

Attributes of the population structure and ventral polychromatism of *Helicops infrataeniatus* Jan, 1865 (Serpentes, Colubridae, Dipsadinae) in subtropical Brazil

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Abstract. Many ecological questions can be answered only with data from hundreds or even thousands of individuals. In some taxonomic groups, such as snakes, the availability of those data is rare due to low population densities and/or the difficulties in collecting them. Hence, studies on the population structure of snakes are still relatively scarce compared to other zoological groups. In this study, we had the opportunity to analyze the population structure from an unusually large sample of the Pampean water snake *Helicops infrataeniatus*. The specimens were collected through a flood event caused by excessive rainfall related to an El Niño period in southern Brazil. Although *H. infrataeniatus* is a common species in the study area, no ecological data regarding its population structure are available so far. Therefore, the main goals of this study were to (1) determine sex ratios, (2) test for sexual dimorphism, and (3) identify the ventral polymorphism in this population. We analyzed 672 individuals (46.4% females, 53.6% males; 50.2% were classified as adults, 48.6% juveniles, and 1.3% hatchlings). The total body length (ToL) ranged from 18.4–77.4 cm for females, and 19.7–67.0 cm for males, tail length (TaL) was 4.5–21.9 cm and 5.8–21.5 cm; sub-caudal scales were 55–73, 74–92, and weight was 2.2–191.0 g, 2.3–93.3 g. Highly significant differences were detected in the number of sub-caudal scales and the TaL:ToL ratios between females vs. males tested via analysis of covariance (ANCOVA), suggesting the presence of sexual dimorphism. Regarding the ventral spotting patterns, 38.0% of individuals had trilinear, 36.0% - intermediate, and 26.0% - checkered color patterns. Besides this, 63.0% of the individuals had a reddish ventral coloration, 25.0% - yellowish, and 12.0% - both colors. No correlation was found between ventral polymorphism and sex or age class. The results presented herein offer the first robust snapshot of the population structure of *H. infrataeniatus*.

Keywords: Hydropsini, length-weight relationships, sexual dimorphism, Squamata, water snake.

Introduction

Population structure data provide important information for monitoring animal populations and allow researchers to answer questions in ecology and evolution (Millar & Libby 1991). Comparable numerical indicators are useful to assess species abundance fluctuations through time. For many squamates (lizards, snakes, and amphisbaenians), key information (e.g., sex ratios, size structure, and size-weight relationships) is often lacking, frequently due to their secretive behavior that prohibits easy sampling (Fitch 1975, Sun et al. 2001). Over the past few decades, studies on the community structure of squamates have increased (e.g., Keogh et al. 2000, Ford & Ford 2002, Ávila et al. 2006), with a greater focus on lizards (e.g., Rocha 1998, Horreo & Fitze 2015). Nonetheless, due to the (perceived) rarity of the species and/or conservation concerns, few studies describing community structures addressed such questions based on large sample sizes (e.g., Voris & Jayne 1979, Blouin-Demers et al. 2002, Winne et al. 2005).

The genus *Helicops* (Colubridae, Dipsadinae) currently comprises 19 recognized species and is the group of water snakes with the widest distribution in the Neotropics (Costa et al. 2016, Moraes-da-Silva et al. 2021, Uetz et al. 2021). One of them, the Pampean water snake *Helicops infrataeniatus* Jan, 1865 occurs in southern Paraguay, northeastern Argentina, Uruguay, and southern and southeastern Brazil (Giraud 2001). In the coastal plain of Rio Grande do Sul, southernmost Brazil, this species is considered one of the

most abundant snakes (Quintela & Loebmann 2009, Regnet et al. 2017). It is also known for its ventral polychromatism within the same population (see Deiques & Cechin 1991, Lema 2002, Quintela & Loebmann 2009). Several aspects of the biology of *H. infrataeniatus* have been addressed, including dietary data (Aguiar & Di-Bernardo 2010), geographic distribution (Landgraf-Filho & Aoki 2011), ecology (Araujo & Ely 1980), morphology (Santos-Costa & Hofstadler-Deiques 2002), natural history (Lema 1958a, Oliveira et al. 2004), reproduction (Aguiar & Di-Bernardo 2005, Braz et al. 2016) and taxonomy (Lema 1958b, Deiques & Cechin 1991, Rossman 2000). However, data on the population structure of this species have not been provided so far.

Herein, we present data on the population structure of *H. infrataeniatus* based on a large sample size. The specimens analyzed in this study were collected through a flood event caused by the El Niño climatic phenomenon on the coastal plain of Rio Grande do Sul, southernmost Brazil. Assuming that the flood event had a homogenous impact on all individuals of the population, we present data on population parameters, which may be useful for monitoring the fluctuations of population attributes over time and help to inform future conservation assessments for this species.

Material and Methods

This study was based on 710 specimens collected after a flood event in October 2015 at Laranjal beach in the municipality of Pelotas, state

of Rio Grande do Sul, Brazil (31°46'S, 52°13'W, datum WGS84, ca. 2 m a.s.l.). Individuals were collected along a transect of 1,000 meters in linear length and 25 meters in width on the coast of the Laranjal beach. These specimens are part of 2002 specimens captured/collected immediately after this event, wherein only fatally injured, debilitated, or dead specimens were fixed in formalin 10% and preserved in alcohol 70% and housed at the Herpetological Collection of Rio Grande Federal University (CHFURG). We expect that the flood had a similar impact on all groups (e.g., sex, age) in this area due to its large-scale effect, likely limiting biases due to selective sampling, e.g., due to potential microhabitat segregation between age and sex classes. Further details on the meteorological event and collection data are provided in Regnet et al. (2017). The following specimens were examined: CHFURG 3477–3512, 3514–3543, 3546–3557, 3558–3560, 3590–3752, 3754–3877, 3896–3979, 4018–4041, 4080–4108, 4109–4140, 4324–4370, and 4640–4641. The length, weight, and sex data, as well as the ventral photos of the individuals, were taken before the specimens were preserved.

Population structure and morphometric parameters

To determine the population parameters of *H. infrataeniatus*, each specimen was sexed through sub-caudal incision and verification of the presence/absence of a hemipenis. Subsequently, measurements of total length (ToL), snout-vent length (SVL), and tail length (TaL) were taken with a flexible ruler to the nearest mm. The specimens' weights were assessed with a digital scale to centesimal precision (0.01 g). Specimens were grouped into size classes using intervals of 5 cm to construct histograms. Age groups were assigned based on the total length of each individual and classified as hatchlings (< 19.9 cm ToL), juveniles (20.0 to 39.9 cm ToL), or adults (> 40.0 cm ToL) (sensu Deiques & Cechin 1991).

Length-weight relationships

The length-weight relationships (LWR) for females and males were calculated using the equation $w = a \times L^b$, where w is the total weight of each snake, a is a coefficient related to body shape, L is the total length, and b is an exponent related to change in body shape (Froese 2006). Parameters a and b were estimated by the linear regression $\log(W) = \log(a) + b \log(L)$.

Sex ratio and sexual dimorphism

We applied a Yates corrected Chi-square test to determine if the studied sample presented a balanced sex ratio of 1:1. Sexual dimorphism was assessed based on external characters and evaluated through three variables: total length (ToL), tail length (TaL) and the number of sub-caudal scales. We tested the existence of significant differences between adult females' and males' TaL using a non-parametric analysis of covariance – ANCOVA – with ToL as a covariate (R 4.0.5; R Core Team 2021) and Mann-Whitney U-test for differences in ToL. In this case, we applied a Bonferroni adjustment for multiple comparisons and considered significant values if $p < 0.025$. Performing a non-parametric ANCOVA was necessary as the assumptions of homogeneity of regression slopes and homoscedasticity were not met even after log, $1/x$, and sqrt transformations. Potential differences in the number of subcaudal scales (count variable) between sexes were assessed using a Poisson regression model in R.

Evaluation of ventral polychromatism

The ventral surface of each individual was photographed with a digital camera Canon PowerShot G10 (14.7 megapixels) to evaluate the frequency of each ventral spotting pattern type (morphotypes). We classified the morphotypes according to Boulenger (1893, 1894), Giraud (2001), and Lema (2002) as follows: type A: trilinear staining pattern – three longitudinal black lines, between the post-cephalic region and the cloaca, with background color in shades of yellow or red; type B: checkered staining pattern – absent longitudinal lines along the body, but with each ventral scale displaying alternating black coloration and background color in shades of yellow or red; type C: intermediate staining pattern – both staining patterns described above on their ventral surface (Fig. 1). For clarity, to indicate the different ventral coloration (e.g., red, yellow, or both) we apply the term polychromatism. Conversely, we apply the term polymorphism for the different morphs of coloring patterns (checked, intermediate, or trilinear) together with the different ventral colors. To test the existence of significant differences in frequencies among morphotypes, we used a Chi-square test. All statistical analyzes were performed using the R 4.0.5 software (R Core Team 2021). All significant differences were considered at the 95% confidence level.



Figure 1. Ventral surface of *Helicops infrataeniatus* and their respective morphotypes, and color variations.

A - intermediate patterns;
B - trilinear patterns and
C - checkered patterns.
Helicops infrataeniatus
individuals from the Praia do
Laranjal, municipality of
Pelotas, state of Rio Grande

Results

Out of 710 *H. infrataeniatus* analyzed, 28 specimens (13 females and 15 males; 7 juveniles and 21 adults) were excluded from the morphometric analysis as they had stubbed tails. Since these non-lethal injuries were already healed, we assume that the stubbed tails were related to attempted predation and possible pseudoautotomy before the flood event. Nine additional individuals were excluded from the analysis because it was

not possible to obtain the complete meristic and morphometric data (e.g., undefined sex and/or skin lesions preventing accurate sub-caudal scale count). A case of an intersexual individual of *H. infrataeniatus* detected in the sample due to its uniqueness was described in more detail by Regnet et al. (2018). So, the meristic, morphometric, and weight data were analyzed for 672 specimens, whose data are presented separately for females and males and according to each age group (adults, juveniles, and hatchlings; Table 1).

Table 1. Meristic, morphometric, and weight data for females and males from a sample of 671 specimens of *Helicops infrataeniatus* collected in the municipality of Pelotas, state of Rio Grande do Sul, Brazil. Data are shown separately by age groups: adults, juveniles, and hatchlings. Number of individuals for each group is in parentheses. Results expressed as mean, standard deviation, and amplitude. SVL = Snout-vent length, ToL = Total Length, TaL = Tail Length, SUB = Number of subcaudal scales.

Sex	Age group	SVL (cm)	ToL (cm)	TaL (cm)	SVL/TaL	SUB	Weight (g)
Females (311)	Adults (160)	41.7±8	55.1±10.1	13.4±2.4	3.1±0.2	64.6±3.5	62.5±36.7
		29.3–60.3	40.1–77.4	9.4–18.5	2.2–3.8	55–73	20.6–191
	Juveniles (143)	19.2±3.6	25.7±4.8	6.4±1.4	3.0±0.3	64.9±3.4	7.1±4.6
		15–29.3	20–39.6	4.6–11.5	2.3–3.8	56–73	2.8–22.4
	Hatchlings (8)	14.3±0.5	19.2±0.4	4.9±0.2	2.9±0.2	63.6±3.8	3.2±0.7
		13.3–15	18.4–19.9	4.5–5.1	2.6–3.3	58–68	2.2–4
Males (360)	Adults (177)	34.2±4.1	49.6±6.1	15.4±2.2	2.2±0.1	81.2±3.1	30.7±9.7
		27.9–46.7	40.1–67	11.7–21.5	1.8–2.9	75–92	15–61.3
	Juveniles (182)	18.6±3.1	26.2±4.4	7.6±1.4	2.5±0.2	81±2.9	6.2±3.7
		14–29.3	20.3–39.9	5.3–13.5	2–3.3	74–90	2.3–20
	Hatchlings (1)	-	-	-	-	-	-
		13.9	19.7	5.8	2.4	84	2.8

Sex ratio and sexual dimorphism

The analyzed 672 specimens consisted of 312 (46.4%) females and 360 (53.6%) males. Of these, 337 (50.2%) were adults, 160 (47.5%) females and 177 (52.5%) males; 326 (48.6%) were juveniles, 143 (21.4%) females and 182 (27.1%) males; and 9 (1.3%) were hatchlings, eight (88.9%) females and one (11.1%) male (Table 1). The smaller number of hatchlings is likely related to the recruitment period of the species (Aguiar & Di-Bernardo 2005). There was no significant difference in the sex ratio between adults (F:M 0.9:1; Chi² = 0.86, N = 337). The frequency distribution of individuals by size classes presented a bimodal pattern (Fig. 2).

The size classes with the highest frequencies were 20 to 24.9 and 25 to 29.9 cm, both composed of juveniles, comprising respectively 166 (24.8%) individuals (49% females and 51% males) and 115 (17.1%) individuals (36% females and 64% males, Fig. 2). In the two largest ToL size classes 75 to 79.9 and 80 to 84.9 cm, there were 11 females and no males. The largest male ToL was detected in class 70 to 74.9 cm (n = 2), which included 24 females. The linear regression for LWRs analysis resulted in high determination coefficients for females and males (R² = 0.986 and 0.979, respectively, both with p < 0.001). The intercepts *a* were -3.18 for females and -2.92 for males, while estimates of the parameter *b* were 2.83 and 2.60 for females and males, respectively (Fig. 3).

The count of the sub-caudal scales in females ranged from 55 to 73 (mean = 64.7; sd = 3.5), and in males it ranged from 74 to 92 (mean = 81.1; sd = 3.0). The most frequent

number of sub-caudal scales for females was 65 (12.0%) and for males 81 (14.2%) (Fig. 4). Females had smaller TaL:ToL ratios than males (Fig. 5). TaL:ToL ratios were highly significant between sexes (Mann-Whitney U-test; p < 0.001) as well as the number of sub-caudal scales (p < 0.001). The non-parametric ANCOVA showed a highly significant difference in tail length between sexes (F_(3,658) = 10660, p < 0.001). Likewise, the difference in the number of subcaudal scales between sexes was highly significant (GLM: p < 0.001, df = 660, R² = 0.86).

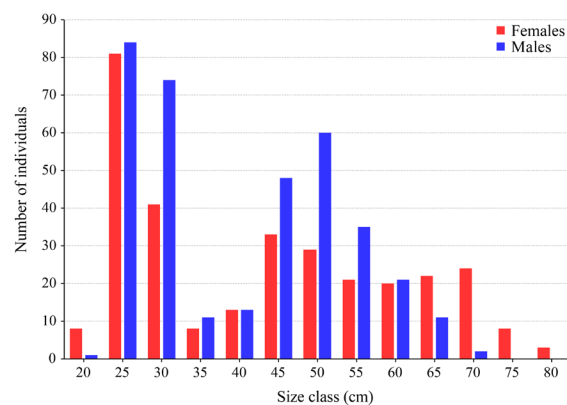


Figure 2. Frequency distributions of size classes for specimens of *Helicops infrataeniatus* from the Praia do Laranjal, municipality of Pelotas, state of Rio Grande do Sul, Brazil.

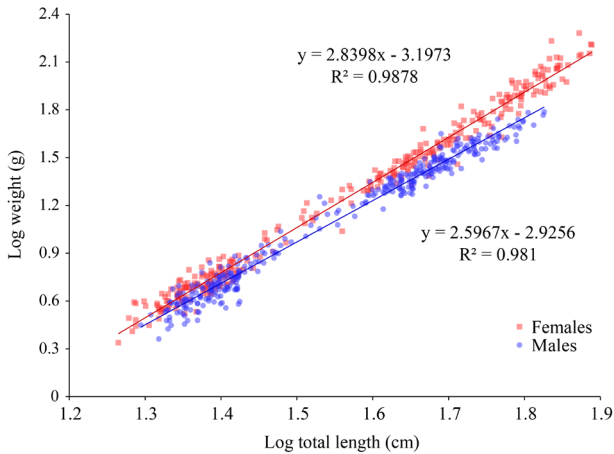


Figure 3. Length-weight relationships and linear regression values for females and males of *Helicops infrataeniatus* from the Praia do Laranjal, municipality of Pelotas, state of Rio Grande do Sul, Brazil.

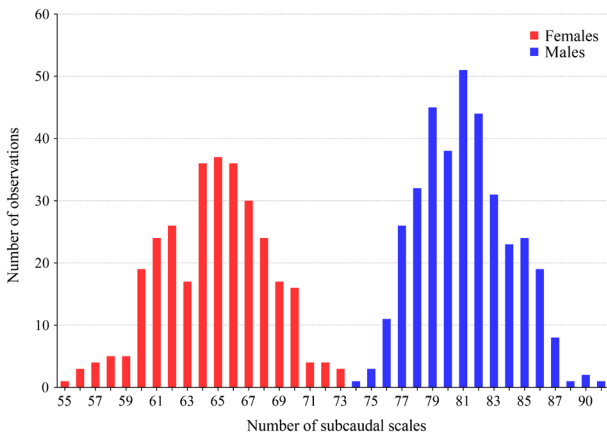


Figure 4. Histograms showing the frequency of occurrence of the number of subcaudal scales for females and males of *Helicops infrataeniatus* from the Praia do Laranjal, municipality of Pelotas, state of Rio Grande do Sul, Brazil.

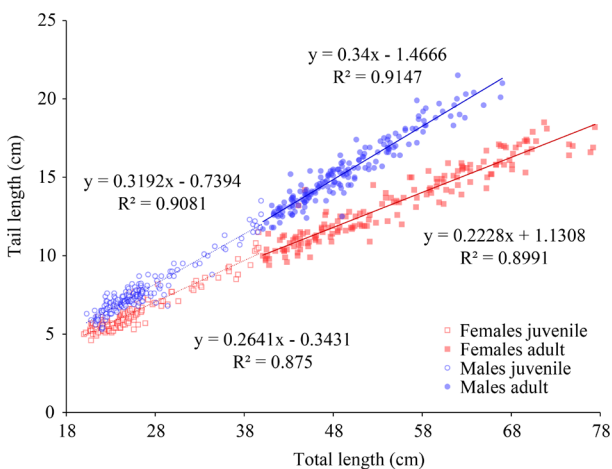


Figure 5. Tail length in relation to total length and linear regression values for juveniles and adults of *Helicops infrataeniatus* from the Praia do Laranjal, municipality of Pelotas, state of Rio Grande do Sul, Brazil.

Evaluation of ventral polychromatism

No dominance of a given ventral pattern or coloration was observed between the different size classes or different age groups (Chi² juvenile, color = 4.94, df = 2, p = 0.085, N = 325; Chi² adult, color = 3.86, df = 2, p = 0.145, N = 337; Chi² juvenile, pattern = 1.04, df = 2, p = 0.596, N = 325; Chi² adult, pattern = 5.69, df = 2, p = 0.058, N = 337). Thus, below we present the data separated by sex and not by age groups. Concerning polychromatism, the highest frequency of individuals showed reddish patterns on the ventral surface (n = 423, 63%; 49% females and 51% males). The ventral surface of the remaining specimens varied in shades of yellow (n = 171, 25%; 46% females and 54% males) and bicolor pattern (n = 78, 12%; 33% females and 67% males). In relation to the ventral polymorphism, we observed a slightly higher frequency of the trilinear pattern (n = 255, 38%; 52% females and 48% males), followed by an intermediate pattern (n = 242, 36%; 44% females and 56% males) and the checkered pattern (n = 175, 26%; 42% females and 58% males).

Discussion

What distinguishes the present study from most snake population structure studies is the high sample size, which we obtained opportunistically due to a stochastic event. Specimens were not obtained by standard scientific methodological techniques (e.g., pitfall traps), but we are confident that they represent a good sample snapshot of individuals from the population as the flood event had a large-scale impact across the area. Indeed, our sample comprises specimens of all sizes, age classes, and both sexes. Considering that there is an interval of births between October and December, it can be expected that hatchlings occur in lower numbers during this event (Aguiar & Di-Bernardo 2005). Overall, our results confirm that *H. infrataeniatus* is indeed very abundant in the study area (Quintela & Loebmann 2009, Braz et al. 2016).

Sex ratios

The herein-studied *H. infrataeniatus* population did not show significant deviation from a 1:1 sex ratio. However, studies on congeners show different patterns. For example, a *H. leopardinus* (Schlegel, 1837) population had more males than females (sex ratio of approximately 1:0.78, n total = 409; Ávila et al. 2006), while a population of *H. angulatus* (Linnaeus, 1758) had a higher proportion of females (n = 64) than males (n = 52, Ford & Ford 2002). In both cases, the authors did not perform any statistical analyses, thus is not possible to assess the statistical significance of these results. Our findings are in concert with many other studies investigating the sex ratios at the population level in snakes (e.g., Shine & Bull 1977, Dodd Jr. 1993, Ford et al. 2004, Pilgrim et al. 2011) and show quite balanced sex ratios. Nonetheless, explorations about sex ratios in snake populations are still in their early stages (Pilgrim et al. 2011), and patterns of variation in sex ratio in the group still need to be more widely documented (see Weatherhead et al. 1995, Brown & Weatherhead 1999).

Sexual dimorphism

Sexual dimorphism in body length in snakes has long been recognized for many species (Blanchard 1931). Adult males tend to have smaller body sizes than females; in some cases, differences can be 50% smaller than that of females. In extreme examples, in the water snakes of the genus *Nerodia*, females may reach up to twice the size of males (Cox et al. 2007). Three hypotheses typically explain the larger size of females; i) sexual selection in species in which males do not engage in male-male combats, such as in viviparous and aquatic species (Shine 1994, Cox et al. 2007); ii) natural selection in which body size is related to different ways of resource uses and partitioning to reduce intersexual competition (Cox et al. 2007); and iii) fecundity selection, where larger females have larger body cavities and thus can generate offspring of a larger number and size (Keogh et al. 2000, Rivas & Burghardt 2001, Ávila et al. 2006).

In a study on the evolution of sexual size dimorphism in reptiles, within eight of the most specious snake lineages analyzed (Acrochordidae, Boidae, Colubrinae, Elapidae, Natricinae, Scolecophidia, Viperidae and Xenodontinae) only in Viperidae larger body proportions were biased towards males (Cox et al. 2007). In this family, male-male combats are reported for many of the species (Shine 1994). For phylogenetically close lineages to the genus *Helicops*, as Natricinae and Xenodontinae (Colubridae), the sexual size dimorphism is clearly biased towards females (Cox et al. 2007), which is similar to our results. The largest individual we analyzed had a total length of 77.4 cm. Larger body sizes have been reported for *H. infrataeniatus*, with maximal lengths up to 100 cm (e.g., Carreira & Maneyro 2013, Cox et al. 2007, Quintela & Loebmann 2009). However, *H. infrataeniatus* has an extensive distribution (Giraud 2001), and these differences in ToL, may potentially be linked to its distribution range and the different environmental ecological aspects of the populations.

Snakes are frequently dimorphic regarding caudal length, wherein males have larger tails and a higher number of sub-caudal scales than females (Shine 1984, Van-Gelder et al. 1988, Dodd Jr. 1993). This can be related to increased reproductive success by providing more space to shelter a larger hemipenis and higher sexual fitness by providing better support during mating (King 1989, Shine et al. 1999). Thus, the loss of a large proportion of the tail, as we observed for some *H. infrataeniatus* individuals, has been pointed out as a factor that decreases male reproductive success and acts as a mechanism of sexual selection (King 1989, Shine et al. 1999).

We observed no overlap of counts of sub-caudal scales between sexes (55–73 in females; 74–92 in males), and thus, we propose it can be used as an effective sexual dimorphic character for this species. Still, in Uruguay, females had 60–73 and males 72–89 sub-caudal scales (Carreira & Maneyro 2013). Despite the minor overlapping and the smaller sub-caudal scales amplitude reported (Carreira and Maneyro 2013), we believe these results can help highlight and support this dimorphic character of the species.

Growth rates

In vertebrates, the vast majority of studies regarding the use of LWR for estimating growth rates are related to fish, where

this approach has been used for almost a century (e.g., Bianco 1909, Orton 1920, Bertalanffy 1934, Beverton & Holt 1957). However, the use of this parameter has been increasingly expanded, including its application for groups like Squamata (lizards: Minnich 1971, Meiri 2010, Feldman et al. 2016; snakes: Kaufman & Gibbons 1975, Feldman & Meiri 2013, Feldman et al. 2016). Herein, we present the LWR data for *H. infrataeniatus* based on a large sample, providing a solid basis for future comparisons. For the analyzed population, the correlation between length and weight was high and remained within the reported range of other reptile taxa (Kaufman & Gibbons 1975, Feldman & Meiri 2013, Feldman et al. 2016). Slope values (parameter b) were similar to those found for a set composed of 166 species of colubrids and dipsadids (Feldman & Meiri 2013). However, intercept values (parameter a) were different from the values presented by Feldman & Meiri (2013) for other dipsadids as well as other snake species.

We assume that the tail loss is related to predation attempts, where parts of the tails could have been ripped directly off by a predator or were lost through pseudautotomy as a defensive strategy. This non-lethal injury requires a mechanical action to promote the tail breakage, often facilitated by twisting or rotating the body to the point of the tail rupture (Savage & Slowinski 1996, Marco 2002), which allows the snake to escape from the predator. However, snakes do not have the ability to regenerate any part of the lost tail (Pough et al. 2001). This strategy is different from that known for lizards, which present an intervertebral pseudautotomy or intravertebral autotomy under neural control and also the ability of tail regeneration (Arnold 1988, Pough et al. 2001).

To the best of our knowledge, this is the first report of stubbed tails and likely pseudoautotomy in the genus *Helicops*. For a phylogenetically close species to *H. infrataeniatus* and with similar life habits, the Northern Watersnake *Nerodia sipedon* (Linnaeus, 1758), stubbed tails were also reported. Where 6.5% of the studied individuals, larger than 30 cm, had cut and healed tails (Willson et al. 2008). Additionally, 12.8 to 29.0% of the adults of *N. sipedon* from three different populations had stubbed tails (Willson et al. 2008). We detected lower proportions of stubbed tails (4.0%, or 28 specimens, of which 25 were longer than 30 cm).

Evaluation of ventral polychromatism

All morphotypes of ventral polymorphism and polychromatism we detected fully coincide with the previously described patterns for the species (Deiques & Cechin 1991, Lema 2002, Quintela & Loebmann 2009). The individual colorations and ventral staining patterns were unrelated to the sex or age groups of the individuals. The red coloration and the trilinear pattern were the predominant chromotypes detected in our study. When compared to yellow, red is a more conspicuous aposematic color (Wang 2011). Similarly, snakes with longitudinal stripes are associated with rapid escape speed (Allen et al. 2013). Thus, the greater presence of red morphotypes may be linked to a warning color recognized by the predator (Wang 2011) and the linear pattern to difficulty in tracking your speed and direction during movement, resulting in greater escape success (Creer 2005, Allen et al. 2013). This probably

results in a lower predation rate in red and trilinear individuals compared to other morphotypes.

Polymorphism has been reported for some snake species, for example, in a couple of species of the genera *Coluber* (Linnaeus, 1758), *Corallus* (Daudin, 1803), *Micrurus* (Wagler, 1824) and *Morelia* (Gray, 1842), (Neill 1963, Soini 1974, Creer 2005, Wilson et al. 2007, Duarte et al. 2015). In *H. infrataeniatus* (Boulenger 1893, 1894, Giraudo 2001, Lema 2002), it varies within the same clutch (Quintela & Loebmann 2009). It is known that polymorphism may be linked to behavior, prey-predator interactions, aposematism, interactions with the environment, thermoregulation, metabolism, camouflage, and increased habitat occupation (Farallo & Forstner 2012, Pizzatto & Dubey 2012). Furthermore, some snake taxa exhibit an ontogenetic change in color pattern correlated to an evolutionary anti-predatory defense strategy, such as *Coluber constrictor* Linnaeus, 1758 (Creer 2005); *Morelia viridis* Schlegel, 1872 (Wilson et al. 2007) and *Thamnophis ordinoides* (Baird & Girard, 1852) (Brodie III 1992). However, such a strategy of ontogenetic color change does not seem to apply to *H. infrataeniatus*.

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