Home of the brave: is similarity of defensive behavior of Neotropical snakes (Dipsadidae: Pseudoboini) predicted by sympatry?

Filipe C. Serrano[1,6*], Juan C. Diaz-Ricaurte[1,4,*], Cristopher A. Antúnez-Fonseca[2,3*], Yulfreiler Garavito-David[4], Aida Luz Garcia[4], Rolland D. Díaz-Morales[4], Silvia R. Travaglia-Cardoso[5]

[1]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 05508-090 São Paulo, SP, Brazil.
[2]Centro Zamorano de Biodiversidad, Departamento de Ambiente y Desarrollo, Escuela Agrícola Panamericana Zamorano, Valle de Yeguare, Francisco Morazán, Honduras.
[3]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Cidade Universitária, 79070-900, Campo Grande, Mato Grosso do Sul, Brazil.
[4]Semillero de Investigación en Ecofisiología y Biogeografía de Vertebrados, Grupo de investigación en Biodiversidad y Desarrollo Amazónico (BYDA), Centro de investigaciones Amazónicas Macagual – Cesar Augusto Estrada Gonzales, Universidad de la Amazonia, Florencia, Caquetá, Colombia.
[5]Museu Biológico, Instituto Butantan, 05503-900, São Paulo, SP, Brazil.
[6]Corresponding author. Filipe C. Serrano (filipe.serrano@usp.br)

*These authors contributed equally to this work.

Running title: Spatial structure of Neotropical snakes

Keywords: anti-predator behavior, ecoregion, geographical distribution, natural history, predation.

Abstract

Predation is a strong driver of prey behavior and sympatric species are exposed to similar selective predatory pressures.We test the hypothesis that this leads to similar anti-predator behaviors using the widespread Neotropical snake tribe Pseudoboini. We reviewed and compiled documented defensive behaviors for all species, adding new unreported behaviors for three species. We used a cluster analysis to generate a matrix of defensive behavior dissimilarity between species. We then used a PGLMM to test how behavior dissimilarity changed with range overlap, similarity in ecological traits and phylogenetic relatedness. Only 41 species had available data on defensive behavior, with only 22 of those represented in the phylogeny. We found that similarity in defensive behavior is significantly (albeit not strongly) correlated with range overlap, but only for species with similar body sizes. Phylogenetic relatedness by itself was a poor predictor of behavior dissimilarity. This corroborates our hypothesis that defensive behaviors are spatially structured at larger scales but that it can be modulated by morphological differences.. Our study tests inter-species ecogeographical differences of defensive behavior, and its implications can be broadly applied to other taxa.

Introduction

Predation is one of the main selective pressures that shape communities (Glasser 1979). Anti-predator behaviors shape species interactions (Glasser 1979) thus they occupy a central position in evolutionary ecology as they directly influence survival and fitness (Lind & Cresswell 2005). Examples of anti-predatory mechanisms include chemical defenses, aposematic coloration, and anti-predatory behaviors (Durso and Mullin 2013). These anti-predatory behaviors depend on diverse morphological and behavioral components (Blomberg et al. 2003) thus being under strong selection (Alcock 2009) and thus represents a fundamental component of fitness (Réale et al. 2007). Nevertheless, the contextual components of animal behavioral traits – and how these are spatially structured – are poorly understood and remain a relevant subject of debate among scientists (Koski 2014; Wilson et al. 2019).

While most defensive mechanisms that depend on morphological structures (e.g., rattles in rattlesnakes, venom glands) are phylogenetically conserved, behavior often varies amongst species of the same clade (Blomberg et al. 2003). Thus, defensive behaviors may have a higher fitness in a specific context but lower fitness in others (Hoverman & Relyea 2009), such as lizards decreasing risk-taking and thermoregulation when dehydrated (Chabaud et al. 2023). The ability to display different anti-predator behaviors may be important for an effective defense (Heynen et al. 2017), thus defensive behavior varies across species of the same genus and often even within species due to factors such as phenotypic plasticity and environmental cues (Aubret et al. 2011). This is especially important because there may be different scenarios of selective pressure in different populations, which results in a correlation of local predator-prey behaviors (Toja & Sota 2006; Meo et al. 2021) and in prey under a higher predation risk developing more complex defenses (Steinberg et al. 1995; Trussell & Smith 2000). Thus, one of the most important aspects shaping behavioral strategies is the selective pressure by local predators, which also varies at different spatial scales (habitat and region) (Placyk 2012).

Geographical differences of prey response to potential predators are poorly studied, with most studies mostly focused on intraspecific differences (at population level) but not on interspecific differences (Herzog & Schwartz 1990; Placyk 2012). These interspecific differences are worth to analyse, especially in taxa with broader geographical ranges since different environmental conditions may have different predatory pressures.(Placyk 2012; Moura et al. 2022). This variation of predation pressure should therefore be a driver of defensive behavior across space. For example, biotic interactions are thought to be stronger at lower latitudes which have higher temperatures and less seasonality (Romero et al. 2018), and thus metabolic rates might impose different cost-efficiency of defensive behaviors (Delaney 2019). This is supported by deliberate tail loss of limbless reptiles being more reported for warmer regions (Moura et al. 2022) or snails having thicker shells in populations with shell-piercing predators in austral populations (Trussell & Smith 2000). At the same time, activity patterns and habitat use – strongly linked to abiotic factors – are important as they modulate the chance of encounter between prey and predator (Moura et al. 2022). On the other hand, the expression of defensive strategies in prey is often correlated with predator abundance or diversity over a range of spatial scales (Trussell & Smith 2000; Santos et al. 2011). Since predators differ in their foraging strategies and predation efficiency, they can favor different traits in prey populations and, therefore, species in areas with markedly dangerous or abundant predators might be under greater selective pressure and exhibit different anti-predatory behaviors compared to those in less risky areas (Placyk 2012). Furthermore, predatory pressure is also linked to larger scale characteristics such as climate and vegetation structure (Moura et al. 2022), favoring similar defensive behaviors for species that occur in sympatry. Thus, sympatric species exposed to similar conditions such as the type and number of potential predators could have similar anti-predator behaviors (Greene 1979), making range overlap a good predictor of similarity of defensive behaviors. However, this hypothesis has never been tested.

Among vertebrates, snakes have one of the most varied repertoires of defensive behaviors to avoid predation, since they have several types of natural predators, both vertebrates and invertebrates (Greene 1988, 1997). Documenting and reporting anti-predator behaviors of snakes in diverse regions is essential to better understand their behavioral ecology, especially in the Neotropical region in which these are still under-reported but also where “paradoxically, the most spectacular and complex defensive repertoires are often found […]” Greene (1988). Among Neotropical snakes, Pseudoboini Wagler, 1830 is one of the most ecologically diverse tribes, especially regarding defensive behaviors (Gaiarsa et al. 2013). This tribe belongs to the Dipsadidae family and comprises 49 species from 11 genera (Uetz et al. 2024) distributed in the Neotropical region (Nogueira et al. 2019; Uetz et al. 2024). Species of the Pseudoboini tribe are predominantly nocturnal and terrestrial (e.g., Díaz-Ricaurte et al. 2018; Díaz-Ricaurte & Arteaga 2021) but some species can be considered as semi-arboreal (e.g., *Siphlophis* genus) or fossorial (*Phimophis* genus). These habits also reflect their greatly diverse range of traits such as morphology, diet, natural history and even coloration (Martins & Oliveira 1998; Marques et al. 2001; Gaiarsa et al. 2013; Serrano et al. in prep). For instance, species of the genus *Oxyrhopus* have aposematic coloration, similar to venomous coral snakes of the genus *Micrurus* such that there is a geographic association between these two genera of snakes, which likely decreases the chance of predation by visual animals such as birds and mammals (Bosque et al. 2016). Due to the comprehensive studies on the natural history of Pseudoboini (Gaiarsa et al. 2013), this tribe is an excellent model to understand how defensive behavior might be spatially structured.

Herein, we assess if defensive behavior is spatially structured, potentially due to similar selective pressures from predation. We test the hypothesis that co-occurring species have similar defensive behaviors, accounting for phylogenetic relatedness and ecological similarity. To do so, we review all reported defensive behaviors for the snake tribe Pseudoboini and add descriptions of unreported behaviors for three species of *Oxyrhopus*.

Materials and Methods

Literature review and new defensive behaviors

To compile all the defensive behaviors present in species of the tribe Pseudoboini and to update the existing information on Gaiarsa et al. (2013), we conducted searches for articles published between 1980 and 2023 in the databases of Scopus, Web of Science, Scielo, and Google Scholar. Also, we reviewed the entire archive of natural history notes published in *Herpetological Review*, *Herpetology Notes* and *Herpetological Bulletin*. We searched the literature for articles mentioning defensive behavior for species using a combination of the terms ‘defensive display’, ‘natural history’, ‘neotropical snake’, ‘false coral snake’, ‘Pseudoboini, ‘behaviors’, ‘defensive behavior’, in English, Portuguese and Spanish regardless of year. Behaviors were included as reported, grouping them whenever redundant (e.g. ‘body depression and ‘body flatenning). We furthermore describe new unreported defensive behaviors for three species from personal field observations and personal communications.

Using compiled defensive behavior for each species, we performed a comparison among species with a cluster analysis, using a ‘binary’ UPGMA (unweighted pair-group average; Saraçli et al. 2013; Supplementary material S1) to generate a matrix of cophenetic distance between species, as dissimilarity in defensive behavior. This method uses proportional averaging weighted by the number of taxa in each cluster. Locomotor escape was considered as present for all species since is the first line of defense in snakes, although often not reported in literature, while mimicry.was not considered in the cluster analysis because it is a passive display (Bosque et al. 2016). Nevertheless, we still report species considered as aposematic mimics to account for the complete defensive aspects of Pseudoboini species.

Statistical analysis

To assess whether range overlap predicts congruence in defensive behavior, we estimate this parameter between each pair of species with at least one reported defensive behavior. We first obtained the distribution ranges of species using the Global Assessment of Reptile Distributions (GARD version 1.7, Roll et al. 2017). We calculated pairwise range overlap by dividing the area of geographical intersection of each pair of species by the total area of geographic union of both species, with values ranging from 1 (fully sympatric) to 0 (fully allopatric) (McKee et al. 2016). Furthermore, we calculated macrohabitat similarity by intersecting each species distribution range with global ecoregions (Dinerstein et al. 2017). We then obtained the proportion of species occurrence in each ecoregion to then generate an macrohabitat dissimilarity matrix, using a Euclidean UPGMA (unweighted pair-group average; Saraçli et al. 2013; Supp. Mat. S1).

We included relevant ecological traits potentially linked to defensive behavior: arboreality and body size. Arboreality modulates both the encounter rate and type of predators, leading to a greater diversity of defensive behaviours in snakes (Martins et al. 2008). Herein, we define arboreality as the relative number of records in trees as made available by Gaiarsa et al. (2013) and use pairwise differences in arboreality as the absolute difference of arboreality between each two species. Body size is also correlated with defensive behavior, with larger individuals exhibiting higher levels of aggression and number of anti-predatory behaviors (Delaney 2019). We obtained maximum length for each species from ReptTraits (Oskyrko et al. 2024) and calculated pairwise differences in body size as the absolute difference between each two species.

Lastly, since behavior can be phylogenetically conserved in clades (Thierry et al. 2000; Miranda et al. 2022; Zocca et al. 2022), we used a dated phylogeny of Dipsadidae (Serrano et al. 2024) to generate pairwise phylogenetic distances for species present in the phylogeny. We used a Generalized Linear Mixed Model (GLMM) approach to test if dissimilarity in defensive behavior is predicted by the interaction of range overlap, ecoregion similarity, phylogenetic distance, and differences in microhabitat (absolute difference in arboreality) and body size (absolute difference of maximum length), using the package 'glmmTMB' (Brooks et al. 2023). We used a beta distribution since dissimilarity in defensive behavior ranges from 0 to 1 and used nested species pairs as a random effect since each species is compared with every other species. We only included species that simultaneously had data on defensive behavior and were present in phylogeny. Before inclusion in the GLMM, we tested collinearity between variables with Pearson's Correlation and excluded ecoregion similarity due to collinearity with range overlap ($r > 0.6$). We then performed full-model averaging using the package 'MuMIn' (Bartoń 2018) since it can provide more reliable confidence intervals compared to model selection and that it lessens issues with over-complex models, especially in behavioral ecology (Symonds & Moussalli 2011). Additionally, in order to assess whether the number of reported behaviors could be biased towards widespread species, we performed a Phylogenetic Generalized Linear Mixed Model (PGLMM) to test the relationship between the number of reported behaviors for each species and the log of its area of distribution, with a Poisson distribution and correcting for phylogenetic relatedness. All analyses were performed in R version 4.0.2 (R Core Team 2020).

Results

New unreported behaviors

Oxyrhopus petolarius (Linnaeus 1758)

On September 22, 2020, at 21:45h and February 22, 2022, at 22:30 h, we observed a male and a female (total length = 251 mm; snout–to-vent length [SVL] = 219 mm; weight = 4 g and total length = 1020 mm; SVL = 740 mm; weight = 63 g, respectively) in the foothills of the Amazon rainforest (Municipality of San José del Fragua, Caquetá, Colombia. (1.336826, -75.966334; 349 m asl, WGS84). The first individual exhibited balling behavior towards the observers followed by thanatosis (Figure 1A–B). After a few minutes, it raised its head and again tried to flee. When approached, the second individual expanded its body and, with its neck in a coil (Figure 1C), made several false strikes towards the observer. Notice the difference between balling (tight coils in a spheric shape; Figure 1A) and head-hiding (a *O. rhombifer* showing much looser coils and a flatter body position, Figure 1D).

Oxyrhopus fitzingeri (Tschudi 1845)

According to César Luque-Fernandéz and Luis Villegas Paredes (pers. comm.), an individual of *O. fitzingeri* caught in Atiquipa, Arequipa (Peru) coiled its neck in a S-shape, raised its head and made lateral movements, shortly after which it tried to escape. This is the first detailed description of this behavior for this species but more details about the individual and the locality can be found in Luque-Fernandez & Villegas Paredes (2017)

Oxyrhopus doliatus Duméril, Bibron & Duméril 1854

According to Luís Esqueda (pers. comm.), individuals of *O. doliatus* in Venezuela attempt to flee when first detected and often make lateral movements and flatten the body (mainly the juveniles), using cloacal discharges when captured. More details on the locality of record can be found in Esqueda et al. (2008).

Figure 1. New defensive behaviors for *Oxyrhopus petolarius* and *O. rhombifer*. For *O. petolarius* the newly reported behaviors are A) balling; B) thanatosis and C) neck S-coil behavior. For *O. rhombifer* the newly reported behavior is D) head-hiding behavior. D) A *Oxyrhopus rhombifer* exhibiting head-hiding behavior, with much looser coils and a flatter body compared to the typical spheric shape of balling snakes.

Literature review

We found data of defensive behavior for 41 species of 11 genera (83.7% and 100%, respectively) of Pseudoboini snakes (Table 1). Only 22 species had simultaneously reported defensive behavior and were present in the phylogeny. The species for which a higher number of behaviors has been reported was *Oxyrhopus rhombifer* with 14, followed by *Siphlophis compressus* and *O. petolarius* both with 12. Among the reported defensive behaviors for Pseudoboini species, the most commonly reported were head-hiding, erratic movements, cloacal discharges and balling (Figure 2).

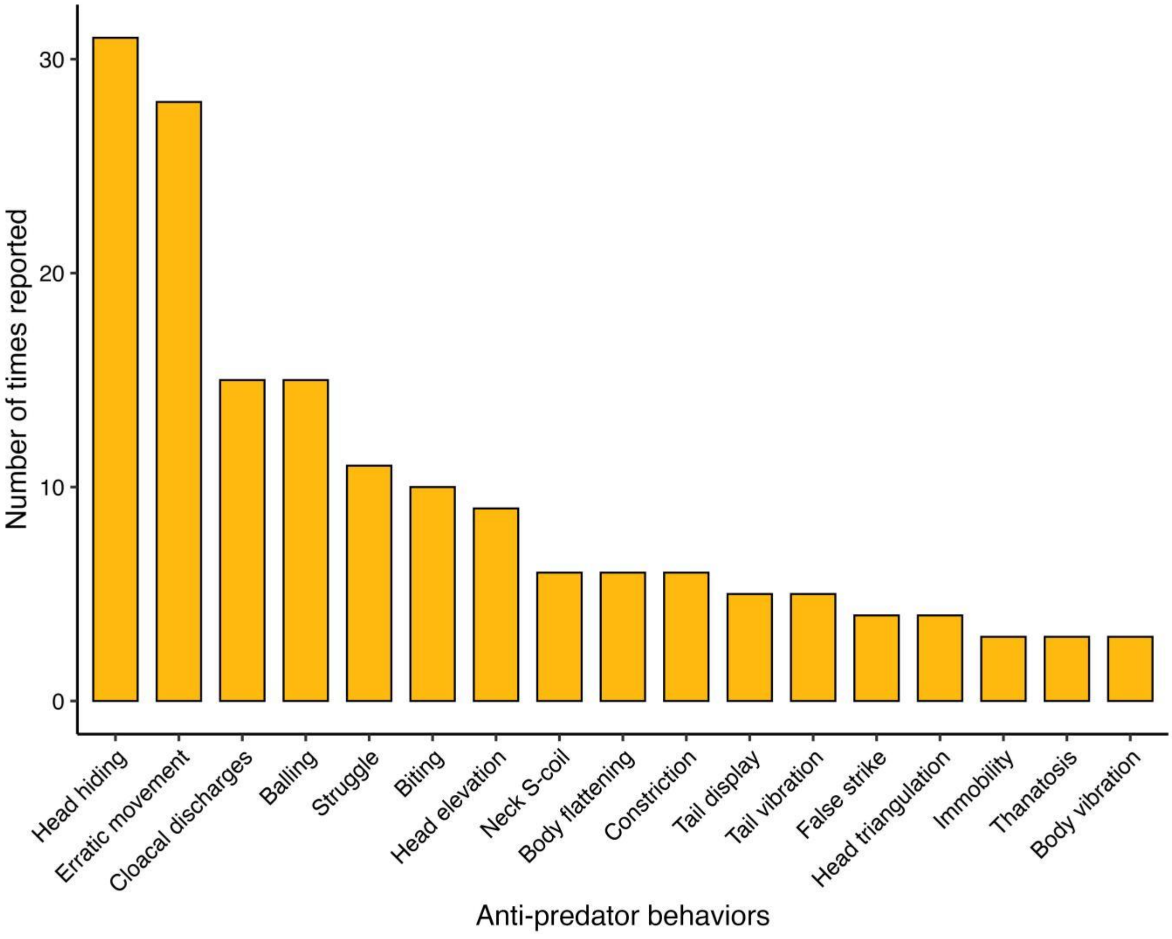

Figure 2. Number of species of Pseudoboini reported to show each defensive behavior. For more details see Table 1. Locomotor escape was excluded since it is often not reported and mimicry was excluded due to being a passive defensive mechanism but not a behavior *per se*.

The UPGMA dendrogram of behavioral dissimilarity of this subset yielded two major clusters (Figure 3A), with the one comprising *Paraphimophis rusticus* (*Oxyrhopus fitzingeri* + *Siphlophis pulcher*) having large average lengths, which indicates high dissimilarity. The other cluster was composed of all other 19 species divided into two sub-clades: one comprising seven species, featuring all three species from *Siphlophis* genus; and the other one comprising 12 species, mainly from the *Boiruna*, *Clelia, Pseudoboa* and *Mussurana* genera (Figure 3A). Species from the *Oxyrhopus* genus were equally present in both sub-clades. The average range overlap between species was 18.8% (± 23.7%) and varied from 0 (e.g., between *Oxyrhopus clathratus* and *O. occipitalis*) and 89.2% (between *Siphlophis compressus* and *S. cervinus*) (Supp. Mat. S3). Overall, average range overlap between species of the same genus (19.5% ± 25.3%, n = 30 pairs) was similar to species belonging to different genus (18.7% ± 23.6%, n = 201 pairs) Our analysis showed that range overlap by itself did not significantly predict dissimilarity in defensive behavior (Table 2). However, the interaction of range overlap and difference in body size (estimate = -0.01, p = 0.02) had a significant negative effect, albeit weak, on the dissimilarity in defensive behavior (Table 2, Figure 3B). The interaction of these factors with phylogenetic distance was weak and marginally non-significant (p = 0.054) but phylogenetic distance by itself was poorly correlated with dissimilarity in defensive behavior (Table 2, Figure 3A). For instance, even though most species of the *Oxyrhopus* genus comprise a monophyletic group (excluding *O. fitzingeri*, see Serrano et al., 2024), they do not cluster together regarding behavioral dissimilarity. On the other hand, species from the *Siphlophis* genus (excluding *S. pulcher*) are cluster both phylogenetically and in behavioral dissimilarity, albeit with different relationships among them. Our PGLMM also showed that species with a higher number of reported behaviors did not have wider distributions (p = 0.17).

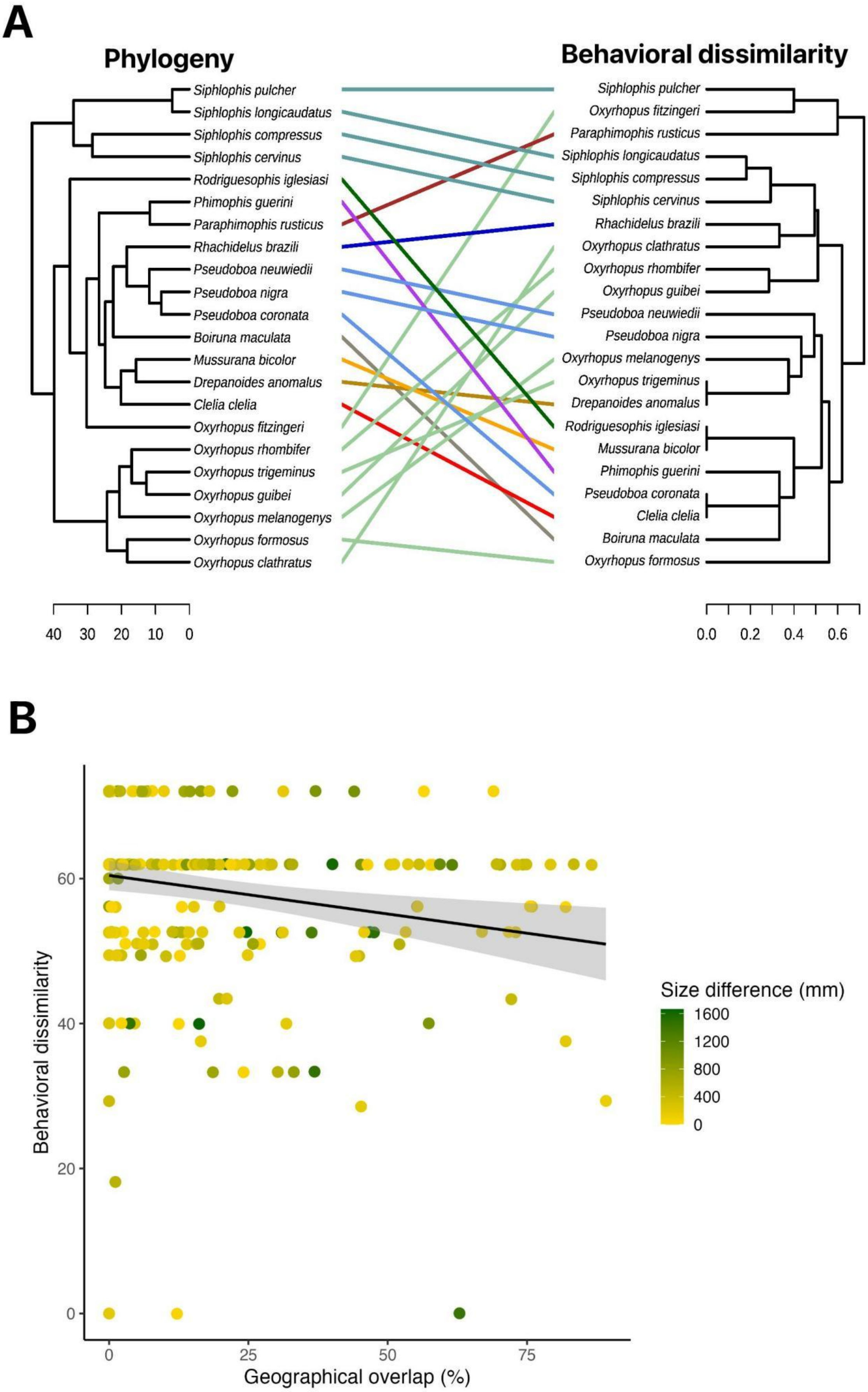
A
Phylogeny
Behavioral dissimilarity
Siphlophis pulcher
Siphlophis longicaudatus
Siphlophis compressus
Siphlophis cervinus
Rodriguesophis iglesiasi
Phimophis guerini
Paraphimophis rusticus
Rhachidelus brazili
Pseudoboa neuwiedii
Pseudoboa nigra
Pseudoboa coronata
Boiruna maculata
Mussurana bicolor
Drepanoides anomalus
Clelia clelia
Oxyrhopus fitzingeri
Oxyrhopus rhombifer
Oxyrhopus trigeminus
Oxyrhopus guibei
Oxyrhopus melanogenys
Oxyrhopus formosus
Oxyrhopus clathratus
Siphlophis pulcher
Oxyrhopus fitzingeri
Paraphimophis rusticus
Siphlophis longicaudatus
Siphlophis compressus
Siphlophis cervinus
Rhachidelus brazili
Oxyrhopus clathratus
Oxyrhopus rhombifer
Oxyrhopus guibei
Pseudoboa neuwiedii
Pseudoboa nigra
Oxyrhopus melanogenys
Oxyrhopus trigeminus
Drepanoides anomalus
Rodriguesophis iglesiasi
Mussurana bicolor
Phimophis guerini
Pseudoboa coronata
Clelia clelia
Boiruna maculata
Oxyrhopus formosus
40
30
20
10
0
0.0
0.2
0.4
0.6
B
Behavioral dissimilarity
0
20
40
60
Geographical overlap (%)
0
25
50
75
Size difference (mm)
1600
1200
800
400
0

Figure 3. A) Correspondence of phylogeny (left; scale in million years, Serrano et al., 2024) and behavioral dissimilarity (right; scale in which the higher the value the most dissimilar species are) for species of the Pseudoboini tribe. Lines connect the same species in both clusters (phylogeny and behavioral dissimilarity). Different colors represent different genera. **A)** Behavioral dissimilarity between snakes from the Pseudoboini tribe decreases with geographical overlap and size difference (increasing from yellow to dark green).

Discussion

Herein we show that the Neotropical snake tribe Pseudoboini has a diverse repertoire of defensive behaviors. We confirmed our hypothesis that species that co-occur tend to be more similar in defensive behavior but only if they have similar body sizes. Furthermore, similarity in defensive behavior is not phylogenetically structured. Our work explicitly tests ecogeographical differences of defensive behavior between species, which might be an important component of species ecology and their interactions.

Behaviors such as locomotor escape, cloacal discharge and head-hiding were more than three times as frequent as thanatosis, body vibration, body flattening or tail display. Although all these aforementioned behaviors are considered non-intimidating defensive behaviors (Gray 2015), they may have different trade-offs in cost and success that reflects their reported frequency and the moment they are employed. While behaviors such as locomotor escape and struggle might have a high energetic cost (e.g., continuous movement to escape from the potential predator), they increase the distance between the snake and the predator upon detection and are usually among the initial anti-predatory behaviors shown prior to contact with predator (Gray 2015). On the other hand, behaviors such as balling, head-hiding and thanatosis likely have a low energetic cost but leave the snake potentially more vulnerable and aim to mainly deter or minimize predator attacks, potentially shown on a secondary phase where physical contact with the predator has occurred but escape is no longer possible (Greene 1988). Thus, initial defensive behaviors such as struggle might be more frequent as they represent a first phase in which the goal is to avoid further contact. In contrast, response behaviors such as thanatosis might be less common as they are employed as a last alternative when escape fails (Greene 1988).

We corroborated our hypothesis that there is a relationship of defensive behavior with co-occurrence at a larger scale (sympatry), which had been previously suggested (Greene 1979) but never tested. However, this similarity of defensive behavior for sympatric species is only strongly supported for species of similar size also. Anti-predator behavior of snakes had already been shown to be linked to body size (Delaney 2009), but our work is the first to assess how it plays a role in similarity of defensive behavior across sympatric species. While being large-bodied increases the chances of being detected by predators, it also decrease the probability of capture by gape-limited predators as well as posing a higher risk (Urban 2007). Body size strongly impacts ecophysiological parameters such as behavioral thermal tolerances (Klockmann et al. 2016) thus activity time and period and consequently exposure to predators (Grigaltchik et al. 2012), Since predation pressure is also linked with environmental parameters such as temperature and precipitation (Brodie & Russell 1999), as shown by increased tail autotomy for snakes in warmer regions (Moura et al. 2022), this may lead to a stronger convergence in defensive behavior by co-occuring species with similar size.

Even though body size is often phylogenetically conserved (Martins et al., 2001), we found that phylogenetic relatedness, by itself, was not a strong predictor of similarity in anti-predator behavior. This may also be influenced by range overlap being similar between congeneric and non-congeneric species, which suggests that phylogenetic relatedness does not determine range overlap of Pseudoboini snakes, at least at broad scales. Other studies have shown that defensive behavior can vary depending on the perceived threat and that it is one of the most labile traits (Brodie & Russell 1999; Blomberg et al. 2003; Martins et al. 2008), even though for some groups there is a phylogenetic component in anti-predator behavior (Davis Rabosky et al. 2021; but see Araújo & Martins 2006). Furthermore, arboreality was not present in the best models that explain dissimilarity in defensive behavior. Even though arboreal snakes typically have a greater diversity of defensive behaviours, which has been linked to higher predation pressures (Moura et al. 2022), this is not true for snakes of the Xenodontinae subfamily – such as those in the tribe Pseudoboini (Martins et al. 2008). Since all Pseudoboine snakes are strongly nocturnal, this may reflect how both arboreal and non-arboreal species use the same anti-predator behaviors, in contrast with diurnal species which often use significantly more diverse behaviors (Martins et al. 2008).

We found that the number of reported anti-predator behaviors is not correlated with range size. Thus, widespread species are not significantly changing our findings and report biases are likely constant across species with different range sizes. However, even though the scarcity of data for Pseudoboini is not as pronounced as for other less widespread but diverse snake clades, further information could help elucidate the role of geography on defensive behaviors, specially for species with restricted ranges such as *O. erdisii, O. leucomelas* and *O. marcapatae* (see distribution in Uetz et al. 2022). More in-depth investigation of the fitness costs and benefits of each anti-predator behavior is also required to fully evaluate the geographic patterns of predator-prey interactions (Arnold 1992; Roth & Johnson 2004). Even though previous studies have studied the geographical variation of anti-predator behavior, most have focused only on different populations of the same species (Herzog & Schwartz 1990; Placyk 2012), with our study being among the first testing inter-species differences. Herein we show that space, especially at large scale, is an important component of anti-predator behavior. We hope that our work stimulates future research on defensive strategies as our findings can be broadly applied to and tested in other taxa.

ACKNOWLEDGEMENTS

We thank César Luque-Fernández, Luis Villegas Paredes and Luis Esqueda for providing us with their valuable behavioral observations of *Oxyrhopus* species.

FUNDING

This study was partly financed by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brazil (CAPES)—Finance Code 001″ and by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP; #2023/06999-1, #2024/10038-0 and #2023/14087-2).

AUTHOR CONTRIBUTIONS

FCS and JCDR planned the study; YGD, ALG, RDDM and SRTC recorded the new defensive behaviors; FCS, JCDR, CAAF, YGD and RDDM reviewed and collected the data in literature; FCS led the writing of the manuscript; FCS analysed the data; FCS, JCDR, and CAAF wrote the original draft; FCS and JCDR contributed critically to the manuscript; FCS supervised the manuscript. All authors approved the final version of this manuscript.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information of this paper.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Filipe C. Serrano, https://orcid.org/0000-0002-8568-678X

Juan C. Díaz-Ricaurte, http://orcid.org/0000-0002-4659-0865

Cristopher A. Antúnez-Fonseca, https://orcid.org/0000-0001-8231-326X

Yulfreiler Garavito-David, https://orcid.org/0000-0002-4411-3432

Aida Luz Garcia, https://orcid.org/0000-0002-3482-9146

Rolland D. Díaz-Morales, https://orcid.org/0000-0002-7963-4211

Silvia Regina Travaglia-Cardoso, https://orcid.org/0000-0002-5351-8853

REFERENCES

Alcock J (2009) *Animal Behavior: An Evolutionary Approach*. 9th edn. Sunderland (MA): Sinauer Associates.

Araujo MS, Martins M (2006) Defensive behavior in pit vipers of the genus *Bothrops* (Serpentes, Viperidae). The *Herpetological Journal* **16**, 297–303.

Arnold SJ (1992) Behavior al variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Animal Behavior* **44**, 705–719.

Aubret F, Michniewicz RJ, Shine R (2011) Correlated geographic variation in predation risk and anti-predator behavior within a wide-ranging snake species (*Notechis scutatus*, Elapidae). *Austral Ecology* **36,** 446–452.

Barton K (2020) MuMIn: Multi-Model Inference. R package version 1.43.17. https://cran.r-project.org/package=MuMIn

Blomberg SP, Garland Jr T, Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**(4)**:** 717–745.

Bosque RJ, Noonan BP, Colli GR (2016) Geographical coincidence and mimicry between harmless snakes (Colubridae: *Oxyrhopus*) and harmful models (Elapidae: *Micrurus*). *Global Ecology and Biogeography* **25**, 218–226.

Brodie III ED, Russell NH (1999) The consistency of individual differences in behavior: temperature effects on anti-predator behavior in garter snakes. *Animal Behavior* **57**, 445–451.

Brooks M, Bolker B, Kristensen K, Maechler M, Magnusson A, McGillycuddy M (2023) Package ‘glmmtmb’. R Packag Vers 1, 7.

Chabaud C, Lourdais O, Decencière B, Le Galliard JF (2023) Behavioural response to predation risks depends on experimental change in dehydration state in a lizard. *Behavioral Ecology and Sociobiology,* **77**, 90.

Davis Rabosky AR, Moore TY, Sánchez-Paredes CM, Westeen EP, Larson JG, Sealey BA, Balinski BA (2021) Convergence and divergence in anti-predator displays: A novel approach to quantitative behavioral comparison in snakes. *Biological Journal Linnaean Society* **132**, 811–828.

Delaney DM (2019) Antipredation behavior covaries with body size in Neotropical snakes. *Amphibia-Reptilia* **40**, 437–445.

Díaz-Ricaurte JC, Serrano FC, Fiorillo BF (2018) *Clelia clelia* (Daudin, 1803). *Catálogo de anfibios y reptiles de Colombia* **4**: 23–31.

Díaz-Ricaurte JC, Arteaga A, 2021. Common Mussurana (*Clelia clelia*). In: Arteaga A, Bustamante L, Vieira J, Guayasamin JM, editors. *Reptiles of Ecuador: Life in the middle of the world*. Available from: www.reptilesofecuador.com.

Dinerstein, E, et al. (2017) An ecoregion-based approach to protecting half the terrestrial realm. *BioScience* **67**, 534–545.

Durso AM, Mullin SJ (2014) Intrinsic and Extrinsic Factors Influence Expression of Defensive Behavior in Plains Hog-Nosed Snakes (*Heterodon nasicus*). Ethology **120**, 140–148.

Endler JA (1986) Defense against predators. In: Feder ME, Lauder GV, editors. *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*. Chicago(IL): University of Chicago Press 109–134.

Esqueda LF, Natera-Muma M, Bazo S, La Marca E(2008) Ecogeographical notes on a rare species of false coral snake, *Oxyrhopus doliatus* Duméril, Bibron & Duméril, 1854. The *Herpetological Bulletin* **104**, 36–38.

Gaiarsa MP, Alencar LR, Martins M (2013) Natural history of Pseudoboine snakes. *Papéis Avulsos de Zoologia*, **53**, 261–283.

Glasser JW (1979) The role of predation in shaping and maintaining the structure of communities. *The American Naturalist* **113**, 631–641.

Gray BS (2015) A study of the defensive behaviors of free-ranging DeKay's brownsnakes, *Storeria dekayi* (Holbrook, 1836). *Journal of North American Herpetology* **2015**, 43–52.

Greene HW (1979) Behavioral convergence in the defensive displays of snakes. *Experientia* **35**, 747–748.

Greene HW (1988) Anti-predator mechanisms in reptiles. In: Gans C, Huey RB, editors. *Biology of the Reptilia.* New York (NY):John Wiley and Sons,1–152.

Grigaltchik VS, Ward AJ, Seebacher F (2012) Thermal acclimation of interactions: differential responses to temperature change alter predator–prey relationship. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4058–4064.

Hendry AP, Bolnick DI, Berner D, Peichel CL (2009) Along the speciation continuum in sticklebacks. *Journal of Fish Biology* **75**, 2000–2036.

Herzog Jr HA, Schwartz JM (1990) Geographical variation in the anti-predator behavior of neonate garter snakes, *Thamnophis sirtalis*. *Animal Behavior* **40**, 597–598.

Heynen M, Bunnefeld N, Borcherding J (2017) Facing different predators: adaptiveness of behavioral and morphological traits under predation. *Current Zoology* **63**, 249–257.

Hoverman JT, Relyea RA (2009) Survival trade-offs associated with inducible defences in snails: The roles of multiple predators and developmental plasticity. *Functional Ecology* **23**, 1179–1188.

Irwin DE, Price T (1999) Sexual imprinting, learning and speciation. *Heredity* **82**, 347–354.

Klockmann M, Günter F, Fischer K (2017) Heat resistance throughout ontogeny: body size constrains thermal tolerance. *Global Change Biology* **23**, 686–696.

Koski SE (2014) Broader horizons for animal personality research. Frontiers in Ecology and Evolution 2, 70.

Lind J, Cresswell W (2005) Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* **16**, 945–956.

Luque-Fernández CR, Villegas Paredes LN (2017) First record of the Fitzinger’s False Coral Snake, *Oxyrhopus fitzingeri* (Tschudi, 1845)(Reptilia: Dipsadidae) in Atiquipa, southwestern Peru. *Check List* **13**, 2085.

Martins M, Araujo MS, Sawaya RJ, Nunes R (2001) Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of Neotropical pitvipers (*Bothrops*). *Journal of Zoology* **254**, 529–538.

Martins M, Marques OA, Sazima I (2008) How to be arboreal and diurnal and still stay alive: microhabitat use, time of activity, and defense in Neotropical forest snakes. *South American Journal of Herpetology*, **3**, 58–67.

Marques OAV, Eterovic A, Nogueira CC, Sazima I (2015) *Serpentes do Cerrado: guia ilustrado*. Ribeirão Preto (SP):Holos Editora.

McKee CD, Hayman DT, Kosoy MY, Webb CT (2016) Phylogenetic and geographic patterns of bartonella host shifts among bat species. *Infection, Genetics and Evolution* **44,** 382–394.

Meo ID, Østbye K, Kahilainen KK, Hayden B, Fagertun CH, Poléo AB, 2021. Predator community and resource use jointly modulate the inducible defense response in body height of crucian carp. *Ecology and Evolution* **11,** 2072–2085.

Miranda RB, Klaczko J, Tonini JF, Brandão RA (2022) Escaping from predators: a review of Neotropical lizards defence traits. *Ethology Ecology & Evolution* **35**, 1–31.

Nogueira CC, et al. (2019) Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South American Journal of Herpetology* **14**, 1–274.

Oskyrko O, Mi C, Meiri S, Du W (2024) ReptTraits: a comprehensive dataset of ecological traits in reptiles. *Scientific Data*, **11**, 243.

Placyk JS (2012) The role of innate and environmental influences in shaping anti-predator behavior of mainland and insular gartersnakes (*Thamnophis sirtalis*). *Journal of Ethology* **30,** 101–108.

R Core Team, 2020. R Core Team R: a language and environment for statistical computing. Foundation for Statistical Computing.

Réale D, Reader SM, Sol D, McDougall PT, Dingemanse NJ (2007) Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**, 291–318.

Roll U, et al. (2017) The global distribution of tetrapods reveals a need for targeted reptile conservation. *Nature Ecology & Evolution* **1,** 1677–1682.

Romero GQ, Gonçalves-Souza T, Kratina P, Marino NA., Petry WK, Sobral-Souza T, Roslin T (2018) Global predation pressure redistribution under future climate change. *Nature Climate Change* **8**, 1087–1091.

Roth ED, Johnson JA (2004) Size-based variation in anti-predator behavior within a snake (*Agkistrodon piscivorus*) population. *Behavioral Ecology* **15**, 365–370.

Santos X, Feriche M, Leon R, Filippakopoulou A, Vidal-Garcia M, Llorente GA, Pleguezuelos JM (2011) Tail breakage frequency as an indicator of predation risk for the aquatic snake *Natrix maura*. *Amphibia-Reptilia* **32**, 375–383.

Saraçli S, Doğan N, Doğan İ (2013) Comparison of hierarchical cluster analysis methods by cophenetic correlation. *Journal of Inequalities and Applications* **2013**, 1–8.

Serrano FC, Pontes-Nogueira M, Sawaya RJ, Alencar LRV, Nogueira, CC, Grazziotin FG (2024) There and back again: when and how the world's richest snake family (Dipsadidae) dispersed and speciated across the Neotropical region. *Journal of Biogeography* **51, 878–893.**

Steinberg PD, Estes JA, Winter FC (1995) Evolutionary consequences of food chain length in kelp forest communities. *Proc Natl Acad Sci U.S.A.* **92**, 8145–8148.

Symonds MR, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral ecology and sociobiology*, **65**, 13–21.

Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behavior of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology* **106**, 713–728.

Toju H, Sota T (2006) Imbalance of predator and prey armament: geographic clines in phenotypic interface and natural selection. *The American Naturalist* **167**, 105–117.

Trussell GC, Smith LD (2000) Induced defenses in response to an invading crab predator: an explanation of historical and geographic phenotypic change. *Proceedings of the National Academy of Sciences* **97**, 2123–2127.

Uetz P, Freed P, Aguilar R, Hošek J (2024) The Reptile Database, http://www.reptile-database.org, Accessed [Nov 07, 2024].

Urban MC (2007) The growth–predation risk trade-off under a growing gape-limited predation threat. *Ecology* **88**, 2587–2597.

Wilson V, Guenther A, Øverli Ø, Seltmann MW, Altschul D (2019) Future directions for personality research: contributing new insights to the understanding of animal behavior. *Animals* **9**, 240.

Zocca C, Lourenço-de-Moraes R, Campos FS, Ferreira RB (2022) The high diversity and phylogenetic signal of anti-predator mechanisms of the horned frog species of

Proceratophrys Miranda-Ribeiro, 1920 (Amphibia: Anura: Odontophrynidae). *Acta Herpetologica* **17**, 77–83.

TABLES

Table 1. Defensive behaviors reported for the snake tribe Pseudoboini. BA = balling; BD = body flattening; BT = biting; BV = body vibration; CD = Cloacal discharges; CO =. Constriction; EM = Erratic movements; FS = False strike; HE = Head Elevation; HH = Hiding the head; HT = Head triangulation; IM = Immobility; LE = Locomotor escape; MI = Mimicry; NC = neck S-coil; ST = Struggle; TD = tail display; TH = thanatosis (death feigning); TV = tail vibration. Abbreviations in bold with * correspond to new behaviors for the species described in this work. List of references can be found in Supplementary material S2.

Genus	Species	Behavior	Nr of behaviors	Source
Boiruna	*Boiruna maculata*	BA, BT, EM, HH, MI	5	Gaiarsa et al., 2013; Marques et al., 2015; Tozetti et al., 2021
	Boiruna sertaneja	BT, CO, EM, HH, LE, MI	6	Lemos et al., 2009; Mesquita et al., 2013; Marques et al., 2015
Clelia	*Clelia clelia*	BT, CO, EM, HH, MI	5	Martins & Oliveira, 1998; Fraga et al 2013; Champagne et al 2021
	Clelia plumbea	BA, BT, EM, HH, MI	5	Marques et al., 2016; Tozetti et al., 2021; Weinstein et al., 2022
Drepanoides	*Drepanoides anomalus*	CD, EM, HH, LE, MI, ST	6	Martins 1996; Martins & Oliveira, 1998; Fraga et al 2013; Gaiarsa et al., 2013

Mussurana	*Mussurana bicolor*	EM, HH, MI	3	Marques et al. 2015; Marques et al., 2016; Tozetti et al., 2021
	Mussurana montana	EM, HH, MI	3	Marques et al. 2015; Tozetti et al., 2021
	Mussurana quimi	EM, HH, MI	3	Marques et al. 2015; Marques et al., 2016; Tozetti et al., 2021
Oxyrhopus	*Oxyrhopus clathratus*	BA, BD, BT, CD, EM, HH, LE, MI, ST	9	Martins et al. 2008; Gaiarsa et al. 2013; Tozetti et al., 2021
	Oxyrhopus doliatus	**BD*, CD*, EM*, LE***, MI	1	Esqueda et al. 2008; Luís Esqueda (pers. comm.); **This study**
	Oxyrhopus emberti	MI	1	Bosque 2012; Bosque et al., 2016
	Oxyrhopus erdisii	MI	1	Bosque 2012; Bosque et al., 2016

Oxyrhopus fitzingeri	**HE*, LE*,** MI, **NC***	4	Bosque 2012; Bosque et al., 2016; Luque-Fernandéz (pers. comm.); **This study**
Oxyrhopus formosus	BT, HH, MI, ST	4	Martins & Oliveira 1998; Martins et al. 2008; Tozetti et al., 2021
Oxyrhopus guibei	BA, BD, CD, EM, HE, HH, IM, LE, MI, ST, TH	11	Sazima & Abe, 1995, Gaiarsa et al. 2013; Da Silva et al. 2018, Marques et al. 2015; França et al, 2017; Pacheco 2018; Tozetti et al., 2021
Oxyrhopus leucomelas	MI	1	Bosque 2012; Bosque et al., 2016
Oxyrhopus marcapatae	MI	1	Bosque 2012; Bosque et al., 2016
Oxyrhopus melanogenys	CD, EM, HH, LE, MI, NC, ST, TD, TV	9	Martins 1996; Martins & Oliveira 1998; Franklin 2003; Gaiarsa et al. 2013; Frota et al. 2021; Rabosky et al. 2021; Tozetti et al., 2021
Oxyrhopus occipitalis	BT, BV, LE, MI, TV	5	Martins & Oliveira 1998, Torres-Carvajal et al., 2020
Oxyrhopus petolarius	**BA***, CD, EM, **FS*, HE*,** HH, IM, LE, MI, NC, ST,	**12**	Campbell & Lamar 2004; Martins et al. 2008; Abe 2010; Marques et al. 2015; Marques et al., 2016; Quezada & Arteaga 2020;

		TH		Magallón et al. 2021; **This study**
	Oxyrhopus rhombifer	BA, BD, BV, CD, EM, FS, HE, HH, IM, LE, MI, NC, ST, TD	14	Martins et al. 2008; Sawaya et al. 2008; Marques et al. 2015; França et al, 2017; Assis et al. 2020; Tozetti et al., 2021; **This study**
	Oxyrhopus trigeminus	CD, EM, HH, MI, ST	5	Martins & Oliveira 1998; Pereira-Filho 2007; Marques et al. 2015; Rabosky et al., 2016; França et al, 2017; Tozetti et al., 2021
	Oxyrhopus vanidicus	BV, LE, MI, ST, TV	5	Martins & Oliveira 1998; Gaiarsa et al. 2013; Quezada & Arteaga 2020
Paraphimophis	*Paraphimophis rusticus*	BA, HH	2	Tozetti et al., 2021
Phimophis	*Phimophis guerini*	BT, CD, EM, HH, MI	5	Gaiarsa et al., 2013; Mesquita et al., 2013; Tozetti et al., 2021
Pseudoboa	*Pseudoboa coronata*	BT, CO, EM, HH	4	Fraga et al 2013; Gaiarsa et al., 2013
	Pseudoboa haasi	BA, EM, HH, MI	4	Marques et al. 2004; Tozetti et al., 2021
	Pseudoboa martinsi	CO, EM, HH, MI	4	Fraga et al., 2013
	Pseudoboa neuweidii	BT, CD, CO, EM, HH,	10	Martins 1996, Fraga et al 2013; Gaiarsa et al., 2013; Lozan &

		IM, LE, MI, ST; TH		Angarita-Sierra 2018; Fuentes et al 2021
	Pseudoboa nigra	CD, CO, EM, HH, LE, MI, TD	7	Mesquita et al., 2013; Fiorillo et al 2021; Tozetti et al., 2021; Ugalde & Prado 2022
	Pseudoboa serrana	MI		Marques et al., 2015
Rhachidelus	*Rhachidelus brazili*	BA, BD, CD, EM, LM, HH, HT	7	Fiorillo et al., 2021; Tozetti et al., 2021
Siphlophis	*Siphlophis cervinus*	BA, CD, EM HE, HH, LE, TV	7	Fraga et al 2013; Gaiarsa et al., 2013; Santos-Costa et al., 2015; Tozetti et al., 2021
	Siphlophis compressus	BA, CD, EM, FS, HE, HH, HT, LE, MI, NC, ST, TV	12	Martins & Oliveira, 1998; Fraga et al 2013; Sena et al 2016; Abegg et al 2017; Acosta-Ortiz & Aponte-Gutiérrez 2021; Tozetti et al., 2021
	Siphlophis leucocephalus	BA, EM, HE, HH	4	Martins & Oliveira, 1998; Marques et al., 2016; Carvalho et al 2017
	Siphlophis longicaudatus	BA, CD, EM, FS, HE, HH, MI, NC, HT, TV	10	Marques et al. 2004; Pereira et al 2018; Fraga et al., 2013
	Siphlophis pulcher	BA, HE, HH, LE, MI, NC	6	Martins & Oliveira, 1998; Marques et al. 2004; Tozetti et al., 2021

	Siphlophis worontzowi	BA	1	Tozetti et al., 2021
Rodriguesophis	*Rodriguesophis iglesiasi*	EM, HH, LE, MI	4	Marques et al., 2016; Miguel Trefaut Rodrigues personal communication
	Rodriguesophis chui	EM, HH, LE, MI	4	Marques et al., 2016; Miguel Trefaut Rodrigues personal communication
	Rodriguesophis scriptorcibatus	EM, HH, LE, MI	4	Marques et al., 2016; Miguel Trefaut Rodrigues personal communication

Table 2. Model output of the PGLMM, testing for the effects of range overlap, difference in body size, difference in arboreality difference and phylogenetic distance on behavioral dissimilarity. * indicates a significant effect.

	Estimate	Adjusted SE	z	p-value
Intercept	-0.18	0.47	0.39	0.70
Size difference	0.00	0.00	1.22	0.22
Range overlap	1.30	1.35	0.96	0.34
Phylogenetic distance	0.01	0.01	0.99	0.32
Size difference x Range overlap	-0.01	0.00	2.35	0.02*
Size difference x Phylogenetic distance	0.00	0.00	0.83	0.40
Range overlap x Phylogenetic distance	-0.04	0.04	0.97	0.33
Size difference x Range overlap x Phylogenetic distance	0.00	0.00	1.90	0.06
Arboreality difference	-0.56	2.35	0.24	0.81
Arboreality difference x Phylogenetic distance	0.01	0.05	0.27	0.79
Arboreality difference x Size difference	0.00	0.00	0.31	0.76
Arboreality difference x Size difference x Phylogenetic distance	0.00	0.00	0.27	0.79
Arboreality difference x Range overlap	0.09	1.70	0.05	0.96
Arboreality difference x Range overlap x Phylogenetic distance	0.00	0.04	0.01	0.99
Arboreality difference x Size difference x Range overlap	0.00	0.00	0.05	0.96
Arboreality difference x Size difference x Range overlap x Phylogenetic distance	0.00	0.00	0.01	0.99

SUPPLEMENTARY MATERIAL

Supplementary material S1. Presence/absence matrix for each species used to perform the cluster analysis.

Supplementary material S2. List of references of Table 1.

Supplementary material S3. % of range overlap for Pseudoboini species. Subset of species that were present in the phylogeny.