Journal of Tropical Ecology

www.cambridge.org/tro

Research Article

Cite this article: Serrano FC, Diaz-Ricaurte JC, Antúnez-Fonseca CA, Garavito-David Y, Luz Garcia-Vargas A, Díaz-Morales RD, and Travaglia-Cardoso SR (2025). Home of the brave: is similarity in defensive behaviour of Neotropical snakes (Dipsadidae: Pseudoboini) predicted by sympatry? *Journal of Tropical Ecology*. **41**(e22), 1–10. doi: https://doi.org/10.1017/S026646742510014X

Received: 19 January 2024
Revised: 19 May 2025
Accepted: 11 July 2025

Keywords:
Anti-predator behaviour; ecoregion; geographical distribution; natural history; predation

Corresponding author:
Filipe C Serrano;
Email: filipe.c.serrano@gmail.com
*These authors contributed equally to this work.

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

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

[1]Departamento de Ecologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, 05508-090 São Paulo, SP, Brazil; [2]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; [3]Centro Zamorano de Biodiversidad, Departamento de Ambiente y Desarrollo, Escuela Agrícola Panamericana Zamorano, Valle de Yeguare, Francisco Morazán, Honduras; [4]Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Cidade Universitária, 79070-900, Campo Grande, MS, Brazil and [5]Museu Biológico, Instituto Butantan, 05503-900, São Paulo, SP, Brazil

Abstract

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

Introduction

Predation is one of the main selective pressures that shape communities (Glasser 1979). Consequently, anti-predator behaviours significantly shape species interactions (Glasser 1979) and hold a central position in evolutionary ecology by directly influencing survival and fitness (Lind & Cresswell 2005). These anti-predatory mechanisms are diverse, encompassing chemical defenses (e.g., venom, poison, pheromones), coloration (e.g., Batesian mimicry, Serrano *et al.* 2024a), morphological defenses such as spines and stinging hairs, and a wide repertoire of anti-predatory behaviours ranging from fleeing to thanatosis (Cloudsley-Thompson 1996; Durso & Mullin 2014). These anti-predatory behaviours depend on diverse morphological and behavioural components (Blomberg *et al.* 2003) and are under strong selection (Alcock 2009), thus representing a fundamental component of fitness (Réale *et al.* 2007). Nevertheless, the contextual components of animal behavioural 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, behaviour often varies amongst species of the same clade (Blomberg *et al.* 2003). Furthermore, defensive behaviours may have a higher fitness in a specific context but lower fitness in others (Hoverman & Relyea 2009), such as rattlesnakes being less likely to engage in rattling behaviour in areas of high human activity (Atkins *et al.* 2022). The ability to display different anti-predator behaviours may be important for an effective defense (Heynen *et al.* 2017) and defensive behaviour 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 behaviours (Toju & 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 behavioural 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 the population level) but not on interspecific differences (Herzog & Schwartz 1990; Placyk 2012). These interspecific differences are worth analysing, especially in taxa with broader geographical ranges, since different environmental conditions may have different predatory pressures (Placyk 2012; Moura *et al.* 2023). This variation of predation pressure should therefore be a driver of defensive behaviour across space. For example, biotic interactions are thought to be stronger at lower latitudes, where temperatures are higher and climate is less (Romero *et al.* 2018), and thus metabolic rates might impose different cost-efficiency of defensive behaviours (Delaney 2019). This is supported by deliberate tail loss of limbless reptiles being reported more for warmer regions (Moura *et al.* 2023) 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.* 2023). On the contrary, 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 drive the evolution of distinct traits in prey populations (Placyk 2012). Furthermore, predatory pressure is also linked to large-greescale characteristics such as climate and vegetation structure in limbless reptiles (Moura *et al.* 2023), favouring similar defensive behaviours 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 behaviours, which has been shown for marine gastropods (Aguilera *et al.*, 2019). However, even though geographical overlap has been suggested as a good predictor of similarity in defensive behaviours (Greene 1979), this hypothesis has never been tested.

Among vertebrates, snakes exhibit a highly varied repertoires of defensive behaviours to avoid predation, likely due to the diverse array of both vertebrate and invertebrate predators as well as a lack of social structures (e.g., herding in ungulates or mobbing in birds), which have likely shaped the evolution of these defenses (Greene 1979, Greene 1988). Documenting and reporting anti-predator behaviours of snakes in diverse regions is essential to better understand their behavioural 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 behaviours (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 (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 geographical 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 behaviour might be spatially structured.

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

Materials and methods

Literature review and new defensive behaviours

To compile all the defensive behaviours 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 behaviour for species using a combination of the terms 'defensive display', 'natural history', 'neotropical snake', 'false coral snake', 'Pseudoboini, 'behaviours' and 'defensive behaviour', in English, Portuguese and Spanish regardless of year. Behaviours were included as reported, grouping them whenever redundant (e.g., 'body depression' and 'body flattening'). We furthermore describe new unreported defensive behaviours for three species from personal field observations and personal communications.

Statistical analysis

Using compiled defensive behaviour 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; Supp. Mat. S1) to generate a matrix of cophenetic distance between species, as dissimilarity in defensive behaviour. This method uses proportional averaging weighted by the number of taxa in each cluster, with resulting clustering species indicating a higher similarity in defensive behaviours than with species in other clusters. Locomotor escape was considered as present for all species since it is the first line of defense in snakes, although often not reported in literature, while mimicry was not included 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.

To assess whether geographical overlap predicts congruence in defensive behaviour, we estimate this parameter between each pair of species with at least one reported defensive behaviour. 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 geographical overlap by dividing the area of the geographical intersection of each pair of species by the total area of the geographical 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 a macrohabitat dissimilarity matrix, using a Euclidean UPGMA (Saraçli *et al.* 2013; Supp. Mat. S1).

We included relevant ecological traits potentially linked to defensive behaviour: 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 behaviour, with larger individuals exhibiting higher levels of aggression and number of anti-predatory behaviours (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 behaviour 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.* 2024b) to generate pairwise phylogenetic distances for each species present in the phylogeny. We used a generalised linear mixed model (GLMM) approach to test if dissimilarity in defensive behaviour is predicted by the interaction of geographical 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 behaviour 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 behaviour and were present in the phylogeny. Before inclusion in the GLMM, we tested collinearity between variables with Pearson's Correlation and excluded ecoregion similarity due to collinearity with geographical overlap ($r > 0.6$). We then performed full-model averaging using the package 'MuMIn' (Barton 2020) since it can provide more reliable confidence intervals compared to model selection and it lessens issues with over-complex models, especially in behavioural ecology (Symonds & Moussalli 2011). Additionally, in order to assess whether the number of reported behaviours could be biased towards widespread species, we performed a phylogenetic generalised linear mixed model (PGLMM) to test the relationship between the number of reported behaviours 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 behaviours

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 behaviour 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. Balling involves tight coils in a spherical shape (Fig. 1A), and differs from head-hiding where the snake (here an *O. rhombifer* hides its head under loose coils and has an overall flatter body position (Fig. 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 an S-shape, raised its head and made lateral movements, shortly after which it tried to escape. This is the first detailed description of this behaviour 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).

Literature review

Our literature review of anti-predatory behaviours in the study species, belonging to the snake tribe Pseudoboini, revealed the presence of 19 distinct defensive anti-predatory behaviours. These observed behaviours correspond to the known repertoire for this tribe and encompass: balling (BA); body flattening (BD); biting (BT); body vibration (BV); cloacal discharges (CD); constriction (CO); erratic movements (EM); false strike (FS); head elevation (HE); hiding the head (HH); head triangulation (HT); immobility (IM); locomotor escape (LE); mimicry (MI); neck S-coil (NC); struggle (ST); tail display (TD); thanatosis (death feigning) (TH); and tail vibration (TV). We found data on defensive behaviour for 41 species of 11 genera (83.7% and 100%, respectively) of Pseudoboini snakes (Table 1). Only 22 species had simultaneously reported defensive behaviour and were present in the phylogeny. The species for which a higher number of behaviours has been reported was *Oxyrhopus rhombifer,* with 14, followed by *Siphlophis compressus* and *O. petolarius,* both with 12. Among the reported defensive behaviours for Pseudoboini species, the most commonly reported were head-hiding, erratic movements, cloacal discharges, and balling (Figure 2).

The UPGMA dendrogram of behavioural dissimilarity of this subset yielded two major clusters (Figure 3A), with one comprising only *Paraphimophis rusticus* + *Oxyrhopus fitzingeri* + *Siphlophis pulcher*). The other cluster was composed of all the other 19 species, divided into two sub-clades: one comprising seven species, featuring all three species from the *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 subclades.

The average geographical overlap between species was 18.8% (± 23.7%) and varied from 0 (e.g., between *Oxyrhopus clathratus* and *O. melanogenys*) and 89.2% (between *Siphlophis compressus* and *S. cervinus*) (Supp. Mat. S3). Overall, average geographical overlap between species of the same genus (19.5% ± 25.3%, $n = 30$ pairs) was similar to species belonging to different genus (18.7% ±

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

23.6%, $n = 201$ pairs) Our analysis showed that geographical overlap by itself did not significantly predict dissimilarity in defensive behaviour (Table 2). However, the interaction of geographical overlap and difference in body size (estimate = -0.01, $p = 0.02$) had a significant negative effect, albeit weak, on the dissimilarity in defensive behaviour (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 behaviour (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.* 2024b), they do not cluster together regarding behavioural dissimilarity. On the contary, species from the *Siphlophis* genus (excluding *S. pulcher*) are clustered both phylogenetically and in behavioural dissimilarity, albeit with different relationships among them. Our PGLMM also showed that species with a higher number of reported behaviours did not have wider distributions ($p = 0.17$).

Discussion

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

Behaviours such as locomotor escape, cloacal discharge and head-hiding were more than three times as frequent than thanatosis, body vibration, body flattening or tail display. Although all these aforementioned behaviours are considered non-intimidating defensive behaviours (Gray 2015), they may have different trade-offs in cost and success that reflect their reported frequency and the moment they are employed. While behaviours 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 behaviours shown before contact with a predator (Gray 2015). In contrast, behaviours such as balling, head-hiding and thanatosis likely have a low energetic cost as they are meant to deter or minimize predatory attacks, but these behaviours have the cost of leaving the snake more vulnerable to predation. These are often employed after physical contact, when escape is no longer feasible (Greene 1988). To corroborate if the frequency of these behaviours reflects different perceptions of threat, further studies should experimentally test the progression of these behaviours (see Davis Rabosky *et al.* 2021).

We corroborated our hypothesis that there is a relationship between defensive behaviour with co-occurrence at a larger scale (sympatry), which had been previously suggested (Greene 1979) but never tested. However, this similarity in defensive behaviour for sympatric species is only strongly supported for species of similar size. Anti-predator behaviour of snakes had already been shown to be linked to body size (Delaney 2019), but our work is the first to assess how it plays a role in the similarity in defensive behaviour across sympatric species. While being large-bodied increases the chances of being detected by predators, it also decreases the probability of capture by predators as well as posing a higher risk (Urban 2007). Body size strongly impacts

Table 1. Defensive behaviours 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 behaviours for the species described in this work. List of references can be found in Supplementary Material S2

Genus	Species	Behaviour	N of behaviours	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	4	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, TH	12	Campbell & Lamar 2004; Martins *et al.* 2008; Abe 2010; Marques *et al.* 2015; Marques *et al.* 2016; Quezada & Arteaga 2020; 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, IM, LE, MI, ST; TH	10	Martins 1996, Fraga *et al.* 2013; Gaiarsa *et al.* 2013; Lozan & 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	1	Marques *et al.* 2015

(*Continued*)

Table 1. (*Continued*)

Genus	Species	Behaviour	N of behaviours	Source
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 (pers. comm.)
	Rodriguesophis chui	EM, HH, LE, MI	4	Marques *et al*. 2016; Miguel Trefaut Rodrigues (pers. comm.)
	Rodriguesophis scriptorcibatus	EM, HH, LE, MI	4	Marques *et al*. 2016; Miguel Trefaut Rodrigues (pers. comm.)

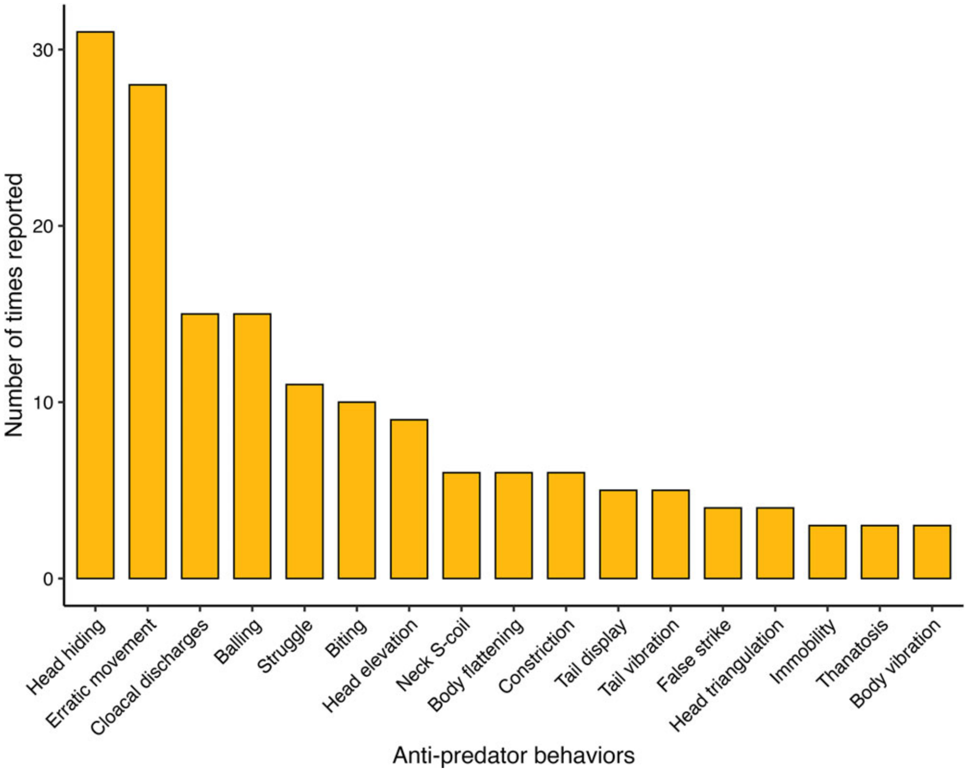

Figure 2. Number of species of Pseudoboini reported to show each defensive behaviour. For more details, see Table 1. Locomotor escape was excluded since it is often not reported, and mimicry was excluded due to being a passive defensive mechanism, but not a behaviour *per se*.

ecophysiological parameters such as behavioural thermal tolerances (Klockmann *et al.* 2017) thus activity time and period and consequently exposure to predators (Grigaltchik *et al.* 2012).

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 behaviour. This absence of relationship between phylogeny and defensive behaviour may also be influenced by geographical overlap being similar between congeneric and non-congeneric species, which suggests that phylogenetic relatedness does not determine geographical overlap of Pseudoboini snakes, at least at broad scales. Other studies have shown that defensive behaviour can vary depending on the perceived threat and that it is one of the most labile traits (Brodie & Russell 1999; Blomberg *et al.* 2003;

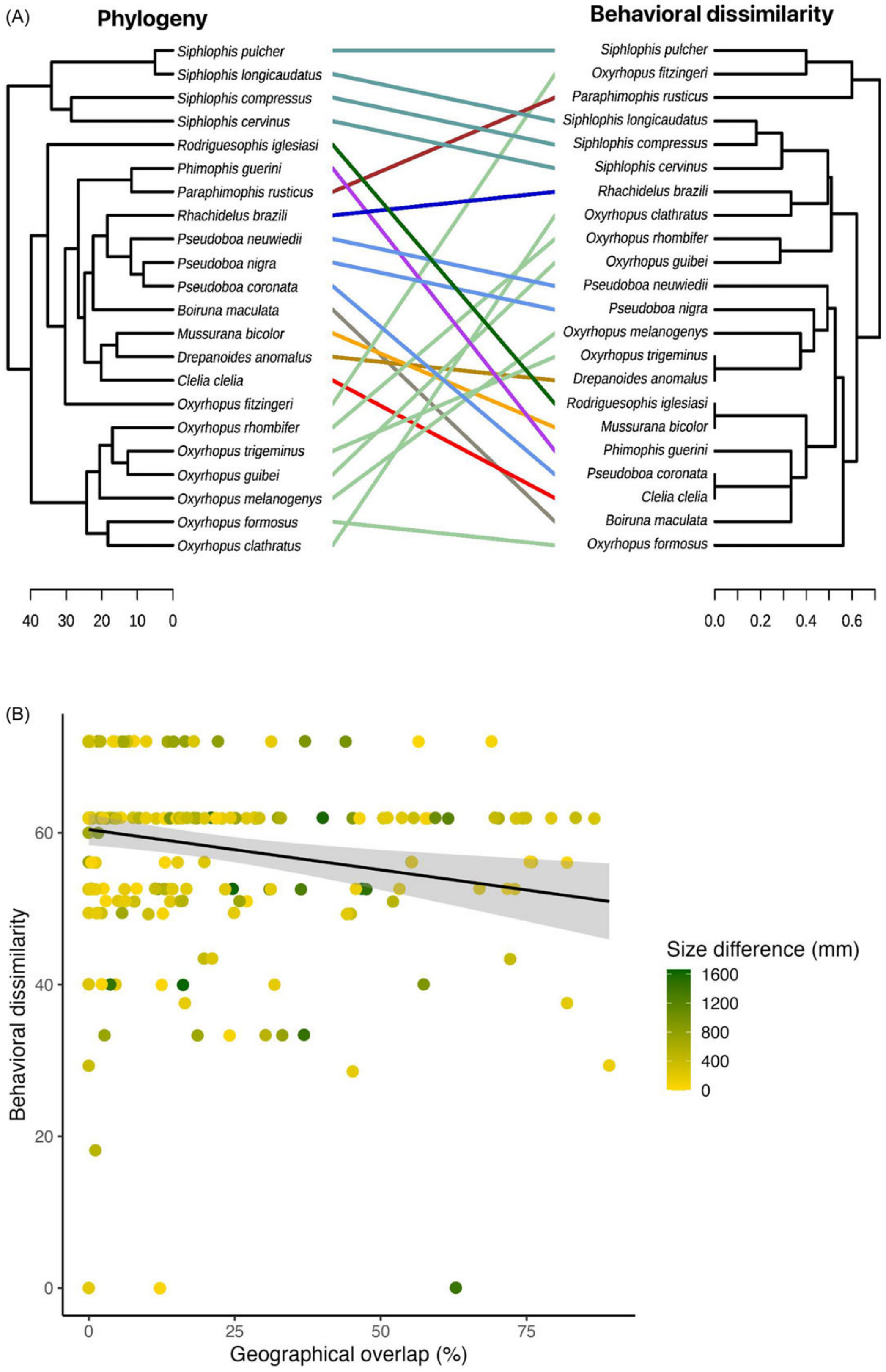

Figure 3. A) Correspondence of phylogeny (left; scale in million years, Serrano *et al.* 2024b) and behavioural dissimilarity (right; scale in which the higher the value, the more dissimilar the species are) for species of the Pseudoboini tribe. Lines connect the same species in both clusters (phylogeny and behavioural dissimilarity). Different colours represent different genera. Notice the two major clusters of dissimilarity of behaviour, with one comprising only three species from different genera and the other with the other 19 species divided into different sub-clades. B) Behavioural dissimilarity between snakes from the Pseudoboini tribe decreases with geographical overlap and size difference (darker colours indicate larger size differences). Even highly sympatric species (those with >75% of geographical overlap) show marked behavioural dissimilarity.

Table 2. Model output of the PGLMM, testing for the effects of geographical overlap, difference in body size, difference in arboreality difference and phylogenetic distance on behavioural 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
Geographical overlap	1.30	1.35	0.96	0.34
Phylogenetic distance	0.01	0.01	0.99	0.32
Size difference x Geographical overlap	−0.01	0.00	2.35	0.02*
Size difference x Phylogenetic distance	0.00	0.00	0.83	0.40
Geographical overlap x Phylogenetic distance	−0.04	0.04	0.97	0.33
Size difference x Geographical 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 Geographical overlap	0.09	1.70	0.05	0.96
Arboreality difference x Geographical overlap x Phylogenetic distance	0.00	0.04	0.01	0.99
Arboreality difference x Size difference x Geographical overlap	0.00	0.00	0.05	0.96
Arboreality difference x Size difference x Geographical overlap x Phylogenetic distance	0.00	0.00	0.01	0.99

Martins *et al.* 2008), even though for some groups there is a phylogenetic component in anti-predator behaviour (Davis Rabosky *et al.* 2021; but see Araújo & Martins 2006). Furthermore, arboreality was not present in the best models that explain dissimilarity in defensive behaviour. Even though arboreal snakes typically have a greater diversity of defensive behaviours, which has been linked to higher predation pressures (Moura *et al.* 2023), 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 behaviours, in contrast with diurnal species, which often use significantly more diverse behaviours (Martins *et al.* 2008).

We found that the number of reported anti-predator behaviours is not correlated with range size. This suggests that the potential for reporting biases—whereby more widespread species might be studied more extensively and have more behaviours documented—is not significantly influencing our findings. Therefore, our conclusions are likely robust across species with different range sizes, as even well-studied, widespread species do not consistently show a higher number of reported behaviours. 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 behaviours, especially for species with restricted ranges such as *O. erdisii, O. leucomelas* and *O. marcapatae* (see distribution in Uetz *et al.* 2024). More in-depth investigation of the fitness costs and benefits of each anti-predator behaviour is also required to fully evaluate the geographical patterns of predator–prey interactions (Arnold 1992; Roth & Johnson 2004). Even though previous studies have studied the geographical variation of anti-predator behaviour, most have focused only on different populations of the same species (Herzog & Schwartz 1990; Placyk 2012), with our study being among the first to test inter-species differences. Herein, we show that space, especially at a large scale, is an important component of anti-predator behaviour. We hope that our work stimulates future research on defensive strategies, as our findings can be broadly applied to and tested in other taxa.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S026646742510014X

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

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

Author contributions. FCS and JCDR planned the study; YGD, ALG, RDDM and SRTC recorded the new defensive behaviours; 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, JCDRs 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.

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

Competing interests. The authors declare no conflict of interest.

References

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

Aguilera MA, Weiß M and Thiel M (2019) Similarity in predator-specific anti-predator behavior in ecologically distinct limpet species, *Scurria viridula* (Lottiidae) and (Fissurellidae)., 1–13.

Araújo MS and 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.

Atkins MC, Howarth CR, Russello MA, Tomal JH and Larsen KW (2022) Evidence of intrapopulation differences in rattlesnake defensive behavior across neighboring habitats. *Behavioral Ecology and Sociobiology* **76**, 3.

Aubret F, Michniewicz RJ and 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 and Ives AR (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* **57**: 717–745.

Bosque RJ, Noonan BP and 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 and 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 and McGillycuddy M (2023) Package 'glmmtmb'. R Packag Vers 1, 7.

Cloudsley-Thompson JL (1996) *Secondary Anti-Predator Devices*. In: Cloudsley-Thompson JL, (ed.), *Biotic Interactions in Arid Lands. Adaptations of Desert Organisms*. Heidelberg (BER): Springer 67–86.

Davis Rabosky AR, Moore TY, Sánchez-Paredes CM, Westeen EP, Larson JG, Sealey BA and 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 and Fiorillo BF (2018) Clelia clelia *(Daudin, 1803)*. In: *Catálogo de anfibios y reptiles de Colombia* **4**: 23–31.

Díaz-Ricaurte JC and Arteaga A (2021). *Common Mussurana (Clelia clelia)*. In: Arteaga A, Bustamante L, Vieira J, Guayasamin JM, (eds.), *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 and Mullin SJ (2014) Intrinsic and extrinsic factors influence expression of defensive behavior in plains hog-nosed snakes (*Heterodon nasicus*). *Ethology* **120**, 140–148.

Esqueda LF, Natera-Muma M, Bazo S and 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 and 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, (eds.), *Biology of the Reptilia*. New York (NY): John Wiley and Sons 1–152.

Grigaltchik VS, Ward AJ and 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.

Herzog Jr HA and 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 and Borcherding J (2017) Facing different predators: adaptiveness of behavioral and morphological traits under predation. *Current Zoology* **63**, 249–257.

Hoverman JT and 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.

Klockmann M, Günter F and 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 and Cresswell W (2005) Determining the fitness consequences of antipredation behavior. *Behavioral Ecology* **16**, 945–956.

Luque-Fernández CR and 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 and 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 and 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 and Sazima I (2015) Serpentes do Cerrado: guia ilustrado. Ribeirão Preto (SP): Holos Editora.

McKee CD, Hayman DT, Kosoy MY and 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 and 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 and Brandão RA (2022) Escaping from predators: a review of Neotropical lizards defence traits. *Ethology Ecology & Evolution* **35**, 1–31.

Moura MR, *et al.* (2023) Unwrapping broken tails: Biological and environmental correlates of predation pressure in limbless reptiles. *Journal of Animal Ecology* **92**, 324–337.

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 and 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 and 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 and Roslin T (2018) Global predation pressure redistribution under future climate change. *Nature Climate Change* **8**, 1087–1091.

Roth ED and 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 and 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 and 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 and Grazziotin FG (2024b) 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.

Serrano FC, Farhat C, Díaz-Ricaurte JC and Martins M (2024a) Citizen science and color pattern analysis indicate unreported Batesian mimicry between Neotropical snakes. *Biotropica* **56**, e13380.

Steinberg PD, Estes JA and Winter FC (1995) Evolutionary consequences of food chain length in kelp forest communities. *Proceedings of the National Academy of Sciences* **92**, 8145–8148.

Symonds MR and 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 and Pellis SM (2000) The influence of phylogeny on the social behavior of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology* **106**, 713–728.

Toju H and 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 and 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 and 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 and 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 and 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.