CHAZ HYSENI[2],[3],[●], MARIA LUIZA GONÇALVES SANTOS[1], EDUARDO RANGEL[4], CAMILA JULIANA DA SILVA DIAS[5], JACOB BEATHEA HEARIN[4], NELSON JORGE DA SILVA JR[6], FABRÍCIUS MAIA CHAVES BICALHO DOMINGOS[7], GUARINO RINALDI COLLI[1] and BRICE PATRICK NOONAN[4]

[1]*Universidade de Brasília, Instituto de Biologia, Departamento de Zoologia, Brasília, Distrito Federal, 70910-900, Brazil*
[2]*Uppsala University, Department of Ecology and Genetics, Uppsala, Uppsala County, 75236, Sweden*
[3]*USDA Forest Service, Southern Research Station, Center for Bottomland Hardwoods Research, Oxford, Mississippi, 38655, USA*
[4]*The University of Mississippi, Department of Biology, University, Mississippi, 38677, USA*
[5]*Universidade Federal de Mato Grosso, Instituto de Ciências Biológicas e da Saúde, Pontal do Araguaia, Mato Grosso, 78698-000, Brazil*
[6]*Pontifícia Universidade Católica de Goiás, Escola de Ciências Médicas e da Vida, Goiânia, Goías, 74175-120, Brazil*
[7]*Universidade Federal do Paraná, Departamento de Zoologia, Curitiba, Paraná, 81531-980, Brazil*

Coral snakes in the genus *Micrurus* are venomous, aposematic organisms that signal danger to predators through vivid coloration. Previous studies found that they serve as models to several harmless species of Batesian mimics. However, the extent to which *Micrurus* species engage in Müllerian mimicry remains poorly understood. We integrate detailed morphological and geographical distribution data to investigate if coral snakes are Müllerian mimics. We found that coloration is spatially structured and that *Micrurus* species tend to be more similar where they co-occur. Though long supposed, we demonstrate for the first time that coral snakes might indeed be Müllerian mimics as they show some convergence in coloration patterns. Additionally, we found that the length of red-coloured rings in *Micrurus* is conserved, even at large geographic scales. This finding suggests that bright red rings may be under more substantial stabilizing selection than other aspects of coloration and probably function as a generalized signal for deterring predators.

ADDITIONAL KEYWORDS: colour – Elapidae – evolution – geographic distribution – *Micrurus* – Neotropics.

INTRODUCTION

New World snakes in the genus *Micrurus*, commonly known as coral snakes, advertise potential danger via their aposematic (warning) coloration, frequently a combination of red, black and light (white or yellow) coloured rings (Roze, 1996). Protected by potent neurotoxins, coral snakes serve as models for many harmless species bearing similar colour patterns to deceive predators (Ruxton *et al.*, 2004), i.e., Batesian mimics (Greene & McDiarmid, 1981; Almeida *et al.*, 2021). Surprisingly, despite decades of research, practically no formal tests have been performed to evaluate the extent to which *Micrurus* species engage in Müllerian mimicry, with the assumption instead relying upon anecdotal reports [Greene & McDiarmid (1981); Roze (1996); Marques (2002) but see Banci *et al.* (2020)]. Müllerian mimicry refers to well-defended (i.e., unpalatable or dangerous) species sharing both the aposematic signal and the cost of training predators to avoid the said signal (Müller, 1878; Ruxton *et al.*, 2004; Sherratt, 2008). This phenomenon has been documented in Asian pit vipers (Sanders *et al.*, 2006), but has yet to be demonstrated in coral snakes.

*Corresponding author. E-mail: renan.janke@gmail.com

The paucity of studies on Müllerian mimicry in coral snakes is probably related to the fact that most works have been performed in the USA, where only a few species of coral snakes exist, and often where their ranges do not overlap. The genus *Micrurus* comprises approximately 80 recognized species, with up to 11 species co-occurring in some areas, such as in western Amazonia (Campbell & Lamar, 2004; Bosque *et al.*, 2016; Silva Jr *et al.*, 2021b). This pattern renders the Neotropical region ideal for studying the evolution of Müllerian mimicry in *Micrurus*. It thus represents an ideal system in which similarly defended species could share the cost of training predators to avoid aposematic coral snake coloration, facilitating the evolution of innate avoidance of coral snake coloration (Smith, 1976).

However, encounters with coral snakes are rare, which results in fewer opportunities for predator learning and weaker selection for innate avoidance. Nevertheless, if Müllerian mimicry is a driver for colour evolution in this system, we predict a morphological similarity between two or more species in areas where they co-occur (Kapan, 2001). Concomitantly, selection for signal similarity would become relaxed outside the range of distributional overlap. In this study, we integrate detailed morphology, coloration and geographic distribution data for several *Micrurus* species to test for the existence of Müllerian mimicry.

MATERIAL AND METHODS

SPECIES

Coral snakes have a variety of colour patterns ranging from monads (red rings separated by a sequence of white-black-white rings) to triads (with two distinct groups occurring in Central and South America with red rings separated by a sequence of black-white-black-white-black rings) or bicolour (alternated red and black rings). Colour pattern variation in the *Micrurus* genus was traditionally used in taxonomic rearrangements, fuelling intense debates among scientists (Silva Jr *et al.*, 2021a).

To test whether coral snakes engage in Müllerian mimicry, we examined museum specimens of the subset of species that possess a tricoloured, triadic aposematic signal (Savage & Slowinski, 1992).

We selected species based on the following criteria: species with overlapping and non-overlapping geographic distributions (Roze, 1996; Bosque *et al.*, 2016; Silva Jr *et al.*, 2021b), species with similar banding patterns and species well represented in museum collections. After an initial exploration of the available material, we selected *Micrurus brasiliensis*, *Micrurus frontalis*, *Micrurus ibiboboca*,

Micrurus lemniscatus and *Micrurus surinamensis* for this study (Supporting Information, Figs S1, S9). We obtained geographic coordinates of species distribution records based on the original collection data.

MORPHOLOGY AND COLOUR QUANTIFICATION

We took high-quality digital photographs from the dorsum of 1528 preserved snakes deposited in Brazilian herpetological collections (CEPB, CHUFPB, CHUNB, INPA, LARUFRN, MHNCI, MNRJ, MPEG, MZUFBA, MZUSP and UFMT; Supporting Information, Figs S1, S7). After excluding damaged snakes, we retained 1453 individuals for further analyses. We recorded the following measurements from each image: total length (from the tip of the snout to the end of the tail) and the number of black, red and white rings. We also selected one triad at the mid-body position (the nearest triad halfway from the snout to the end of the tail) to measure the length of the first, second and third black rings, the length of the first and second white rings, and the length of the red ring anteriorly to the selected triad. The length of the white rings and the length of the first and third black rings were nearly identical, so we averaged them. After checking which variables were highly correlated (Spearman correlation ≥ 0.9), we selected five variables to be used in further analyses: number of red rings, relative length of red rings (length of red ring/ total length), relative length of external black rings [(length of black ring I + length of black ring III/ total length)/ 2], relative length of white rings [(length of white ring I + length of white ring II/ total length)/ 2] and relative length of internal black rings (length of black ring II/ total length). We used ImageJ-Fiji, v.2.0.0-rc-69/1.52i (Schindelin *et al.*, 2012) to analyse all images and take measurements.

STATISTICAL ANALYSES

To calculate colour variation through the geographic distribution of each species, we used a multivariate spatial analysis (spatial principal component analysis: sPCA), with the function *multispati* from the *adespatial* package (Dray *et al.*, 2018), which maximizes the product of variance and spatial autocorrelation. To assess spatial autocorrelation at broad geographic scales in the coloration data, we ran a Monte Carlo test of global spatial structure with 999 simulations using the function *global.rtest* from the package *ade4* (Dray & Dufour, 2007). To calculate the number of nearest neighbours and the spatial weights (using row-standardized style), we used the functions *knearneigh* and *nb2listw*, respectively, using the package *spdep*

(Bivand, 2002). To produce continuous maps of the geographic distribution of morphological variation for each species, we interpolated sPCA lagged scores using the function *interp* from the *Akima* package (Akima & Gebhardt, 2016).

To test whether each species pair is more morphologically similar where their distributions overlap, we created a one-degree grid (each cell with *c*. 111 km²) for each species. We extracted the lagged scores from each cell to generate a matrix with cells as rows and species as columns. If multiple samples of the same species occurred in the same cell, we averaged their lagged scores to obtain a single value per cell for each species. Next, we compared pairs of species using *t*-tests. We repeated this procedure for the first three sPCA axes. We predicted that there should be no statistical difference between the lagged scores of two species where they co-occur, and there should be differences in their lagged scores where they do not co-occur.

Additionally, we tested if morphological dissimilarity between pairs of species increases with geographic distance by performing a Mantel test (999 permutations) using the package *ecodist* (Goslee & Urban, 2007) with a dissimilarity matrix of the Euclidean distances of each PCA score and geographic distance of each individual with the package *geosphere* (Hijmans, 2017). If Müllerian mimicry occurs, we expect an increase in morphological dissimilarity with geographic distance between two species pairs. We conducted all statistical analyses in the R statistical environment (R Core Team, 2021).

RESULTS

We found no evidence for ontogenetic variation in the number of rings (correlation test between the number of red rings and total length: rho = -0.003; $P = 0.905$). That is, the five coral snake species analysed tended to maintain a constant number of rings throughout their lives (including juvenile and adult life stages), only increasing the length of each ring. Accordingly, we performed subsequent analyses using all available individuals (adults and juveniles). The first three spatial principal components explained 93% of the variance in the original morphological variables (Supporting Information, Fig. S2). Based on the Monte Carlo simulation, we rejected the null hypothesis of no spatial structure in our data (Monte Carlo test: observed = 0.08, simulated *P*-value = 0.001). The first spatial principal component (sPCA1) alone accounted for 47% of the variance, and the number of rings and length of the internal black rings were the most important variables (Table 1).

Table 1. sPCA loadings of all morphological variables for the first three Spatial Principal Components axes (sPCAa)

	sPCAa1	sPCAa2	sPCAa3
Number of rings	-0.607	-0.259	0.092
External black ring length	0.450	0.249	0.780
Internal black ring length	0.582	-0.350	-0.416
White ring length	-0.127	0.851	-0.310
Red ring length	0.271	0.154	-0.340

The second spatial principal component (sPCA2), which explained 30% of the variance in the original variables, was strongly correlated with the length of the white rings (Table 1; Supporting Information, Fig. S3). The third spatial principal component (sPCA3, 16% of the variance) was strongly correlated with the length of external black rings (Table 1; Supporting Information, Fig. S4).

The maps produced by interpolation separated each species into specific colour pattern groups (Fig. 1; Supporting Information, Figs S3, S4), except for *M. lemniscatus*. Despite indicating that species can be grouped based on colour pattern, the maps revealed similar trends between species for length and number of rings (i.e., species tend to be more similar where they overlap; Fig. 1; Table 1; Supporting Information, Fig. S2). Based on sPCA1, *M. lemniscatus* has the most extensive morphological variation, which was unsurprising given that it has the broadest and most discontinuous geographic distribution of all analysed species. *Micrurus surinamensis* has long internal black rings and a reduced number of rings, whereas many individuals of *M. frontalis* have short internal black rings (Supporting Information, Table S1).

Most *t*-tests indicated morphological differences in areas of allopatry where species ranges do not overlap (seven out of ten comparisons; Supporting Information, Fig. S5; Table S2). Conversely, there were no differences in coloration patterns in areas of sympatry where species ranges overlap (ten out of ten comparisons, Supporting Information, Fig. S5; Table S2). The Mantel test results indicated that, in general, the dissimilarity between species pairs increased with geographic distance (Supporting Information, Fig. S6; Table S3). The only exception to this pattern occurred in comparing *M. surinamensis* with *M. frontalis/ibiboboca/lemniscatus*. In general, our findings indicate that two or more species tend to be morphologically similar where their distributions overlap and dissimilar where they do not overlap (Fig. 1; Supporting Information, Fig. S8).

DISCUSSION

Micrurus species have long been considered models for several harmless mimics. Numerous studies
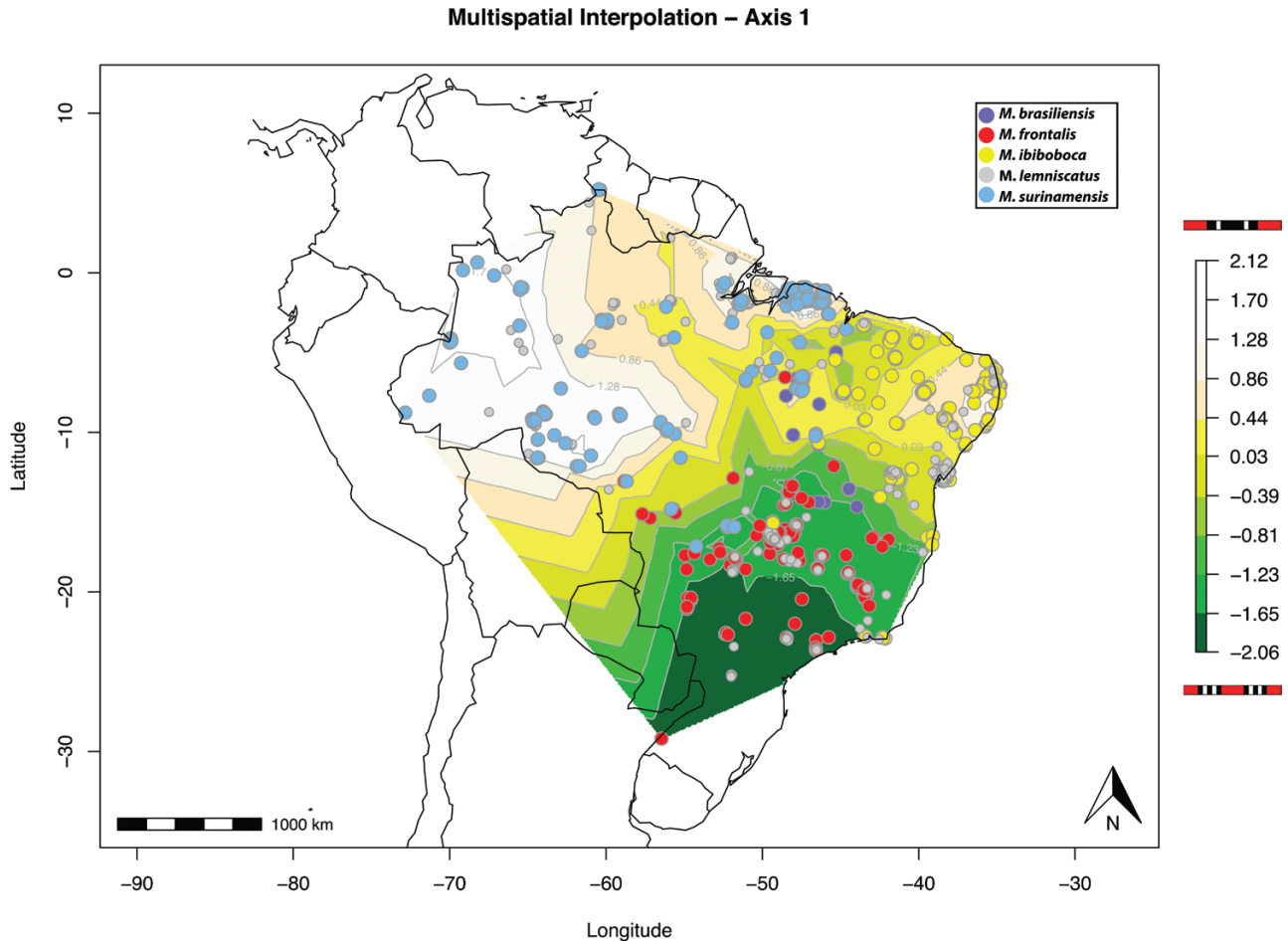
Multispatial Interpolation – Axis 1

Figure 1. Spatial interpolation of the first sPCA axis. Coloured dots represent the five different *Micrurus* species used in the present study. Background colour, ranging from green (negative values: increased number of rings, reduced internal black ring length) to white (positive values: reduced number of rings, increased internal black ring length), represents interpolated lagged scores based on the sPCA of *Micrurus* morphological variables. In general, in areas of co-occurrence, *Micrurus* species tend to be morphologically similar.

have shown that these species engage in Batesian mimicry (Brodie, 1993; Davis Rabosky *et al.*, 2016; Akcali & Pfennig, 2017; França *et al.*, 2017; Akcali *et al.*, 2019; Hudson *et al.*, 2021). Nevertheless, there has been no formal demonstration that *Micrurus* species increase their protection against predation by converging on similar coloration when in sympatry. Our study is the first to demonstrate that *Micrurus* species display similar colour patterns where they co-occur. This is consistent with Müllerian mimicry, but not proof thereof, as other valid hypotheses predict convergence in sympatry (Brattstrom, 1955; Komárek, 1998; Ruxton *et al.*, 2004; Kronforst *et al.*, 2012; Davis Rabosky *et al.*, 2016) and experimental work should be done to confirm the existence of Müllerian mimicry in this system.

Given that the density of individuals is generally lower towards the edge of a species' distribution, we expect even more similarity between two species in such areas (Harper & Pfennig, 2007). This phenomenon is believed to occur because predators have fewer encounters with coral snakes at the edge of their geographic distribution, leaving little room for deviations of the local pattern. Selection favouring better mimicry at the distributional edges was tested in a previous study of coral snake replicas, indicating that Batesian mimics are more like their model at the distributional edges of the model (Harper & Pfennig, 2007). The low density of individuals at the edge of the distribution probably contributes to the convergence towards coloration similarity between multiple *Micrurus* species. This edge-density effect might be another factor contributing to the strong patterns we found in this study.

The length of the red rings was not an essential variable in any of the three sPCA axes. This finding suggests that the length of red rings is under strong selection even at large geographic scales and may be functioning as a generalized signal for predator deterrence (Pryke, 2009). However, some *Micrurus* species, like *M. albicinctus*, do not have red coloration, which indicates that the ring pattern itself is another way to transmit a deterrent signal (Brodie, 1993). The red coloration is usually attributed to a broadly avoided colour pattern (Pryke, 2009; Pravossoudovitch *et al.*, 2014), and banding patterns are used as a signal in other taxa such as hymenopterans (Williams, 2007) and lepidopterans (Ingalls, 1993). Further investigation is warranted to understand the interaction between coloration and ring patterns in *Micrurus* snakes and their role in signalling unprofitability.

Although our results indicate a pattern of Müllerian mimicry, Batesian and Müllerian mimicry likely work together in complex mimicry systems, and sometimes the distinction between these two types of mimicry can be blurred (Speed & Turner, 1999; Balogh *et al.*, 2008). The difficulty of distinguishing between these two types of mimetic interactions can be exacerbated by interspecific variation in venom composition in *Micrurus* (Silva Jr & Aird, 2001; Lomonte *et al.*, 2016), which might pose different threat levels to each predator species. Neotropical coral snakes and their harmless mimics also show overlapping coloration patterns (Bosque *et al.*, 2016). However, it remains to be tested whether coloration tends to be more similar in areas of sympatry between *Micrurus* and harmless snakes. Finally, we advocate that field tests of predator avoidance, quantification of population densities and a better comprehension of the evolutionary history are essential to provide unambiguous evidence of Müllerian mimicry in coral snakes.

CONCLUSION

We indicate that the five species of coral snakes analysed are potential Müllerian mimics, with increased morphological similarity in regions where they co-occur. To further investigate the evolution of Müllerian mimicry in such a diverse clade, a comprehensive phylogenetic hypothesis of *Micrurus* that includes both intra- and interspecific structures is essential, particularly one that includes a representative sampling of species with large geographic distributions. Future studies investigating Müllerian mimicry in this group should also consider the diversity of banding patterns in coral snakes. Additionally, demographic parameters, particularly from the core and the periphery of species ranges,

would provide extra context for further tests of coral snake mimicry.

DATA AVAILABILITY

All the geographic coordinates and coloration data can be found in the Dryad digital repository (Bosque *et al.*, 2021).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Images of coral snakes used in the present study: (A) *M. frontalis* (Corumbá, Goiás), (B) *M. ibiboboca* (Xingo, Alagoas), (C) *M. lemniscatus* (Usina Hedrelétrica Jirau (UHE Jirau), Rondônia), (D) *M. surinamensis* (UHE Jirau, Rondônia), (E) *M. brasiliensis* (Mambaí, Goiás). Photos A, C, D: Naturae Consultoria Ambiental. Photos B, E: Nelson Jorge da Silva Jr.

Figure S2. Three-dimensional scatterplot displaying the first three axes of the spatial principal components analysis (sPCA). Each dot represents a lagged (i.e., spatially weighted) score resulting from the sPCA of morphological variables of five species of the genus *Micrurus*.

Figure S3. Spatial interpolation of the second sPCA axis. Coloured dots represent the five different *Micrurus* species. Background colour, ranging from green (negative values) to white (positive values), represents interpolated lagged scores based on the sPCA of *Micrurus* morphological variables.

Figure S4. Spatial interpolation of the third sPCA axis. Coloured dots represent the five different *Micrurus* species. Background colour, ranging from green (negative values) to white (positive values), represents interpolated lagged scores based on sPCA of *Micrurus* morphological variables.

Figure S5. *t*-tests comparing pairs of coral snake species. *t*-tests comparing mean lagged scores (first axis) using a size grid of one degree of latitude by one degree of longitude. The upper diagonal shows the number of grid cells where species pairs overlap. The lower diagonal shows the number of cells where there is no distributional overlap among pairs of species. Values inside each square represent degrees of freedom. Squares are coloured based upon whether a pair of species are similar (black; $P > 0.05$) or dissimilar (red; $P < 0.05$).

Figure S6. Mantel test results using scores of the first axis of the PCA. Squares are coloured based upon whether dissimilarity between a pair of species increases with distance (red squares; $P < 0.05$) or decreases with distance (black squares; $P > 0.05$).

Figure S7. List of specimens used in this study and museum acronyms.

Figure S8. Maps of colour variation in *Micrurus*. Colour variation of *Micrurus* species represented by one-degree grids that are correspondent to the averaged lagged score of the first sPCA axis. Scale represents the lagged score values. Positive values: reduced number of rings and increased internal black ring length. Negative values: increased number of rings and reduced internal black ring lenght. (A) *M. surinamensis*, (B) *M. brasiliensis*, (C) *M. frontalis*, (D) *M. ibiboboca*, (E) *M. lemniscatus*.

Figure S9. Preserved specimens of coral snakes. Examples of photographs used to take morphological measurements of coral snakes: (A) *M. brasiliensis*, (B) *M. frontalis*, (C) *M. ibiboboca*, (D) *M. lemniscatus*, (E) *M. surinamensis*.

Table S1. Morphological variables of five species of the genus *Micrurus*.

Table S2. *t*-tests comparing lagged scores of the first axis of the sPCA using one-degree cells.

Table S3. Mantel test results using PCA scores of the first component.