

# Body shape and diet reflect arboreality degree of five congeneric snakes sympatric in the Atlantic forest

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## Funding information

Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Number: 300992/79-ZO and 312359/2020-9-EL; Fundação de Amparo à Pesquisa do Estado de São Paulo, Grant/Award Number: 04/12135-9 and 20/12658-4; FAPESP

**Associate Editor:** Jennifer Powers

**Handling Editor:** Lisa Schulte

## Abstract

The substrate use by animals may influence both their morphology and diet. Species of the genus *Chironius* are among the most conspicuous frog-eating, arboreal snakes in South America. The aim of the present study was to investigate whether diet and morphology relate to substrate use in five sympatric *Chironius* species from the Atlantic Forest. Our hypothesis is that habitat pressure is strong enough so that even closely related species will present differences. We collected morphological and diet data from specimens of *C. bicarinatus*, *C. exoletus*, *C. foveatus*, *C. fuscus*, and *C. laevicollis* housed in scientific collections. Information on habitat use were obtained by monitoring free-ranging animals using thread-bobbins and also from the literature. Our results demonstrate that *C. foveatus* is the most arboreal species, and *C. laevicollis* is the most terrestrial among the five studied species. *Chironius foveatus* is the slenderest, with one of the longest relative tail lengths, the narrowest ventral scales, the highest vertebral density, the largest eye diameter, green body color, and diet based on tree frogs (Hylidae). These traits indicate a higher arboreality for this species. On the other extreme, *C. laevicollis* is the stoutest species, and has the shortest tail, the largest head, the lowest vertebral density, and diet based on ground-living frogs (Leptodactylidae). These traits indicate pronounced terrestriality for this species. The other three species have traits intermediate between the extremes showed by *C. foveatus* and *C. laevicollis*. We found evidence for a close relationship between arboreality or terrestriality, morphology, and diet.

## KEYWORDS

*Chironius*, Colubridae, ecology, frog-eating, morphology

## 1 | INTRODUCTION

Habitat plays a key role in the evolution of body shape in vertebrates (Cadle & Greene, 1993; Lillywhite & Henderson, 1993; Miles & Ricklefs, 1984; Moermond, 1979; Wikramanayake, 1990),

and snakes are a good example of it, considering their large adaptive radiation and morphological diversification (Greene, 1997). The habitat, in particular the substrate used by snakes, seems to have influenced body shape modifications (Cadle & Greene, 1993), and several morphological syndromes may be recognized (cf.

Cadle & Greene, 1993; Guyer & Donnelly, 1990; Lillywhite & Henderson, 1993; Martins et al., 2001; Vitt & Vangilder, 1983). Arboreal species, belonging to different phylogenetic lineages, share morphological syndromes (Cadle & Greene, 1993), such as large eyes, slender and compressed body and long tail, usually accompanied by a green, brownish or grayish color similar to leaf or twigs (Lillywhite & Henderson, 1993; Marques et al., 2019; Martins et al., 2008; Sheehy III et al., 2015). Therefore, it is reasonable to consider that such morphological traits provide advantages of performance on arboreal substrates (cf. Alencar et al., 2017; Guyer & Donnelly, 1990; Lillywhite, 2014; Lillywhite & Henderson, 1993; Martins, 1994; Peters, 1960).

In addition to external morphology, the internal anatomy of climbing snakes can also be modified. This has been observed in the size and position of the heart and vertebral density (Guimarães et al., 2013; Hampton, 2011; Lillywhite et al., 2012; Lillywhite & Henderson, 1993). Aside from relating to morphology, substrate use also reflects diet composition in snakes (Hartmann & Marques, 2005), and prey items may be associated with the foraging strategies of each species (Cadle & Greene, 1993; Greene, 1983; Miles & Ricklefs, 1984; Pough & Groves, 1983; Shine, 1988). Arboreal snakes usually rely on small prey (Greene, 1983; Henderson et al., 1979; Marques & Sazima, 2004; Pough & Groves, 1983). For instance, pit vipers of the genus *Bothrops* display great variation in prey types, and two of the most arboreal and slender species in the genus, *B. bilineatus* and *B. taeniatus*, feed on treefrogs, while stouter terrestrial species, such as *B. alternatus*, *B. cotiara* e *B. fonsecai*, feed on mammals (Martins et al., 2001; Martins et al., 2002).

*Chironius* Fitzinger 1826 is a monophyletic genus of the Colubridae family, which includes 23 recognized species (Uetz et al., 2021) that inhabit mainly forested areas from the northern coast of Honduras and Brazil to Uruguay and northeastern Argentina (Klaczko et al., 2014). These frog-eating snakes are among the most conspicuous arboreal snakes in South America, due to their large body size and abundance (Dixon et al., 1993; Henderson et al., 1979). In the field, these snakes are usually found resting perched on branches at any time of day or active either on the ground or on vegetation searching for prey during daylight (Dixon et al., 1993; França & Braz, 2013; Marques et al., 2017; Marques & Sazima, 2004; Torres-Carvajal et al., 2019).

Given the close relationship between ecological and morphological patterns, some degree of variation would be expected even in closely related species, and studying species' traits may be greatly instrumental for understanding the evolution within a phylogenetic lineage such as *Chironius*. Although snakes of the genus *Chironius* are widely recognized as climbers, it is still unclear whether the species differ in the frequency of use of each substrate in their habitat. Previous information on interspecific differences in morphology and prey consumed suggest differences in the proportion of ground and vegetation use by species (Dixon et al., 1993; Marques & Sazima, 2004), but a more detailed analysis is necessary to clarify this question. Thus, the aim of the present study is to investigate if five sympatric *Chironius* species from the Atlantic Forest (Figure 1) differ in the use of forest strata. Our hypothesis is that habitat pressure is strong enough so that even

closely related species will present differences. In this way, we predict that diet, body morphology and substrate use will be different among species, reflecting terrestrial and arboreal habits.

## 2 | METHODS

Among the fifteen species of *Chironius* occurring in Brazil, nine are found in the Atlantic Forest (Nogueira et al., 2019). To conduct our study, we selected five sympatric species from the Atlantic Forest in the Serra do Mar range, namely *C. bicarinatus*, *C. exoletus*, *C. foveatus*, *C. fuscus*, and *C. laevicollis* (Figure 1). We obtained morphological, diet and substrate use measures that we detail below.

### 2.1 | Morphology

Morphological data were obtained from specimens housed in herpetological collections, as follows: Coleção Alphonse Richard Hoge do Instituto Butantan (IB/ São Paulo), Museu de Zoologia da Universidade de São Paulo (MZUSP/ São Paulo), Museu de História Natural do Capão da Imbuia (MHNCI/ Curitiba), and Museu Nacional (MNRJ/ Rio de Janeiro). Analyzed specimens come from Atlantic Forest areas in the Serra do Mar range (19° 23' 27" S and 40° 4' 17" W to 25° 52' 58" S 48° 34' 30" W). The following morphological data were sampled: sex, snout-vent length (SVL), tail length (TL), trunk length (TKL), body mass (BM), head length (HL), head width (HW), eye diameter (ED), body height (BH), body width (BW), ventral scale width (VSW), number of ventral scales (NVS), and number of subcaudal scales (NSS). The variables BH, BW, and VSW were taken from midbody. All variables were sampled using a measuring tape (precision of 1 mm), digital caliper (precision of 0.05 mm), and portable dynamometers (precision of 1 g). Body mass (BM) was measured after draining the excess of preservative liquid using paper towel (Martins et al., 2001) for an arbitrary period of two hours. Females with eggs or ovarian follicles in advanced stage were excluded from stoutness analyses. Our sample included 68 specimens of *C. bicarinatus* (40 males and 28 females), 45 *C. exoletus* (14 males and 31 females), 36 *C. foveatus* (24 males and 12 females), 57 *C. fuscus* (34 males and 23 females), and 82 *C. laevicollis* (37 males and 45 females). In order to avoid ontogenetic biases, only adult animals were considered exclusively in these morphological analyses. Data on sexual maturity for other species of the genus indicate that the average SVL of mature snakes is around 700 mm (Pinto et al., 2010). Therefore, we examined only those animals whose SVL was equal to or larger than 700 mm.

The number of ventral scales in Colubroidea snake's body correspond to the number of vertebrae (Alexander & Gans, 1966). Therefore, ventral scale counting was used for investigating the relationship between habitat use, number of vertebrae, and vertebral density (number of vertebrae per length unity). We also tested for the occurrence of pleomerism in the five species of *Chironius*, that is, whether the number of scales increase with body size. For this reason, we used both juveniles and adults of all sizes in vertebral analyses. In this sense, we used 97

**FIGURE 1** Five sympatric species of *Chironius* in the Atlantic Forest. In increasing order of arboreality. *Chironius laevicollis* (top left). *C. fuscus* (top right). *C. bicarinatus* (center). *C. exoletus* (bottom left). And *C. foveatus* (bottom right)



*C. bicarinatus* (52 males, and 45 females), 51 *C. exoletus* (36 males, and 16 females), 38 *C. foveatus* (20 males, 18 and females), 15 *C. fuscus* (11 males, and 4 females), and 11 *C. laevicollis* (5 males, and 6 females).

## 2.2 | Diet

Information on diet was obtained from stomach contents of specimens housed in herpetological collections, through ventral incision. For diet analyses, we used both juveniles and adults, totaling 196 specimens of *C. bicarinatus*, 195 of *C. exoletus*, 88 of *C. foveatus*, 151 of *C. fuscus*, and 90 of *C. laevicollis*. The percentage of individuals with stomach content per species was 5.1%, 13.8%, 7.9%, 5.3%, and 6.7%, respectively. Whenever possible, prey mass was also estimated. Each prey was removed for further identification to the lowest taxonomic level possible. We classified anuran prey according to their habitat use based on data from the literature (e.g., Haddad & Sawaya, 2000; Haddad & Sazima, 1992; Heyer et al., 1991). Anuran prey found as stomach content belonged either to the family Leptodactylidae or Hylidae, and we calculated the percentages of each one of them for each *Chironius* species. During the day hylid tree frogs usually rest on vegetation, while leptodactylid frogs usually rest on the ground. *Chironius* snakes are active diurnal foragers, thus we assumed that the predominance of one of these anurans in the diet was indicative of the substrate on which snakes forage.

## 2.3 | Habitat use

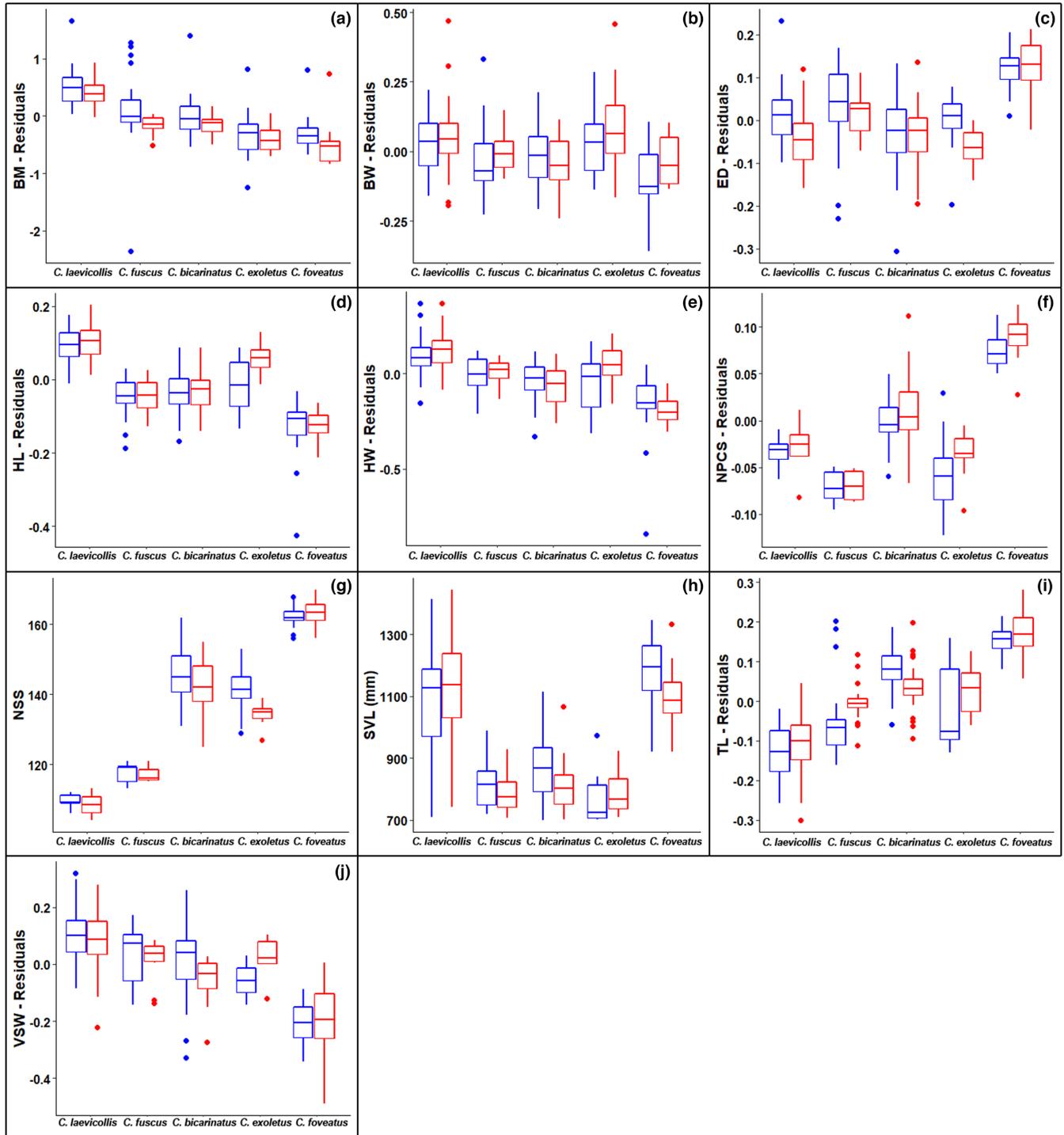
Habitat use was inferred by gathering data from the literature and from field observations on adults of *Chironius*. Information was obtained by us, by interviewing field herpetologists, and also from the literature (Bovo & Sueiro, 2012; Carvalho-Silva & Fernandes, 1994; Di-Bernardo, 1998; Hartmann, 2005; Hartmann et al., 2009a, 2009b; Marques & Sazima, 2004; Morato, 2005; Muscat et al., 2017; Oliveira, 2008; Rocha et al., 1999; Sazima & Haddad, 1992). Such information was grouped in two categories: (1) total number of individuals found on each substrate, and (2) considering only active individuals observed. Such categorization was necessary to discriminate between active and inactive individuals.

Additionally, we carried out field monitoring of free-ranging individuals of *Chironius*, using thread-bobbins (with 150 meters of line) to investigate substrate use (e.g., Tozetti & Martins, 2007). Such field study was performed in the Projeto Dacnis private reserve in Ubatuba municipality (−23.462947, −45.132943; WGS84; 15 m - 500m a.s.l.) during the period from 2015 to 2017. We monitored the following snakes: two *C. exoletus* (♂), five *C. foveatus* (3♀ + 2♂), five *C. fuscus* (3♀ + 2♂), and one *C. laevicollis* (♀). Each individual was monitored until the end of the line (or until it was broken), recording every day the height used in the vegetation, which was measured by a laser distance meter.

## 2.4 | Data analyses

We made all comparisons on individuals of the same sex, due to sexual dimorphism found in *Chironius* (Dixon et al., 1993). All continuous variables were log-transformed. SVL was compared intra- and interspecifically by two-way Analysis of Variance (ANOVA). Analysis

of Covariance (ANCOVA) was used to control for size effects (independent) on body shape (dependent) variables (Losos, 1990; Zar, 1999). Snout-vent length (SVL) was used as covariable for the variables TL and VSW, whereas for BM, the covariable was TTL. For HL, HW, and NVS the covariable TKL was used, whereas the covariable HL was used for the variable ED. The covariable BH was



**FIGURE 2** Five sympatric species of *Chironius* in the Atlantic Forest. Boxplots showing the residuals of body mass (BM; in a). Body width (BW; in b). Eye diameter (ED; in c). Head length (HL; in d). Head width (HW; in e). Number of ventral scales (NVS – In f). Tail length (TL; in i). And ventral scale width (VSW; in j). And also the number of subcaudal scales (NSS; in g) and snout-vent length (SVL; in h). Red boxplots represent the females, and blue one represent the males

used for the variable BW, and TL was used as a covariable for NSS. Whether no significant effect of the covariate upon the dependent variable was found, we conducted two-way ANOVA. Bonferroni's test was used as a post-hoc test whenever necessary. For ANOVA, and ANCOVA,  $p$ -values below 0.05 were considered significant. For the Bonferroni proceeding ANCOVA, we used,  $p$  adjusted, so that  $p$ -values below 0.01 and 0.025 were considered significant in interspecific comparisons. Arithmetic means were reported in case there was no interaction between the dependent variable with the covariate. Otherwise, adjusted means were reported. All statistical tests were based on Zar (1999). All analyses were performed in R (R Core Team, 2021), using the packages "ggplot2" (Wickham, 2016), "tidyverse" (Wickham et al., 2019), "dplyr" (Wickham et al., 2021), "emmeans" (Lenth, 2021), "rstatix" (Kassambara, 2021).

### 3 | RESULTS

#### 3.1 | Morphology

Morphometric data revealed interspecific differences among the five species analyzed, as detailed below. Due to the complexity of pairwise comparisons, we only show here the main results (Figures 2 and 3; but see all data in Tables 1 to 3). Both males and females of *C. foveatus* and *C. laevis* are the largest among the studied species (ranges: 920–1345 mm, and 710–1445 mm, respectively;  $F_{[4,277]} = 3.316$ ,  $p = .000$ ; Tables 1 and 2). *Chironius laevis* had the shortest TL ( $F_{[4,225]} = 3.623$ ,  $p = .000$ ), while *C. foveatus* had the longest TL ( $F_{[4,225]} = 3.623$ ,  $p < .016$ ) of all but *C. bicarinatus* ( $p > .029$ ).

*Chironius laevis* was the heaviest species ( $F_{[4,222]} = 44.614$ ,  $p > .000$ ), and also had the largest head (HL:  $F_{(4,245)} = 4.655$ ,  $p = .000$ ; HW:  $F_{(4,241)} = 3.238$ ,  $p \leq .025$ ). Females of *C. exoletus* had longer heads than females of *C. bicarinatus*, *C. foveatus* and *C. fuscus* ( $F_{(4,245)} = 4.655$ ,  $p = .000$ ). They also had wider heads than

*C. bicarinatus* and *C. foveatus* ( $F_{(4,241)} = 3.238$ ,  $p < .001$ ). Females of *Chironius foveatus* had the largest ED of the five species ( $F_{[4,246]} = 30.298$ ,  $p < .001$ ).

Females of *C. foveatus* had the narrowest VSW ( $F_{[4,166]} = 46.692$ ,  $p < .005$ ), and the males had narrower VSW ( $p = .000$ ), except for *C. exoletus* ( $p = .193$ ). *C. laevis* was the stoutest species ( $F_{[4,256]} = 9.356$ ,  $p = .001$ ).

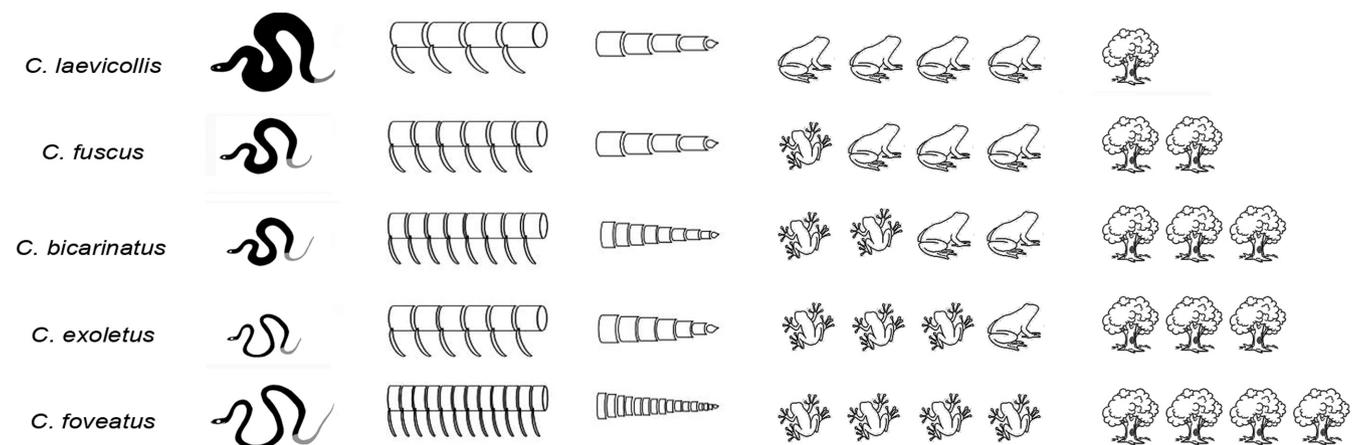
*Chironius foveatus* had the highest NVS (more than 16% larger than *C. fuscus*, the smallest;  $F_{[4,199]} = 184.904$ ,  $p < .001$ ) and NSS (more than 48% larger than *C. laevis*, the smallest;  $F_{[4,132]} = 233.688$ ,  $p = .000$ ) of the studied species. It is noteworthy that unlike NVS, which showed significant interaction with TKL ( $F_{[1,199]} = .837$ ,  $p = .000$ ), there was no association between NSS and TL ( $F_{[1,126]} = 233.688$ ,  $p = .362$ ).

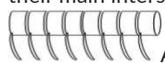
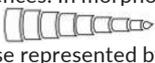
#### 3.2 | Diet

The five species fed on treefrogs (Hylidae) or terrestrial frogs (Leptodactylidae) in different proportions. *Chironius exoletus* and *C. foveatus* fed mainly on Hylidae (see Table 4), whereas *C. fuscus* and *C. laevis* fed mainly on Leptodactylidae. No prevalence for either Hylidae or Leptodactylidae was found for *C. bicarinatus*. Prey/predator ratio ranged from 0.006 to 0.28 (Table 5).

#### 3.3 | Habitat use and activity

Daytime activity data was obtained both from other researchers and the literature (Bovo & Sueiro, 2012; Carvalho-Silva & Fernandes, 1994; Di-Bernardo, 1998; Dixon et al., 1993; Hamdan & Fernandes, 2015; Hartmann et al., 2009a, 2009b; Marques et al., 2019; Marques & Sazima, 2004; Morato, 2005; Muscat et al., 2017; Oliveira, 2008; Sazima & Haddad, 1992), except for one



**FIGURE 3** Representation of five sympatric species of *Chironius* in the Atlantic Forest. In increasing order of arboreality. Summarizing their main interspecific differences. In morphology (note body. Head. And eye size. Stoutness. And tail length in snakes) note proportions of  = ventral and  = subcaudal vertebral density). Diet (legend:  = Hylidae;  = Leptodactylidae). And habitat use represented by levels of arboreality (number of trees).

*C. fuscus* (SVL = 214mm) recorded in nocturnal activity (Hartmann et al., 2009a, 2009b). The number of snakes observed on the vegetation was lower than on the ground for all species, *C. fuscus* and *C. foveatus* being the most frequently (>80%) seen active on the forest floor. On the other hand, *C. exoletus* was the species most frequently found above ground, with 40% of individuals active on vegetation (Table 6).

Thread-bobbins data were obtained for only a few individuals, so no statistical tests were performed. *Chironius foveatus* and *C. fuscus* had the largest number of individuals monitored ( $n = 5$ ). Individuals of *C. foveatus* reached maximum substrate heights ranging from 4 to 16m, while *C. fuscus* used much lower maximum heights (from 0.9 to 3.3 m). The two *C. exoletus* individuals reached heights above 5 m and the only individual of *C. laevicollis* used heights below 1.3 m (Table 7).

## 4 | DISCUSSION

Body size and shape of reptiles and amphibians often reflect adaptation to microhabitats in which they occur (Citadini et al., 2018; Lillywhite, 1996; Lillywhite & Henderson, 1993; Losos, 1990; Martins et al., 2001; Perez et al., 2019). Our results on the five sympatric *Chironius* species reveal a marked variation in body morphology and a strong relationship with substrate use and diet. The two largest species, *C. foveatus* and *C. laevicollis*, contrast strongly in body morphology, and ecological data indicate that they also represent two extremes in the frequency with which *Chironius* species use each substrate. *Chironius foveatus* is the slenderest, presents one of the longest relative tail lengths, shows the narrowest ventral scales, and the highest vertebral density (both ventral and subcaudal), has the largest eye diameter, as well as green body color, and diet based on Hylidae. Altogether, these traits indicate a higher arboreality in this snake (Lillywhite & Henderson, 1993; Sheehy III et al., 2015). On the other extreme, *C. laevicollis* is the stoutest species, presents the shortest tail, the largest head, the lowest vertebral density, and diet based on Leptodactylidae.

These data are inconsistent with the frequency with which the two species were observed on the ground or in vegetation, as *C. foveatus* was found more frequently on the ground than *C. laevicollis*. Although *C. foveatus* individuals are often seen on the ground, this snake is usually out of sight in the field. Most forest snake species are found in the field between 0.5 and 2 m (Martins & Oliveira, 1998), which should be the human visual range in which it is easier to find a snake. It is noteworthy that *C. foveatus* is the least sampled species in studies in the Atlantic Forest (Hartmann, 2005; Marques, 1998), as well as in herpetological collections (Dixon et al., 1993; present study), which is likely related to its use of higher forest strata, rarely accessible to human observation. The Amazonian *C. multiventris*, a sister species of *C. foveatus* (Torres-Carvajal et al., 2019), is recorded resting up to 4 m on the vegetation (Martins & Oliveira, 1998). Therefore, individuals of *C. foveatus* would be easily found when moving close to the ground or on it,

TABLE 1 Means and standard errors of the morphological variables of five sympatric species of *Chironius* in the Atlantic Forest

SPECIES	SVL (mm)		TL (mm)		BM (g)		HL (mm)		HW (mm)	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
<i>C. bicarinatus</i>	806.9 ± 14.5	872.6 ± 17.0	528 ± 7.1	549 ± 5.6	189 ± 18.9	219 ± 15.8	33.8 ± 0.4	34.0 ± 0.4	15.9 ± 0.5	17.0 ± 0.4
<i>C. exoletus</i>	787.6 ± 11.9	761.4 ± 21.1	524 ± 6.9	507 ± 9.7	162 ± 20.1	185 ± 26.0	36.3 ± 0.4	33.8 ± 0.6	17.7 ± 0.4	16.0 ± 0.6
<i>C. foveatus</i>	1099.7 ± 31.8	1182.1 ± 23.8	592 ± 10.7	579 ± 9.7	100 ± 31.2	162 ± 25.4	31.7 ± 0.6	31.8 ± 0.5	14.8 ± 0.7	15.6 ± 0.6
<i>C. fuscus</i>	789.6 ± 14.1	815.3 ± 13.2	511 ± 8.1	488 ± 6.7	192 ± 24.0	236 ± 18.1	33.1 ± 0.5	33.2 ± 0.4	17.0 ± 0.6	16.8 ± 0.4
<i>C. laevicollis</i>	1136.3 ± 22.1	1096.8 ± 26.2	429 ± 7.1	422 ± 7.2	377 ± 17.6	416 ± 18.2	41.2 ± 0.4	40.5 ± 0.4	21.0 ± 0.4	20.3 ± 0.4
SPECIES	ED (mm)		VSW (mm)		BW (mm)		NVS		NSS	
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
<i>C. bicarinatus</i>	6.7 ± 0.1	7.15 ± 0.1	31.5 ± 1.0	33.4 ± 0.8	15.5 ± 0.7	17.8 ± 0.6	160 ± 0.6	158 ± 0.5	142.1 ± 1.3	145.5 ± 1.4
<i>C. exoletus</i>	6.8 ± 0.1	7.17 ± 0.2	33.7 ± 1.5	32.0 ± 2.5	16.4 ± 0.6	15.0 ± 1.0	153 ± 1.0	149 ± 0.7	134.3 ± 1.2	141.2 ± 1.5
<i>C. foveatus</i>	8.24 ± 0.2	7.95 ± 0.1	26.0 ± 1.1	24.8 ± 0.8	16.9 ± 1.1	17.6 ± 0.8	173 ± 0.9	171 ± 0.9	163.5 ± 1.0	162.2 ± 0.9
<i>C. fuscus</i>	7.27 ± 0.2	7.45 ± 0.1	33.4 ± 1.2	34.0 ± 1.0	16.0 ± 0.7	16.8 ± 0.6	147 ± 2.0	147 ± 1.2	117.3 ± 1.9	117.6 ± 0.9
<i>C. laevicollis</i>	7.01 ± 0.2	7.4 ± 0.2	35.5 ± 0.7	36.2 ± 0.7	24.1 ± 0.5	23.2 ± 0.6	154 ± 1.5	154 ± 1.4	108.5 ± 1.9	109.4 ± 1.0

Abbreviations: BM, body mass; BW, body width; ED, eye diameter; HL, head length; HW, head width; NSS, number of subcaudal scales; NVS, number of ventral scales; SVL, snout-vent length; TL, tail length; VSW, ventral scale width.

but not on higher strata. Monitoring snakes with thread-bobbins clarified this issue, since all *C. foveatus* individuals used vegetation above 4 m, and up to 16 m, which makes their encounter difficult and confirms its marked arboreality.

Data from literature show that *C. laevicollis* individuals are also frequently recorded on the ground (Hartmann et al., 2009a; Marques & Sazima, 2003), but unfortunately only one individual was monitored with thread-bobbins. However, it always occupied low heights of the substrate (<1.5 m). If field data obtained with thread-bobbins is insufficient to indicate that *C. laevicollis* climbs less than *C. foveatus*, their diet based on leptodactylid frogs (which are terrestrial)

strongly indicates that they search for prey on the ground, in contrast to *C. foveatus*, which preys mainly on hylid frogs that mostly rest on vegetation. Apparently, the head size of *C. laevicollis* is also associated with its more terrestrial habitat. Among the analyzed species, *C. laevicollis* shows the largest head. In several snakes, large heads are associated with stout prey as mammals, or a rigid prey as fishes (Greene, 1983; Martins et al., 2002; Savitzky, 1983; Vincent et al., 2006). Thus, the large head of *C. laevicollis* may be related to its diet, based on terrestrial leptodactylids, since some species (e.g., *Leptodactylus ocellatus* complex) are among the stoutest frogs in the Atlantic forest (França et al., 2004).

TABLE 2 *T*-ratio-values of the interspecific comparisons of morphological variables in the females of five sympatric species of *Chironius* in the Atlantic Forest. Asterisks indicate significant values, considering *p* adjusted after Bonferroni

SPECIES ♀ ♀	SVL				TL			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	0.663	-7.62*	0.544	-12.3*	0.514	-4.72*	1.72	8.94*
<i>C. exoletus</i>		-8.24*	-0.064	-13.4*		-5.07*	1.28	8.51*
<i>C. foveatus</i>			7.76*	-1.01			5.70*	14.2*
<i>C. fuscus</i>				-12.0*				6.86*
SPECIES ♀ ♀	BM				HL			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	2.56	0.760	0.315	-7.09*	-3.69*	-2.38	1.20	-15.7*
<i>C. exoletus</i>		-1.07	-1.94	-9.33*		0.212	4.41*	-12.1*
<i>C. foveatus</i>			-0.468	-6.40*			3.11(0.0212)	-9.22*
<i>C. fuscus</i>				-6.45*				-14.8*
SPECIES ♀ ♀	HW				ED			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	-2.72	-2.48	-1.43	-11.5*	0.789	-4.62*	-1.64	-0.792
<i>C. exoletus</i>		-0.536	0.888	-8.89*		-5.30*	-2.31	-1.51
<i>C. foveatus</i>			1.16*	-6.06*			3.07*	3.83*
<i>C. fuscus</i>				-8.31*			(0.023)	0.553
SPECIES ♀ ♀	VSW				BW			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	-1.62	3.52*	-1.68	-2.70	-2.43	-0.877	-0.984	-6.37*
<i>C. exoletus</i>		4.19*	0.187	-0.501		0.875	1.33	-4.03*
<i>C. foveatus</i>			-4.58*	-7.42*			0.120	-3.90*
<i>C. fuscus</i>				0.810				-5.15*
SPECIES ♀ ♀	NVS				NSS			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	5.93*	-11.7*	6.58*	3.61*	3.61*	-10.5*	7.58*	12.2*
<i>C. exoletus</i>		-14.2*	2.87	-0.740		-11.4*	4.98*	8.74*
<i>C. foveatus</i>			12.0*	10.5*			12.6*	17.5*
<i>C. fuscus</i>				-3.13*				2.48

Abbreviations: BM, body mass; BW, body width; ED, eye diameter; HL, head length; HW, head width; NSS, number of subcaudal scales; NVS, number of ventral scales; SVL, snout-vent length; TL, tail length; VSW, ventral scale width.

**TABLE 3** *T*-ratio-values of the interspecific comparisons of morphological variables in the males of five sympatric species of *Chironius* in the Atlantic Forest. Asterisks indicate significant values, considering *p* adjusted after Bonferroni

SPECIES ♂♂	SVL				TL			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	3.22* (0.0145)	-10.8*	2.21	-8.83*	3.94*	-2.52	7.32*	13.4*
<i>C. exoletus</i>		-11.2*	-1.52	-9.60*		-4.85*	1.70	6.52*
<i>C. foveatus</i>			12.4*	2.92			7.08*	14.9*
<i>C. fuscus</i>				-10.6*				6.16*
SPECIES ♂♂	BM				HL			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	3.82*	0.402	0.226	-6.26*	2.81	-3.53	3.37	0.000*
<i>C. exoletus</i>		-2.76	-3.69*	-8.17*		-5.24*	-0.214	-12.6*
<i>C. foveatus</i>			-0.196	-5.54*			6.16*	-8.14*
<i>C. fuscus</i>				-5.85*				-15.9*
SPECIES ♂♂	HW				ED			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	3.21 (0.0152)	-2.41	1.16	-7.87*	-0.106	-2.81 (0.054)	-1.85	-1.49
<i>C. exoletus</i>		-4.70*	-2.25	-9.06*		-2.09 (0.374)	-1.30	-1.07
<i>C. foveatus</i>			3.31 (0.0109)	-4.63*			1.23	1.30
<i>C. fuscus</i>				-8.75*				-0.0483
SPECIES ♂♂	VSW				BW			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	0.628	6.73*	-0.959	-2.34	0.650	0.752	0.359	-4.60*
<i>C. exoletus</i>		2.36	-1.03	-1.51		-0.049	-0.399	-3.68*
<i>C. foveatus</i>			-6.48*	-10.9*			-0.420	-4.65*
<i>C. fuscus</i>				-1.10				-4.65*
SPECIES ♂♂	NVS				NSS			
	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>	<i>C. exoletus</i>	<i>C. foveatus</i>	<i>C. fuscus</i>	<i>C. laevicollis</i>
<i>C. bicarinatus</i>	10.7*	-12.1*	8.56*	2.76	2.47	-8.40*	13.5*	14.2*
<i>C. exoletus</i>		-19.2*	1.33	-3.68*		-9.88*	11.1*	12.4*
<i>C. foveatus</i>			15.7*	10.6*			18.2*	18.2*
<i>C. fuscus</i>				-4.10*				3.11*

Abbreviations: BM, body mass; BW, body width; ED, eye diameter; HL, head length; HW, head width; NSS, number of subcaudal scales; NVS, number of ventral scales; SVL, snout-vent length; TL, tail length; VSW, ventral scale width.

**TABLE 4** Number and percentage of Hylidae and Leptodactylidae frogs recorded in the stomach of specimens of five sympatric species of *Chironius* in the Atlantic Forest. In parenthesis, the number of prey registered in the present study

Species	Hylidae	(%)	Leptodactylidae	%	$\chi^2$	<i>p</i>
<i>C. bicarinatus</i>	26 (7)	49%	27 (2)	51%	0.018868	.8907
<i>C. exoletus</i>	94 (13)	79.7%	24 (1)	20.3%	41.525	1.16E-07*
<i>C. foveatus</i>	21 (8)	84%	4	16%	11.56	.0006739*
<i>C. fuscus</i>	10 (2)	20.8%	38 (3)	79.2%	8.5263	.0035*
<i>C. laevicollis</i>	0	0%	13 (7)	100%	13	.0003115*

**TABLE 5** Predator and prey mass, and prey/predator ratio of stomach contents found in five sympatric species of *Chironius* in the Atlantic Forest

Species	Sex	SVL (mm)	Predator mass (g)	Prey mass (g)	Prey/predator ratio
<i>C. bicarinatus</i>	♂	852	228	7.8	3.4
<i>C. bicarinatus</i>	♂	600	76	3.6	4.7
<i>C. bicarinatus</i>	♀	916	212	12	5.6
<i>C. bicarinatus</i>	♀	518	60.5	1.9	3.1
<i>C. exoletus</i>	♂	629	84	3.4	4
<i>C. exoletus</i>	♂	701	87	8.1	9.3
<i>C. exoletus</i>	♀	882	197	21	10
<i>C. exoletus</i>	♀	767	155	32.5	20
<i>C. foveatus</i>	♂	511	38	11	28
<i>C. foveatus</i>	♂	1020	230	16	6
<i>C. foveatus</i>	♂	1234	300	4.5	1.5
<i>C. foveatus</i>	♂	1178	200	14	7
<i>C. foveatus</i>	♀	1145	315	14.5	4.6
<i>C. fuscus</i>	♂	933	220	1.5	0.6
<i>C. fuscus</i>	♂	600	70	4.2	6
<i>C. laevicollis</i>	♂	1234	982	100	10
<i>C. laevicollis</i>	♂	1197	684	51	7
<i>C. laevicollis</i>	♂	844	300	6.3	2.1

**TABLE 6** Number and percentage individuals of five sympatric species of *Chironius* in the Atlantic Forest observed using terrestrial or arboreal substrates. And the values of the chi-square test and *p*-value. Divided into total records and only those of active individuals

Species	Total records			Active animals		
	Terrestrial	Arboreal	$\chi^2; p$	Terrestrial	Arboreal	$\chi^2; p$
<i>C. bicarinatus</i>	53 (77.9%)	19 (22.1%)	21.235; $p < .05$	32 (72.7%)	16 (27.3%)	9.0909; $p < .05$
<i>C. exoletus</i>	35 (77.8%)	10 (22.2%)	13.889; $p < .05$	12 (60%)	8 (40%)	0.8; $p > .05$
<i>C. foveatus</i>	24 (85.7%)	4 (14.3%)	14.286; $p < .05$	18 (81.8%)	4 (18.2%)	8.9091; $p < .05$
<i>C. fuscus</i>	49 (69%)	22 (31%)	10.268; $p < .05$	41 (87.2%)	6 (12.8%)	26.064; $p < .05$
<i>C. laevicollis</i>	25 (78.1%)	7 (21.9%)	10.125; $p < .05$	17 (77.3%)	5 (22.7%)	6.5455; $p < .05$

A clear contrast of body morphology and habitat use is also seen when comparing the two smallest *Chironius* species to each other. *Chironius exoletus* is less slender and has a longer tail than *C. fuscus*. The fact that *C. exoletus* is mostly found active above ground in the field, as well as occupying heights above 5 meters, indicates its greater arboreality degree compared to *C. fuscus*, which is usually found on the ground and heights up to about 3 m. Field data indicate that *C. bicarinatus* uses less substrates above the ground than *C. exoletus*, although more than *C. fuscus*. Diet data support field observations, as *C. exoletus* feeds mainly on hylid frogs (predominantly arboreal) while *C. fuscus* feeds mostly on leptodactylid frogs (predominantly terrestrial). On the other hand, *C. bicarinatus* feeds on approximately equal numbers of hylid and leptodactylid frogs.

In addition to the morphological syndromes usually related to arboreality in snakes (see Lillywhite & Henderson, 1993), other characters may be associated with the frequent use of higher forest

strata. Our results show that *C. foveatus* presents narrower and more numerous ventral and subcaudal scales than the other species, including the large *C. laevicollis*, which has an equivalent body size and shows the lowest vertebral density. Since the number of ventral scales correspond to the number of vertebrae (Alexander & Gans, 1966) it is evident that *C. foveatus* shows the highest vertebral density. In spite of ventral scales' width not being a diagnostic characteristic for differentiating terrestrial from arboreal snakes (Bury et al., 2019), relative width of the ventral scales may vary according to the snake's habit. In terrestrial snakes, driving forces of the lateral undulation are transmitted against irregular ground, and enlarged scales may reduce friction against the ground (Gans, 1974). In aquatic snakes, narrowing of ventral scales may favor swimming, as shown in species belonging to different lineages (cf. Scartozzoni, 2005). Arboreal habitats are formed by branches and leaves, being characterized by discontinuous surfaces with different size and slopes

TABLE 7 Individuals of five sympatric species of *Chironius* in the Atlantic Forest monitored using thread-bobbins

Species	Individual	Sex	SVL (cm)	Maximum height (m)	Days of monitoring
<i>C. exoletus</i>	1	Male	114	5.12	3
	2	Male	120	5.87	2
<i>C. foveatus</i>	1	Female	140	16	14
	2	Male	153	12	4
	3	Male	190	4	1
	4	Female	160	4.6	1
	5	Female	210	14.7	4
<i>C. fuscus</i>	1	Female	120	3	3
	2	Male	90	2.7	2
	3	Male	113	0.9	1
	4	Male	98	2.78	2
	5	Female	103	3.25	1
<i>C. laevicollis</i>	1	Female	72	1.24	3

that require more complex three-dimensional movements of snakes (Jayne, 2020). The elongate shape and large numbers of vertebrae in snakes form a body plan that readily bends and allows its long axis to conform to a wide variety of surfaces (Jayne et al., 2015). Thus, shape and number of ventral scales and the highest vertebral density in *C. foveatus* may facilitate vertebral bending, improving locomotor performance in arboreal microhabitats.

The largest and most protruding eye of *C. foveatus* stands out among all species within the genus. Arboreal snakes are exposed to predators approaching from all sides whereas terrestrial snakes are exposed to predators approaching from above (Lillywhite & Henderson, 1993; Senter, 1999). Thus, it is expected that selection favors large eyes for increased visual information in species that spend more time active on vegetation and could be more exposed to predators. This may explain the most differentiated eyes in *C. foveatus*, the most arboreal of the five *Chironius* species.

Defensive tactics displayed by the five studied *Chironius* species also are congruent with substrate predominantly used by each species. The defensive repertoire shared by these snakes includes lateral flattening, gaping, gular inflation, head triangulation and elevation, and neck S-coil (Marques et al., 2019; Muscat & Entiauspene Neto, 2016). This set of behaviors is typical of arboreal snakes (Greene, 1979; Marques, 1999; Martins et al., 2008). However, tail vibration is restricted to *C. fuscus* and *C. laevicollis* (Marques et al., 2019). Tail vibration usually makes a sound caused by quick and repeated tail tip movement in the litter on forest ground. This behavior is displayed by other terrestrial neotropical colubrids (e.g., *Dendrophidum*, *Drymoluber*, *Mastigodryas*), thus it is possible that it has been lost in more arboreal *Chironius* species, such as *C. bicarinatus*, *C. exoletus* and *C. foveatus*, as it would be less effective on vegetation than on forest ground.

Phylogenetic analysis indicates that *C. grandisquamis* and *C. challenger* are a sister group of the other *Chironius* species (Torres-Carvajal et al., 2019). Ecological information is absent for the latter, but data for *C. grandisquamis* indicate marked activity on the ground, since individuals are usually found active on the floor and only leptodactylid frogs

are recorded as prey (Dixon et al., 1993). The five *Chironius* studied here belong to two clades, and *Chironius fuscus* and *C. laevicollis* are grouped into one of them (Torres-Carvajal et al., 2019). If the phylogenetic hypothesis is correct, the predominant use of terrestrial substrate shared by both species could be a conserved trait. On the other hand, the more arboreal habit of the other species (*C. bicarinatus*, *C. exoletus*, and *C. foveatus*) could be a derived character. The number of *Chironius* species recorded at Serra do Mar is usually higher than in many other regions, such as in Amazonia (e.g., Bernarde & Abe, 2006; Cunha & Nascimento, 1982; Dixon & Soini, 1986; Duellman, 1978; Martins & Oliveira, 1998). The Atlantic Forest in the Serra do Mar range has great structural complexity, characterized by high abundance of epiphytes and lianas found from canopy to understory (Leitman et al., 2015; Villagra et al., 2013). Thus, this forest provides plentiful resources distributed along the forest's vertical axis, allowing the presence of a high number of *Chironius* species that explore different microhabitats along this gradient.

Our analysis included only the adult snakes. In all species presently studied, the color pattern of juveniles is very different from that of the adults (Dixon et al., 1993; Marques et al., 2019). While adults are uniformly colored (or almost), small individuals have conspicuous bands or spots on the body, with the exception of *C. laevicollis*, which is uniformly green (Marques et al., 2019; Marques & Sazima, 2003). Bands can help blend the body with heterogeneous backgrounds, such as the leaf litter of the forest, while the uniformly green color provides effective camouflage over the vegetation. Thus, juveniles likely differ from adults in substrate use in most species. Field data for juveniles are necessary to assess possible ontogenetic differences in substrate use.

In conclusion, our results indicate a clear difference in the frequency that each of the five sympatric species of *Chironius* uses substrates along the forest vertical gradient. We provide evidence that habitat plays an important role influencing diet and body morphology, even within closely related species. Further more comprehensive analyses are needed for understanding the evolutionary relationships among the traits we discuss.

## ACKNOWLEDGMENTS

Francisco Franco, Hussam Zaher, Julio Moura-Leite, Ronaldo Fernandes, and Felipe Graziotin provided access to herpetological collections. Eugênio Izecksohn, José Peres Pombal Jr., Vanessa K. Verdade, and Marcos Raposo identified prey species. We thank Antonio Carlos da Costa, Carlos Frederico da Rocha, Fausto Barbo, Felipe Curcio, Fernanda Centeno, Fernando Couto, Mateus Lima, Monique Van Sluys, Renato Bérnils, Ricardo Sawaya and Roberta Pinto for providing field data on *Chironius* species. We specially thank Valdir Germano for his great assistance, support, knowledge and friendship. Carolina Castro-Mello, Claudia Ribas, Eliza Soares, Fernanda Stender, Geise Rangel and Lilian Parpinelli helped on data collection. MG received a scholarship grant from FAPESP (04/12135-9). IS thanks to Marlies Sazima for her loving support in the field and at home, and acknowledges CNPq for several grants (300992/79-ZO) that allowed vertebrate natural history studies for about three decades. OAVM thanks CNPq for grants (312359/2020-9- EL). The authors thank Biotropica's editors and the two anonymous reviewers for the valuable suggestions. This study was supported in part by FAPESP (grant number 20/12658-4).

## CONFLICT OF INTEREST

The authors have no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.jh9w0vtdk>.

## ETHICAL APPROVAL

This study was authorized by the Ethic Commission for Animal Usage of Instituto Butantan (certificate CEUAIB #983-12), the Brazilian Ministry of the Environment (SISBIO #6295-7 and #16119), and the Brazilian Instituto of Environment and Renewable Natural Resources (IBAMA n° 25.650-1).

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**How to cite this article:** Banci, K. R., Guimarães, M., Siqueira, L. H., Muscat, E., Sazima, I. & Marques, O. A. (2022). Body shape and diet reflect arboreality degree of five congeneric snakes sympatric in the Atlantic forest. *Biotropica*, 00, 1–13. <https://doi.org/10.1111/btp.13107>