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Taxonomy, allometry, sexual dimorphism, and conservation of the trans-Andean watersnake *Helicops danieli* Amaral, 1937 (Serpentes: Dipsadidae: Hydropsini)

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Abstract: The extensive lack of knowledge on the morphological aspects of South American watersnakes includes a poor understanding of phenotypic parameters, intraspecific variation, and conservation of the trans-Andean *Helicops* species, Daniel's Keelback (*Helicops danieli* Amaral, 1937). For the first time, we provide a multidisciplinary view using key features (e.g., morphology and niche modeling) to improve the taxonomic recognition of this species, as well as describing ontogenetic color changes, allometry, sexual dimorphism, and the conservation status of this poorly studied snake. First, we emended the morphological diagnosis of *H. danieli* with 23 characters and detected that juvenile tail length is positively related to allometric growth, and that juveniles differ from adults through the presence of the white nuchal collar. Females are larger than males for snout–vent length, whereas males showed proportionally longer tails and smaller head length growth. Suitable areas for *H. danieli* are restricted to the trans-Andean regions from the Magdalena drainage to the Caribbean coast, which also showed high values of anthropic impacts. Our multidisciplinary approach provided new insights into this South American watersnake's morphology, intraspecific variation, and distribution.

Key words: Daniel's Keelback, ecological niche modeling, *Helicops danieli*, linear morphometry, hemipenis morphology, intraspecific variation, ontogeny, taxonomy.

Résumé : Le vaste manque de connaissances sur les aspects morphologiques des couleuvres d'eau sud-américaines comprend une piètre compréhension de paramètres phénotypiques, de la variation intraspécifique et de la conservation d'une espèce transandine d'*Helicops* (*Helicops danieli* Amaral, 1937). Nous en présentons un premier portrait multidisciplinaire en utilisant des éléments clés (p. ex. morphologie et modélisation de la niche) pour améliorer l'identification taxonomique de l'espèce, en plus de décrire des changements de coloration ontogéniques, l'allométrie, le dimorphisme sexuel et l'état de conservation de ce serpent peu étudié. Nous modifions d'abord le diagnostic morphologique de *H. danieli* sur la base de 23 caractères et relevons que la longueur de la queue des spécimens juvéniles présente une relation positive avec la croissance allométrique et que les jeunes spécimens se distinguent des adultes par la présence d'un collet nucal blanc. Les femelles sont plus grandes que les mâles en ce qui concerne la longueur du museau à l'orifice anal, alors que les mâles ont des queues proportionnellement plus longues et une plus faible croissance de la longueur de la tête. Les secteurs qui conviennent à l'espèce se limitent aux régions transandines allant du bassin versant de Magdalena au littoral caribéen, qui présentent aussi de forts degrés d'impact de l'activité humaine. Notre approche multidisciplinaire fournit de nouveaux renseignements sur la morphologie, les variations intraspécifiques et l'aire de répartition de cette couleuvre d'eau sud-américaine. [Traduit par la Rédaction]

Mots-clés : modélisation de la niche écologique, *Helicops danieli*, morphométrie linéaire, morphologie de l'hémipénis, variation intraspécifique, ontogenèse, taxonomie.

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Introduction

In general, phenotypic traits are responses to evolutionary forces that drive adaptations to different niches or environmental constraints on nature, thus producing a myriad of morphologies and lifestyles (e.g., Pizzatto et al. 2007; Cicero et al. 2020). Snakes are very interesting models for evolutionary biology studies when considering their unique baupläne (Brandley et al. 2008), successful performance as predators (e.g., Pizzatto et al. 2009; Whitford et al. 2019), and their ability to use several, and sometimes extreme, habitats (e.g., Segura et al. 2007; Rasmussen et al. 2011; Fabre et al. 2016).

As with other vertebrates, the morphological patterns of snakes can be explained both by phylogenetic inertia (Westeen et al. 2020) and by ecological pressures (Klaczko et al. 2016). Some phenomena are usually understood as a result of intraspecific variability (sensu Klingenberg 2005; Murta-Fonseca and Fernandes 2016), such as sexual and ontogenetic differences — including allometry — between certain characteristics (e.g., Shine 1994*a*; Murta-Fonseca and Fernandes 2016; Tamagnini et al. 2018; Loebens et al. 2019; Abegg et al. 2020). On the other hand, intraspecific variation in snakes between sexes and ontogenetic trajectory show that subtle differences are selected by behavioral and ecological pressures, such as sexual selection, prey types, and habitat (or microhabitat) use. Within these intraspecific variations, there are some recurrent examples, such as greater body lengths of adult males that present male–male combat (Shine 1978, 1994*b*), different head shapes and sizes between males and females that depend on dietary preferences (Shine 1991; Vincent et al. 2004), more variable head sizes in adult males compared with females in semi-fossorial snakes (Abegg et al. 2020), and larger female aquatic snakes (Fitch 1981; Camargo et al. 2021; García-Cobos et al. 2020).

The genus *Helicops* Wagler, 1828 comprises 19 currently recognized species of watersnakes that are widely distributed across South America (Moraes-da-Silva et al. 2019, 2021; Nogueira et al. 2019). Despite their richness and relevance in aquatic ecosystems, there are deep gaps in the knowledge of their morphology, taxonomy, systematics, and conservation (Braz et al. 2016; Murphy et al. 2020; Moraes-da-Silva et al. 2021).

Amaral (1937) described Daniel's Keelback (*Helicops danieli* Amaral, 1937) based on a single specimen from Carare (= Carare River), Colombia, and proposed that the new taxon is related to another two species, the Mountain Keelback (*Helicops angulatus* (Linnaeus, 1758)) and the Ladder Keelback (*Helicops scalaris* Jan, 1865). Years later, Yuki (1994) examined two more specimens (one female and one male) and briefly described the species' hemipenis. Posteriorly, Rossman (2002*a*) examined 44 specimens of *H. danieli* and characterized the species as having dorsal scales in a 19/19/17 series; between 125–135 ventral scales in males and 130–141 ventral scales in females; between 76–86 subcaudal scales in males and 61–70 subcaudal scales in females; a spotted dorsum; and a venter with semilunar marks arranged in interrupted lines over a clear background. Currently, the species is known to be endemic to Colombia, occurring in seven country regions throughout lowlands and moderately elevated uplands, ranging from the Magdalena drainage to the Caribbean coast (Rossman 2002*a*).

Helicops danieli is the only congener that is endemic to Colombian coastal forests and is restricted to the trans-Andean region. This species has been poorly studied in terms of its morphological, anatomical, and conservation aspects (e.g., Braz et al. 2016, 2018; Moraes-da-Silva et al. 2019, 2021). The distribution of *H. danieli* has also been misunderstood, appearing only in Colombian species lists (Daniel 1949), and regional inventories (e.g., Medina-Rangel 2013; Ruíz 2014; Angarita-M. et al. 2015; Lynch 2015), with a dubious cis-Andean record in Vaupés, Colombia (Yuki and Castaño 1998). Despite the taxonomic studies developed by Yuki (1994) and Rossman (2002*a*), the diagnosis of *H. danieli* is still in its initial stages, especially considering the advances made in the taxonomic gaps and geographical ranges of the genus in the last 10 years (thus reducing the Linnean and Wallace shortfalls for South American watersnakes) (Kawashita-Ribeiro et al. 2013; Costa et al. 2016; Moraes-da-Silva et al. 2019, 2021).

Herein, we are interested in (*i*) providing new data on the taxonomy of the species and emending the *H. danieli* diagnosis; (*ii*) evaluating if the presence of the white nuchal collar varies according to age; (*iii*) testing for ontogenetic and static allometry; (*iv*) testing if *H. danieli* has sexual dimorphism, i.e., presenting females that are larger than males, which is a common pattern of other watersnakes; and (*v*) revising the distribution and conservation aspects of this enigmatic species.

Materials and methods

Sampling and morphological characteristics

We examined 124 specimens of *H. danieli* housed in the following institutions: Instituto Butantan (IBSP), São Paulo, São Paulo, Brazil; Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH), Villa de Leyva, Boyacá, Colombia; Museo de Historia Natural, Universidad de La Salle (MLS), Bogotá, Cundinamarca, Colombia; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, São Paulo, Brazil; Museo Javeriano de Historia Natural "Lorenzo Uribe, S.J." (MPUJ), Pontificia Universidad Javeriana, Bogotá, Cundinamarca, Colombia; Universidad de Los Andes (UNIANDES-R), Bogotá, Cundinamarca, Colombia; Universidad Industrial de Santander (UIS-R), Bucaramanga, Santander, Colombia; and Instituto de Ciencias Naturales (ICN-R), Universidad Nacional da Colombia, Bogotá, Cundinamarca, Colombia. Institutional abbreviations follow Sabaj (2020). A complete list of specimens is provided in Supplementary Table S1.[1]

We followed Dowling (1951) and Moraes-da-Silva et al. (2019) for meristic and pholidosis characters: data on the congeners with trans-Andean records compared with *H. danieli* was acquired from Rossman (2002*b*) for *H. scalaris* and from Rossman (1976) for Shreve's Keelback (*Helicops pastazae* Shreve, 1934).

We followed Moraes-da-Silva et al. (2019) for the measurements of the following morphometric characters: snout–vent length (SVL), tail length (TL), eye diameter (ED), head length (HL), head width (HW), and snout length (SL) (= eye–nostril distance). We also measured eye–mouth distance (EM), from the upper tip to the lower border of the eye; head height (HH), from the medial portion of parietal scales to medial portion of chinshields (= the highest point of the head); and interocular length (IL) between the outer border of the supraocular scales. We took all measurements using a digital caliper to the nearest ±0.01 mm, except for SVL and TL measurements, where we used a flexible ruler to the nearest millimetre. The sex of individuals with no everted hemipenis was identified through an incision at the base of the tail to detect the presence of hemipenes and retractor muscles. To compare our results about dimorphism with other species of the genus, we compiled data from the literature for the morphometric traits SVL, HL, and TL.

To complement the description of the hemipenis of *H. danieli* presented by Yuki (1994), we extracted, everted, and prepared the hemipenis of the preserved specimen AMNH 97461 following Pesantes (1994) and Zaher and Prudente (2003). The fully everted hemipenis was filled with petroleum jelly to ease the visualization of the ornamentation structures, and we followed the terminology of Zaher (1999) for the description. The organ was photographed, manually drawn, and digitized. All morphological measurements were taken using the ImageJ software version 1.8.0 (Rasband 2016).

We evaluated the condition of the white nuchal collar (= juvenile collar) to test the putative relationship between collar conspicuity and age. For this, we defined three categories: (1) present, white

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[1] Supplementary table and figure are available with the article at https://doi.org/10.1139/cjz-2021-0073.

collar conspicuously visible and well defined; (2) smooth, white collar not clearly visible and poorly defined; and (3) absent, white collar absent or indistinct from the background dorsum.

Statistical analyses

It was not possible to use all the samples for all the analyses because some specimens were not sexed, had a broken tail, or had damage to the pholidosis. Therefore, we employed different datasets for each analytical approach: (*i*) the dataset used for the emended diagnosis and variation comprised 61 individuals (36 females and 25 males, of all ages); (*ii*) the dataset used for sexual dimorphism and static allometry analyses comprised only adults (32 females and 32 males); and (*iii*) the dataset used for ontogenetic allometry comprised 72 adults and 41 juveniles with indefinite sex. Since the analysis of ontogenetic allometry was aimed at identifying the differences between growth rates between ages, the potential sexual differences between juveniles were not considered.

Since the range of SVL related to sexual maturity among *Helicops* species is high, i.e., between 215 and 387 mm in males (Scartozzoni 2009),[2] and this information for *H. danieli* is still unknown, we employed a combined approach based on Rossman 2002*a* and our observations of the white nuchal collar, which is an associated age-specific characteristic (= ontogenetic), for age-class estimation were based on SVL. Rossman 2002*a* determines that *H. danieli* individuals with more than 230 mm are subadults and adults, and highlights the fact that the white nuchal collar may be a juvenile characteristic, fading with increasing SVL. Therefore, we used a Kruskal–Wallis test to estimate the effect of age on the presence of the white nuchal collar using SVL as a proxy for age class (see the Results section). Finally, to avoid the inclusion of subadults as adults in our analyses, we chose to use a conservative threshold, i.e., we only considered specimens with SVL of more than 250 mm to be adults.

Before performing the allometric analysis, we imputed 16 missing values (0.8% of the total dataset), to avoid substantial data loss by removing a complete set of observations for a given specimen, using the MissForest R package (Stekhoven and Buhlmann 2012). All morphometric variables were log-transformed to ensured data normality and homogeneity. Prior to the analysis, we test for data normality and homoscedasticity. Static and ontogenetic allometry were tested using the slope test function on Smatr R package (Warton et al. 2012). We estimated the allometric coefficient for each morphological trait, using the allometric equation $y = a + x^b$, where a is the intercept and b corresponds to the slope of the linear regression of the trait value against SVL. Slopes that are not statistically different from $b = 1$ indicate isometry, whereas values significantly higher or lower than $b = 1$ indicate positive or negative allometry, respectively (Warton et al. 2006; De-Lima et al. 2019). We employed ANCOVA tests to identify the differences between the regression values of adults versus juveniles and the sex regression values of males versus females (dimorphism). We also estimated an index of sexual dimorphism following Shine (1994*b*), which is expressed as positive when females are larger than males and negative when males are larger than females. All analyses and graphics were performed using R environment version 3.4.1 (R Core Team 2021).

Endemism and potential distribution modeling

We recorded all the geographical coordinates of *H. danieli* occurrences provided by the collections. For specimens without geographic coordinates (<30% of the total dataset), we georeferenced the specimen's records through a search by collection locations using Google Earth (see Supplementary Table S1).[1] We also converted all coordinates to decimal degrees using SAD69 projection and removed all duplicates. To identify the ecoregions where *H. danieli* occurs, we used the shapefile of World Ecoregions 2017 (Dinerstein 2017). Furthermore, to identify the anthropic influence values on the distribution of *H. danieli*, we used the Human Footprint (HFP) index. This index is based on a quantitative analysis of human influence across the globe, where 0 represents no impact and 50 is the maximum impact value (Venter et al. 2016*a*, 2016*b*). We extracted and calculated the median and modal values of the human footprint for each region with *H. danieli* occurrence.

To build distribution models, we downloaded 19 climate variables plus elevation, available on the WorldClim – Global Climate Data version 2.1 (https://www.worldclim.org), for the current period (between 1970 and 2000), with a resolution of 2.5 arc minutes (ca. 5 km × 5 km) (Fick and Hijmans 2017). We then performed a principal component analysis (PCA) and Pearson's correlation to choose a subset of variables that were not correlated ($r^2 < 0.7$). These analyses were performed using vegan (Oksanen et al. 2018), dismo (Hijmans et al. 2017), and rgdal packages (Bivand et al. 2019). We selected the variables according to the ecological niche parameters of *Helicops* (Ávila et al. 2006; Moraes-da-Silva et al. 2019, 2021; Murphy et al. 2020), such as temperature seasonality (BIO 04), annual temperature range (BIO 07), precipitation of wettest month (BIO 13), precipitation seasonality (BIO 15), and elevation (elev).

We used the maximum entropy algorithm "MaxEnt" (Phillips et al. 2006) to identify the potential distribution of *H. danieli*, considering its high performance and lower sensitivity to possible geographical positioning errors (Hijmans and Graham 2006; Fourcade et al. 2014; Runquist et al. 2019). Occurrences were randomly separated into 70% of all records for training and 30% for validating the model, with 100 bootstrap pseudo-replicates. To assess the model performance, we used the area under the receiver operating characteristic (ROC) curve (area under the curve (AUC)), where values closer to 1 indicate a better agreement between model outputs and the test occurrences.

Results

Taxonomy

Helicops danieli Amaral, 1937
(Figs. 1A–1D)

HOLOTYPE: Juvenile female, IBSP 9872, donated by Brother Daniel of the La Salle Catholic Order, collected on an unknown date, from Carare River, department of Santander, Colombia. The specimen was lost in the accidental fire that affected the Herpetological Collection "Alphonse Richard Hoge" of the Butantan Institute, on 15 May 2010 (F. Grazziotin, personal communication, to N. Citeli, 7 September 2020).

EMENDED DIAGNOSIS: *Helicops danieli* can be distinguished from all its congeners by the following unique combination of characters: (1) scale rows in series of 20–19/19/20–19–17; (2) preocular single; (3) postoculars two; (4) temporal formula 2+3; eight supralabials; (5) fourth supralabial usually contacting orbit; (6) two pairs of chinshields; (7) posterior chinshields in contact (= without intergenial scales); (8) 10 infralabials; (9) 130–145 ventral scales in females and 125–135 ventral scales in males; (10) 58–71 subcaudals in females and 73–86 subcaudals in males; (11) cloacal plate always divided; (12) subcaudals divided (throughout the tail); (13) keeled dorsal scales, but weakly in paraventral region; (14) eye bigger than its distance to oral border (1.4%); (15) internasal wider than long, triangular in shape touching the rostral; (16) nasals semi-divided; (17) dorsum and tail covered by four or five lines of circular spots; (18) dorsal spots 2–3 scales long; (19) posterior region of the head

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[2] R.R. Scartozzoni. 2009. Estratégias reprodutivas e ecologia alimentar de serpentes aquáticas da tribo Hydropsini (Dipsadidae, Xenodontinae). Unpublished Ph.D. thesis, Universidade de São Paulo, São Paulo, Brasil.

Fig. 1. Morphological variation of Daniel's Keelback (*Helicops danieli*): (A) uncollected specimen from Caucasia, Antioquia, Colombia, photographed in life; (B, C) dorsal and ventral views of the adult preserved specimen UIS-R 4464; (D, E) dorsal and ventral views of the juvenile preserved specimen IAvH 7757 showing a white nuchal collar. Photographs taken by, and reproduced with permission of, Hernan Martinez (A) and Nathalie Citeli (B–E). Color version online.

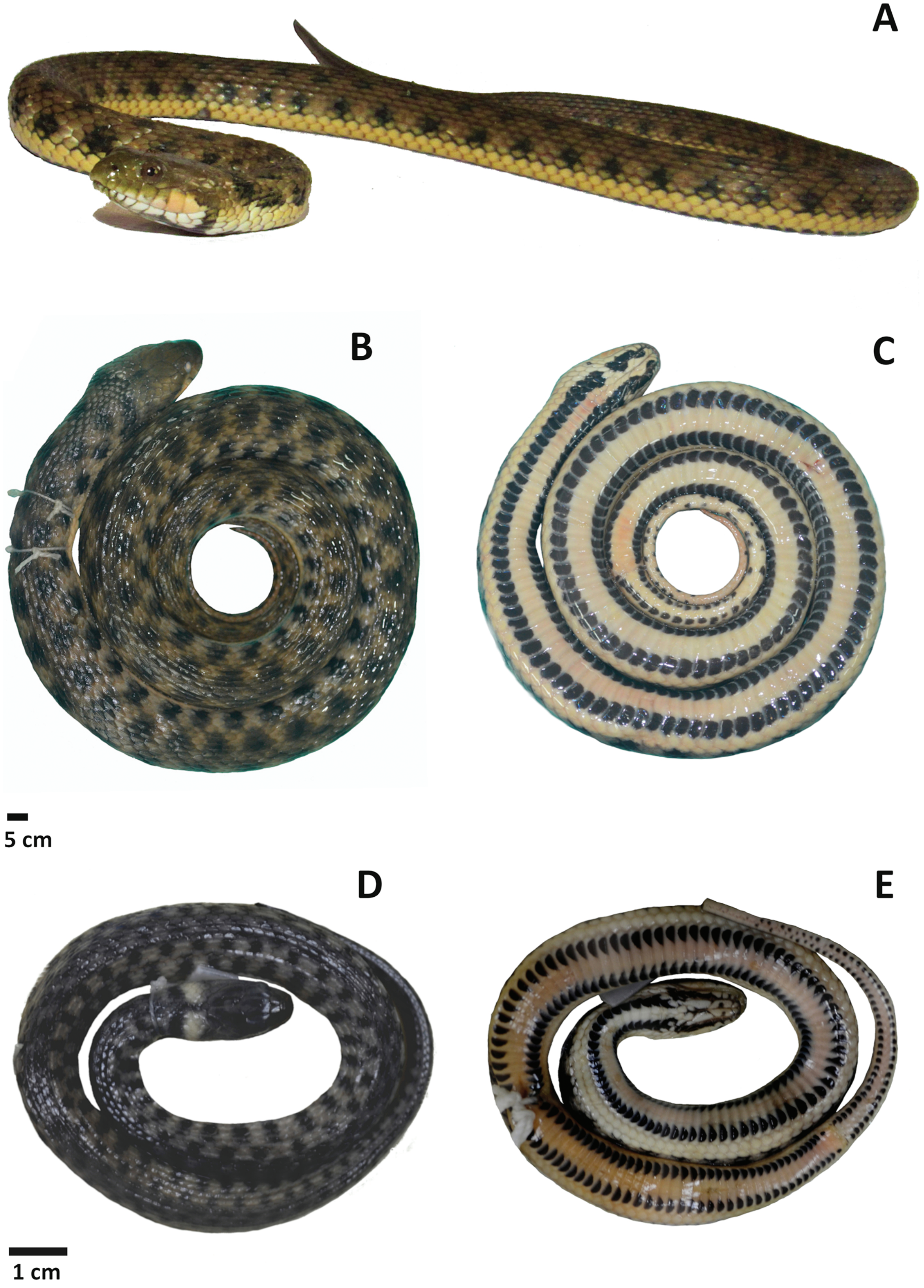
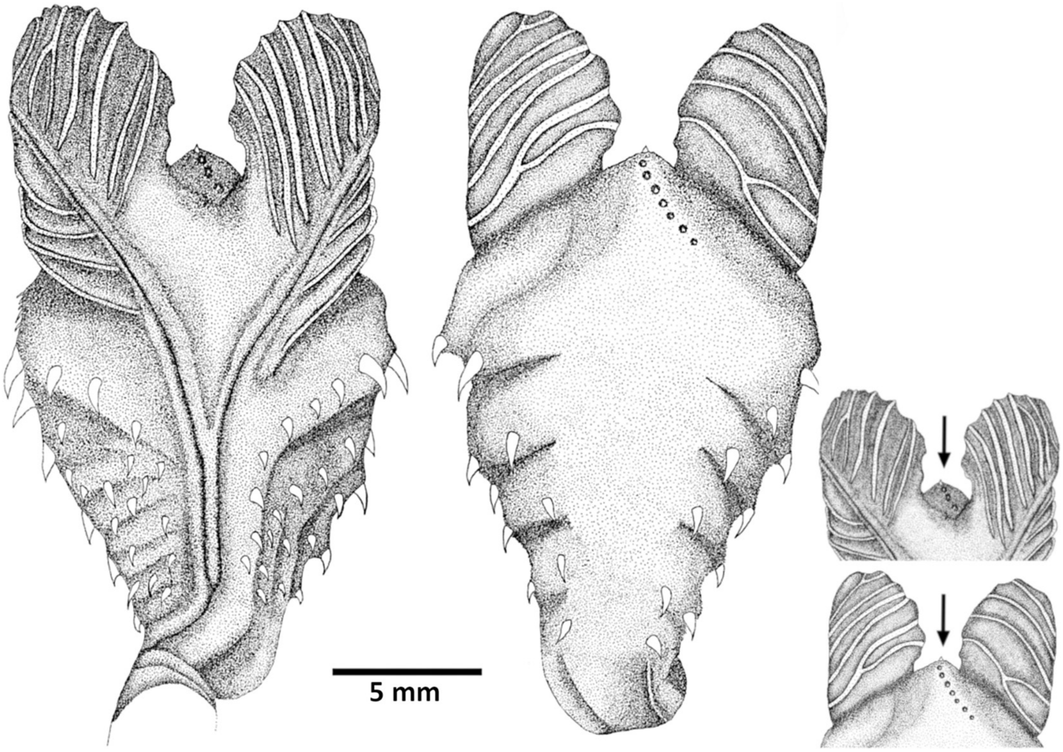


Fig. 2. Sulcate and asulcate faces, respectively, of the right hemipenis of specimen AMNH 97461 of Daniel's Keelback (*Helicops danieli*). Scale bar = 5.0 mm. In the inset, arrows point to the area between the lobes containing a longitudinal row of papillae at sulcate (top) and asulcate (bottom) faces.



with a stripe that starts from the junction of parietal scales to first dorsal spots, forming a dark nuchal band; (20) supralabials yellowish with the first ones (1–4) brownish; (21) whitish infralabials with brownish spots in the sutures and in the region of contact with chinshields; (22) yellowish-colored venter with two semilunar marks on each ventral scale; (23) whitish gular region with some brown speckled spots.

HEMIPENIS REDESCRIPTION: Hemipenis elongated, bilobed, bicalyculated, and semicapitated (Fig. 2); sulcate and asulcate faces surrounded by lateral spines that increase in size from basal region toward lobe apices; sulcate face shows 44 spines, arranged on each half of hemipenial body; intrasulcular region nude; asulcate face of hemipenial body nude, except for two longitudinal rows of lateralized spines, each composed of five to six spines; each lobe surrounded by seven to nine spiral rows of small papillae, and the area between the lobes with a longitudinal row of papillae; the total length of the organ is 22 mm, and the width, measured at hemipenial body and before capitation, is 12.34 mm; the mean length of the lobes is 5.5 mm, corresponding to 25% of the total length of the organ; the mean width of the lobes, measured in the middle of the structure, is 4.6 mm; sulcus spermaticus bifurcates at the first third of hemipenial body (3 mm from the base of the organ) and centrifugally oriented starting from the base of the organ, to median portion of sulcate face, lateral of the lobes and top of the lobes.

VARIATION: Scale rows usually in 19/19/17 series (*n* = 48, about 78.7%), 19/19/19 (*n* = 11; 18%), and rarely 20/19/17 (*n* = 1) or 20/19/20 (*n* = 1; less than 0.02%); single preocular (*n* = 60), rarely two (*n* = 1); two postoculars (*n* = 61); temporal formula usually 2+3 (*n* = 42), 2+2 (*n* = 15), and rarely 1+2 (*n* = 2); supralabials usually eight (*n* = 56) and rarely nine (*n* = 5); fourth supralabial usually contacting orbit (*n* = 57), rarely fourth and fifth (*n* = 2) or only the fifth (*n* = 2); two pairs of chinshields (*n* = 61); infralabials usually 10 (*n* = 50), 11 (*n* = 8), and rarely 9 (*n* = 1); first to fifth infralabials contacting anterior pair of chinshields (*n* = 57) or rarely first to fourth (*n* = 3); sixth to seventh infralabials contacting posterior pair of chinshields (*n* = 57) or rarely fifth to sixth (*n* = 3); posterior chinshields in medial contact (= without intergenial scales) (*n* = 61); 130–145 ventral scales in females (137.61 ± 3.08, *n* = 36), and 125–135 ventral scales in males (131.4 ± 3.34, *n* = 25); 58–71 subcaudals in females (64.52 ± 2.53, *n* = 24) and 73–86 subcaudals in males (77.05 ± 5.26, *n* = 18); cloacal plate always divided (*n* = 61); subcaudals divided (throughout the tail) (*n* = 61); total length of the smallest (juvenile) specimen is 217 mm (male) and of the largest specimen is 909 mm (female); eye is 1.4% bigger than its distance to oral border (= eye–mouth distance) (*n* = 55), rarely smaller (*n* = 6); internasal wider than long, triangular in shape (*n* = 60), touching the rostral (*n* = 51), or rarely separated by nasals (*n* = 9); loreal as long as wide (*n* = 61); nasals semi-divided (*n* = 61); dorsum and tail covered by four lines of circular spots (*n* = 40), sometimes five when a vertebral line of spots is present (*n* = 21); dorsal spots 2–3 scales long (*n* = 61); posterior region of the head with a stripe (starting from the junction of the parietal scales) and extends to first dorsal spots, forming a dark nuchal band (*n* = 60), a single specimen showed no stripe; white nuchal band evident in juveniles and almost absent or indistinct in adults (see ontogenetic and static allometry section); supralabials yellowish with the first (1–4) brownish (*n* = 42), or with speckled brownish spots on all scales (*n* = 19); whitish infralabials with brownish spots in the sutures and in the encounter with chinshields (*n* = 56), or with speckled brownish spots on all scales (*n* = 5); yellowish venter (anecdotal appointment, in life also with reddish tones) with pairs (*n* = 55) or three (*n* = 6) semilunar marks on each ventral scale, the third line usually starts from the second third of the body, and rarely forms two interconnected brownish lines across whole venter (*n* = 1); whitish gular region with some brown speckled spots (*n* = 61)

Table 1. Ontogenetic allometry in Daniel's Keelback (*Helicops danieli*).

			Allometry				Difference in allometric coefficient (slope)		Difference in adjusted trait size (intercept)	
Trait	Stage	Mean ± SD	*b*	r^2	*P*	Adjusted mean ± SD	*F*	*P*	*F*	*P*
Snout–vent length	J	191.22 ± 33.65	—	—	—	5.76	—	—	—	—
	A	441.78 ± 130.01				5.76				
Tail length	J	66.05 ± 20.09	1.21	0.60	**<0.001**	4.72 ± 0.03	7.50	**0.007**	3.73	0.06
	A	144.58 ± 36.23	0.73	0.58	0.057	4.78 ± 0.09				
Head length	J	13.04 ± 1.58	0.52	0.57	**<0.001**	2.83 ± 0.03	16.20	**<0.001**	0.49	0.48
	A	28.82 ± 5.72	0.79	0.93	**<0.001**	2.91 ± 0.01				
Head width	J	6.88 ± 1.09	0.63	0.48	0.38	2.24 ± 0.06	4.18	**0.04**	1.43	0.23
	A	13.19 ± 3.73	0.88	0.79	0.87	2.28 ± 0.02				
Head height	J	4.83 ± 0.81	0.75	0.64	0.53	1.95 ± 0.52	4.88	**0.03**	7.99	**<0.01**
	A	9.50 ± 3.04	0.98	0.87	0.23	1.93 ± 0.02				
Interocular length	J	3.63 ± 0.47	0.54	0.53	**<0.01**	1.56 ± 0.04	2.66	0.11	3.16	0.08
	A	5.89 ± 1.25	0.67	0.86	**<0.001**	1.56 ± 0.01				
Snout length	J	3.04 ± 0.45	0.61	0.50	0.18	1.41 ± 0.05	2.568	0.11	0.06	0.81
	A	5.53 ± 1.31	0.75	0.87	**<0.001**	1.41 ± 0.02				
Eye–mouth distance	J	1.18 ± 0.20	0.54	0.33	0.66	0.43 ± 0.07	8.72	**<0.01**	0.88	0.35
	A	2.35 ± 0.73	0.94	0.80	0.37	0.53 ± 0.02				
Eye diameter	J	1.87 ± 0.23	0.53	0.56	**<0.001**	0.89 ± 0.05	0.32	0.57	0.24	0.63
	A	2.74 ± 0.49	0.47	0.61	**<0.001**	0.85 ± 0.02				

Note: J, juveniles; A, adults; *b* = 1 indicates isometry, whereas a value significantly higher or lower than 1 indicates positive or negative allometry, respectively. Traits that showed significant differences are set in boldface type.

that may form a stripe connected to the first ventral semilunar spots ($n = 39$), and to the lateral spots of the head, forming a "sickle-shaped" spot around the mouth ($n = 30$).

COMPARISONS: Only two other *Helicops* species have trans-Andean records: *H. pastazae*, which is found in the Andean foothills, with one record in the Magdalena River Valley of Colombia (Rossman 1976) and other records from the southern portion of Maracaibo Lake (Rossman 1976; Markezich and Rossman 1992), and *H. scalaris*, which is restricted to northwestern Venezuela and adjacent to Colombia in drainages into Maracaibo Lake Basin (Rossman 2002*b*). In general, *H. danieli* differs from all its congeners due to the combination of the spotted dorsum with two lines of semilunar marks on the venter (Rossman 2002*a*). Specifically, *H. danieli* differs from *H. pastazae* and *H. scalaris* by having scale rows usually in 19/19/17 (vs. 23/23–25/19 in *H. pastazae* and 21–25/19–21/16–19 in *H. scalaris*), 58–71 subcaudals in females (vs. 72–97 in *H. pastazae* and 67–81 in *H. scalaris*), and 73–86 subcaudals in males (vs. 93–117 in *H. pastazae* and 83–95 in *H. scalaris*); venter with two lines of semilunar spots (vs. venter with dark crossbands or alternating checkered pattern in *H. pastazae* and venter with black lateral or medial stripes, sometimes with interconnected checkered pattern in *H. scalaris*). Furthermore, *H. danieli* differs from *H. pastazae* by having two pairs of chinshields in contact (intergenial scales present in *H. pastazae*), and from *H. scalaris* since females have 130–145 ventrals and males have 125–135 ventrals (vs. 113–125 in females and 110–119 ventrals in males of *H. scalaris*).

REMARKS: We found a *H. danieli* female (IAvH 84, collected on 10 November 1970) showing six well-developed embryos in the oviduct, with no sign of eggshell formation, representing the first record of litter size and thus confirming viviparity in this species. The mean size of the largest coiled embryo was 31.24 mm in diameter. The measurements of the female were SVL = 730 mm, tail length = 179 mm, head length = 35.24 mm, head height = 15.57 mm, head width = 17.25 mm, interocular length = 6.96 mm, eye–mouth distance = 3.08 mm, and snout length = 8.04 mm.

Ontogenetic and static allometry

We identified significant differences between presence and absence of a white nuchal collar between age classes ($\chi^2 = 68.068$, $P < 0.001$, $n = 106$), where 90% of juveniles showed a clear white nuchal collar, of which 10% showed a smooth band, and only 4% of adults showed a white nuchal collar, of which 36% had smooth bands and 60% completely lacked a collar. The clear white nuchal collar was found to be more related to younger snakes (less than 250 mm) (Figs. 1A–1E; Supplementary Fig. S1[1]).

We found that tail length was the only trait with positive allometry in juveniles. Head length, interocular length, and eye diameter showed negative allometry for both stages. Snout length only showed negative allometry in adults. Tail length, head length, head width, and eye–mouth distance showed significant differences in allometric coefficients between ages (see Table 1 and Figs. 3A–3H). Despite isometric growth, head height varied according to ontogenetic stage, showing different isometric growth trajectories for juveniles and adults (Table 1).

Males and females showed the same allometric pattern, with negative allometry for interocular length, snout length, eye diameter, and head length. The latter also showed differences in the allometric coefficient between sexes (see Table 2 and Figs. 4A–4H).

Dimorphism in traits

The largest female SVL was 730 mm and the largest male SVL was 490 mm. Females were generally larger than males, showing

Fig. 3. (A–H) Regressions of eight log-transformed morphometric traits vs. log-transformed body size (snout–vent length (SVL)) of Daniel's Keelback (*Helicops danieli*) for both adults (black squares) and juveniles (gray circles).

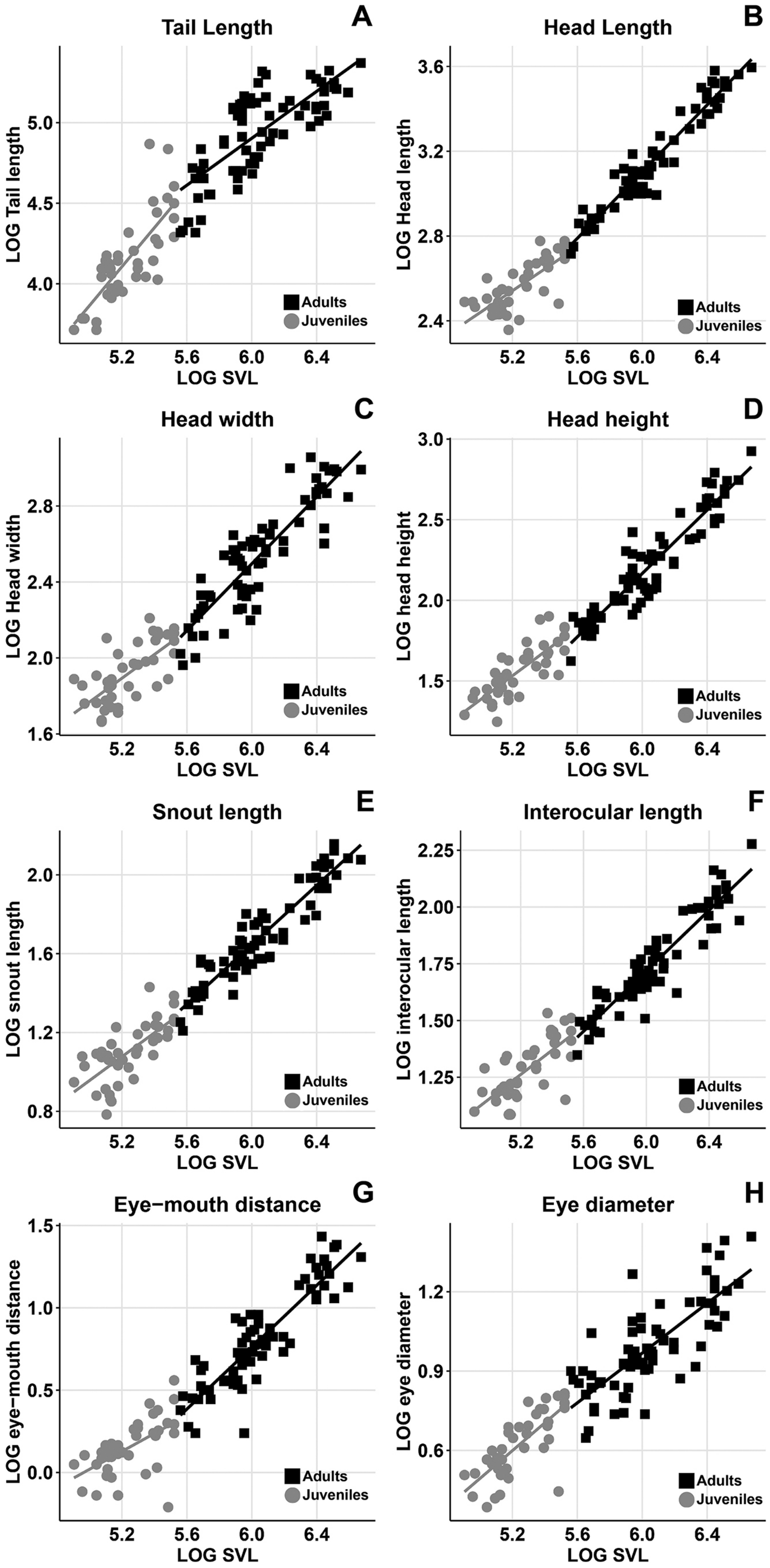


Table 2. Static allometry in Daniel's Keelback (*Helicops danieli*).

Trait	Sex	Mean ± SD	Allometry			Adjusted mean ± SD	Dimorphism in allometric coefficient (slope)		Dimorphism in adjusted trait size (intercept)	
			b	r^2	P		F	P	F	P
Snout–vent length	F	446.78 ± 164.40	—	—	—	5.91	—	—	—	—
	M	338.41 ± 80.40				5.91				
Tail length	F	133.73 ± 42.03	0.84	0.85	0.20	4.74 ± 0.027	1.89	0.18	38.89	**<0.001**
	M	136.35 ± 37.50	1.00	0.76	0.12	4.99 ± 0.029				
Head length	F	24.02 ± 7.40	0.81	0.97	**<0.001**	3.03 ± 0.014	4.57	**0.03**	0.02	0.88
	M	19.42 ± 3.50	0.68	0.83	**<0.001**	3.03 ± 0.014				
Head width	F	13.38 ± 4.86	0.89	0.85	0.63	2.42 ± 0.028	0.45	0.50	0.05	0.81
	M	10.39 ± 2.57	0.81	0.68	0.86	2.40 ± 0.030				
Head height	F	9.69 ± 3.68	0.93	0.88	0.87	2.09 ± 0.023	1.75	0.19	0.03	0.86
	M	7.43 ± 1.64	0.79	0.78	0.21	2.40 ± 0.030				
Interocular length	F	5.92 ± 1.57	0.62	0.87	**<0.001**	1.67 ± 0.016	0.27	0.60	0.20	0.65
	M	4.98 ± 0.75	0.53	0.79	**<0.001**	1.66 ± 0.016				
Snout length	F	5.55 ± 1.77	0.79	0.94	**<0.001**	1.57 ± 0.015	2.74	0.10	3.13	0.08
	M	4.67 ± 0.85	0.66	0.83	**<0.001**	1.61 ± 0.016				
Eye–mouth distance	F	2.39 ± 0.85	0.91	0.87	0.76	0.70 ± 0.025	1.22	0.27	1.00	0.32
	M	1.79 ± 0.37	0.71	0.72	0.07	0.66 ± 0.025				
Eye diameter	F	2.72 ± 0.65	0.51	0.73	**<0.001**	0.92 ± 0.020	0.56	0.46	0.65	0.42
	M	2.45 ± 0.36	0.42	0.58	**<0.001**	0.94 ± 0.021				

Note: F, female; M, male; $b = 1$ indicates isometry, whereas a value significantly higher or lower than 1 indicates positive or negative allometry, respectively. Traits that showed a significant difference for sexual dimorphism are set in boldface type.

larger SVL, head length, head width, head height, interocular length, and eye–mouth distance (Table 2). However, tail length was the only dimorphic trait when using SVL as a covariate (F = 40.452, P = <0.001, n = 64), and head length was equal for males and females also when using SVL as a covariate (Table 2 and for data compilation on *Helicops* spp. see Table 3). The index of sexual dimorphism for *H. danieli* was 0.32.

Distribution and conservation

We obtained 43 unique records of *H. danieli* distributed throughout five Colombian ecoregions, with 65% of the records located in Magdalena–Urabá moist forests, 16% in Sinú Valley dry forests, 7% in Chocó-Darién moist forests, 7% in Magdalena Valley montane forests, and 5% in Amazon–Orinoco–southern Caribbean mangroves (Fig. 5A). This species occurs from sea level up to 1083 m above sea level.

Our *H. danieli* samples were collected between the years 1950 and 2018, and distributed across the following departments: Antioquia, Atlántico, Bolívar, Boyacá, Caldas, Cesar, Chocó, Córdoba, Magdalena, Santander, and Sucre. The highest HFP values were found in the departments Atlántico (median 14, mode 14), Caldas (median 10.7, mode 11), Sucre (median 10.3, mode 17), and Cordoba (median 10.27, mode 13) (Fig. 5B), whereas the less impacted departments were Magdalena (median 9.6, mode 15), Cesar (median 9.5, mode 16), Santander (median 8.2, mode 10), Antioquia (median 7.4, mode 4), Boyacá (median 7.3, mode 3), Bolívar (median 6.6, mode 4), and Chocó (median 3.7, mode 4).

The generated distribution model showed high statistical performance, with a higher mean AUC = 0.963 ± 0.010. The area of suitability for the occurrence of *H. danieli* was found to be restricted to lowlands and moderate highlands in northwestern Colombia, in the surroundings of the Andes Mountain ranges, with two well-demarcated regions in the ecoregion Magdalena–Urabá moist forests and other portions around the Lake Maracaibo, in Venezuela (Fig. 5C). The variables with the greatest contribution to the model were temperature seasonality (56% of contribution) and elevation (27.4%), followed by precipitation seasonality (10.8%), annual temperature range (3.3%), and precipitation of the wettest month (2.5%).

Discussion

In this study, we used a multidisciplinary approach to improve the taxonomic, morphological, distribution, and conservation efforts for a poorly understood aquatic snake, restricted to a small biogeographical region of South America. We update the species' diagnosis, investigate two types of growth rates (i.e., ontogenetic and static allometry), and report on sexual dimorphism in *H. danieli*. We also reassessed this species' distribution, detected anthropic impacts on its range, and indicate suitable areas within its distribution range.

Our data confirmed most of the morphological variation obtained by Rossman (2002*a*), with the exception of greater amplitude of variation for ventrals in females (130–145 vs. 130–141 in Rossman 2002*a*) and subcaudals in females (58–71 vs. 61–70) and males (73–86 vs. 76–86). *Helicops danieli* is part of the *Helicops* species cluster, which has 19 dorsal scale rows in the middle of the body (sensu Moraes-da-Silva et al. 2021). This group also includes Leopard Keelback (*Helicops leopardinus* (Schlegel, 1837)) and *H. angulatus* complexes (both widely distributed in South America), Wied's Keelback (*Helicops carinicaudus* (Wied-Neuwied, 1824)) (southeastern and southern Brazil), *Helicops infrataeniatus* Jan, 1865 (southern and central-western Brazil), Sao Paulo Keelback (*Helicops gomesi* Amaral, 1921), and Olive Keelback (*Helicops modestus* Günther, 1861) (central-western Brazil), *Helicops phantasma* Moraes-da-Silva, Cecília

Fig. 4. (A–H) Regressions of eight log-transformed morphometric traits vs. log-transformed body size (snout–vent length (SVL)) of Daniel's Keelback (*Helicops danieli*) for both females (black squares) and males (gray circles).

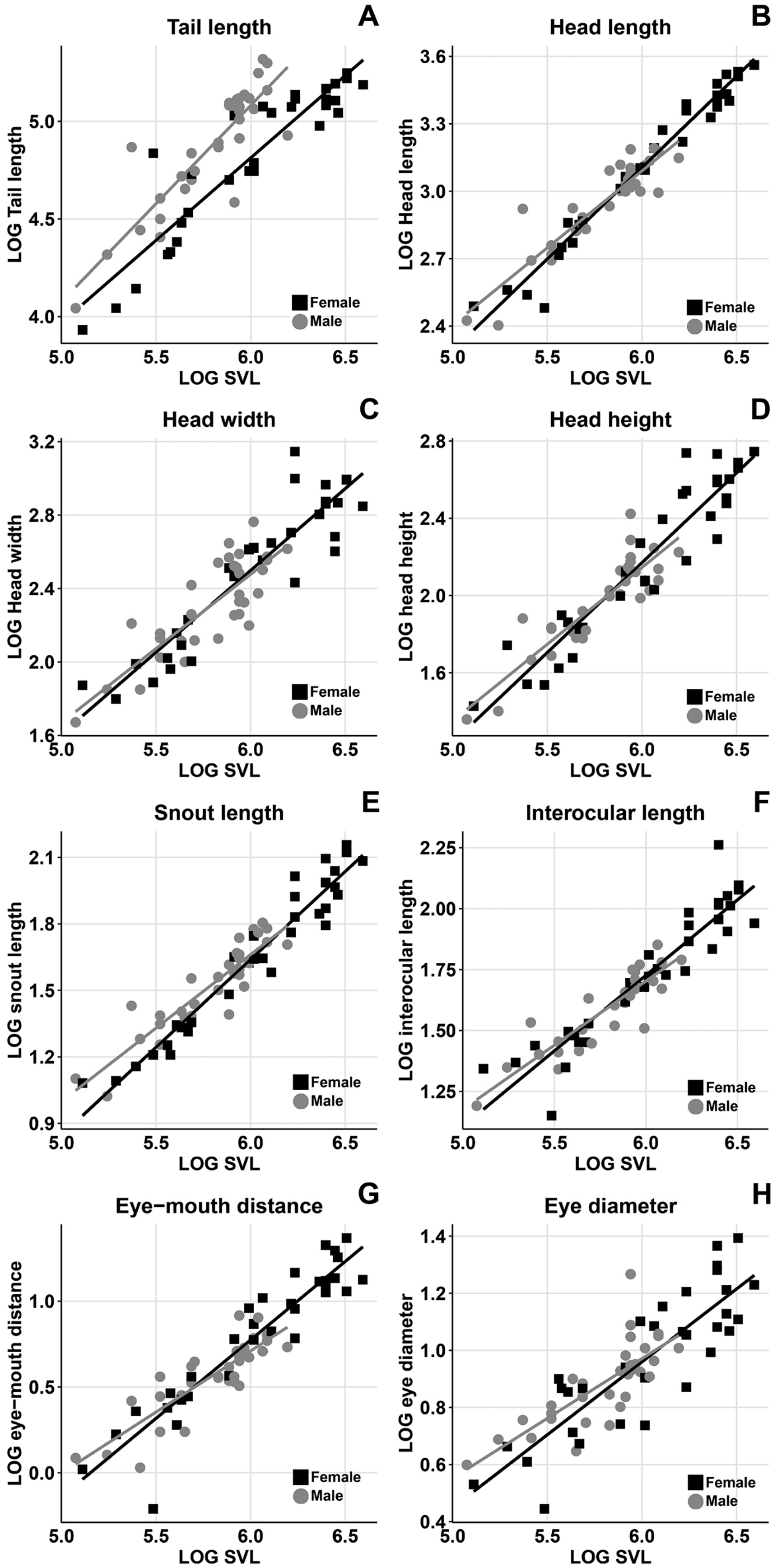


Table 3. Comparisons of sexual dimorphism in morphometric traits, snout–vent length (SVL), head length (HL), and tail length (TL) among the species of the watersnake genus *Helicops*.

	Sexual dimorphism				
Species	Morphometric traits	SVL	HL	TL	References
Mountain Keelback, *Helicops angulatus*	Yes	F > M	F = M	F < M	Scartozzoni 2009[2]; Murphy et al. 2020*
Helicops apiaka Kawashita-Ribeiro, Ávila and Morais, 2013	?	?	?	?	
Helicops boitata Moraes-Da-Silva, Cecília Amaro, Sales-Nunes, Strüssmann, Teixeira, Andrade, Sudré, Recoder, Rodrigues, Curcio, 2019	?	?	?	?	
Wied's Keelback, *Helicops carinicaudus*	Yes	F > M	F = M	F < M	Scartozzoni 2009[2]
Daniel's Keelback, *Helicops danieli*	Yes	F > M	F = M	F < M	Rossman 2002*a**; present study
Sao Paulo Keelback, *Helicops gomesi*	Yes	F > M	F > M	F < M	Scartozzoni 2009[2]
Hagmann's Keelback, *Helicops hagmanni*	Yes	F > M	F = M	F < M	Scartozzoni 2009[2]
Helicops infrataeniatus	Yes	F > M	F > M	F < M	de-Aguiar and Di-Bernardo 2004; Scartozzoni 2009[2]
Leopard Keelback, *Helicops leopardinus*	Yes	F > M	F > M	F < M	Ávila et al. 2006; Scartozzoni 2009[2]
Olive Keelback, *Helicops modestus*	Yes	F > M	F > M	F < M	Scartozzoni 2009[2]; Maia et al. 2015
Helicops nentur	?	?	?	?	
Shreve's Keelback, *Helicops pastazae*	Yes	F > M	F > M	F < M	Rossman 1976*; García-Cobos et al. 2020
Spiral Keelback, *Helicops petersi*	Yes	?	?	F < M	Rossman 1976*
Helicops phantasma	?	?	?	?	
Norman's Keelback, *Helicops polylepis*	Yes	F > M	F > M	F < M	Scartozzoni 2009[2]; Camargo et al. 2021
Ladder Keelback, *Helicops scalaris*	Yes	F > M	F > M†	F < M	Rossman 2002*b**
Helicops tapajonicus	Yes	?	?	F < M	Frota 2005*
Equatorial Keelback, *Helicops trivittatus*	Yes	F > M	F > M	F < M	Scartozzoni 2009[2]
Peru Keelback, *Helicops yacu*	?	?	?	?	

Note: F, female; M, male.

*Authors presented only descriptive data.

†Differences in head size were considered subtle by the author.

Amaro, Sales-Nunes, Rodrigues and Curcio, 2021 (Tocantins–Araguaia Basin), and *Helicops tapajonicus* Frota, 2005 (Amazonia Basin) (Nogueira et al. 2019; Murphy et al. 2020; Moraes-da-Silva et al. 2021). However, with the exception of the *H. leopardinus* complex (sensu Moraes-da-Silva et al. 2021), the spotted dorsal pattern of *H. danieli* mainly appears in *Helicops* species that are restricted to the northern portion of South America, i.e., Hagmann's Keelback (*Helicops hagmanni* Roux, 1910), *H. pastazae*, Spiral Keelback (*Helicops petersi* Rossman, 1976), Norman's Keelback (*Helicops polylepis* Günther, 1861), and Peru Keelback (*Helicops yacu* Rossman and Dixon, 1975) (sensu Moraes-da-Silva et al. 2021). The black semilunar ventral marks of *H. danieli* are shared with *H. carinicaudus*, *Helicops nentur* Costa, Santana, Leal, Koroiva and Garcia, 2016 (both from southeastern Brazil), and Equatorial Keelback (*Helicops trivittatus* (Gray, 1849)) (Amazon and Tocantins–Araguaia basins) (Rossman 2010; Nogueira et al. 2019; Costa et al. 2016).

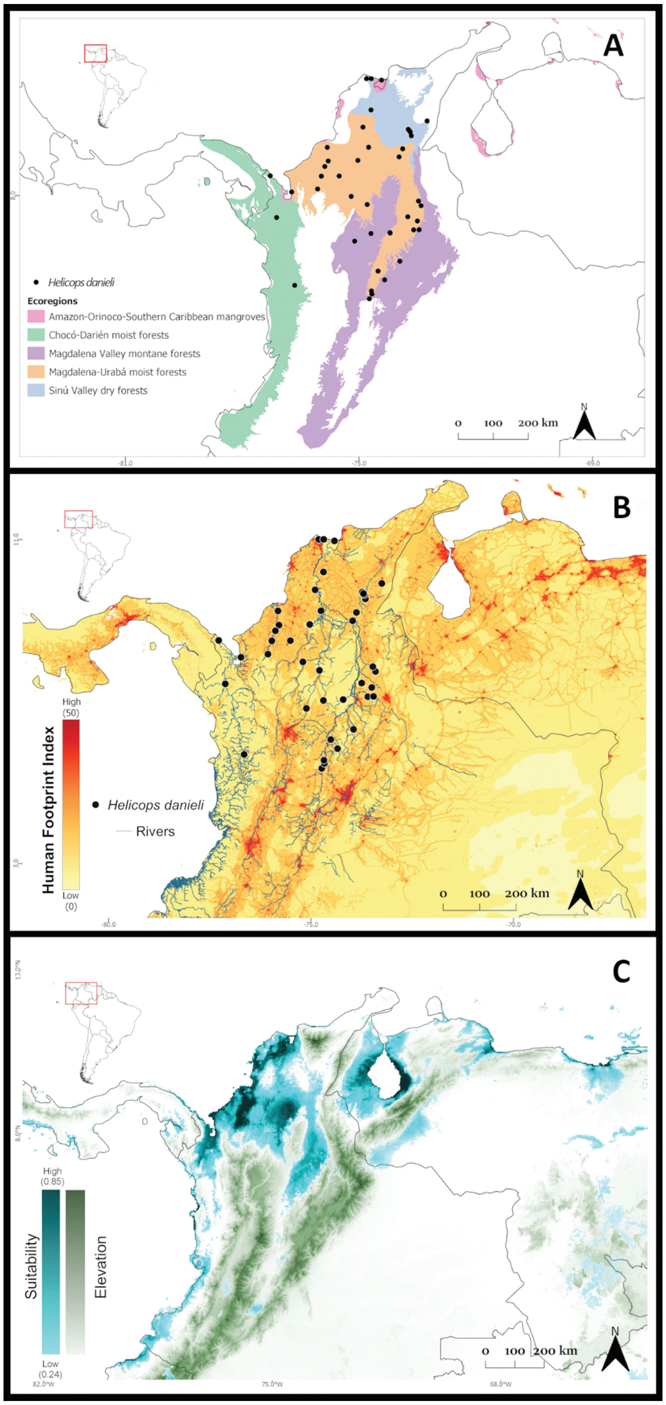
The presence of a white nuchal collar in *H. danieli* juveniles may play a disruptive role against visually oriented predators, depending on the background of the niches exploited by developing individuals (Stevens et al. 2006; Stevens 2007). Other color traits act more strongly on small individuals, as smaller rings increase the effect of blurring with the background for visually oriented predators (Pough 1976). *Helicops danieli* and many other aquatic snakes have bright aposematic colors that are concentrated on the belly (Batista et al. 2020), these characteristics likely act as a defense mechanism against predation by carnivorous fishes in aquatic environments (Batista et al. 2020). Thus, we hypothesize that the presence of the white nuchal collar in *H. danieli*, together with bright ventral coloration, may be driven by selective forces, thereby reinforcing aposematic/disruptive non-conflicting strategies (see Titcomb et al. 2014) against terrestrial and visually oriented aquatic predators.

The sexual dimorphism detected in *H. danieli*, where females are larger than males, is widely documented in snakes and is common in aquatic species (Shine 1978; Shine 1994*b*; Fitch 1981; for *Helicops* spp. see Table 3). Larger female body size is likely not only related to litter size and fat accumulation for embryo development, but also for the use of different niche parameters (Shine 1986, 1994*a*). Unlike many other studies with aquatic snakes (e.g., Shine 1986; Houston and Shine 1993; Shine et al. 2002) and with *Helicops* (Table 3), we did not detect females with proportionally larger heads than males. However, our results are similar to those found for the other three *Helicops* species: *H. angulatus* (which likely represents a species complex according to Murphy et al. 2020), *H. hagmanni*, and *H. carinicaudus* (Table 3). Considering that this trait may be triggered by ecological pressures related to diet and habitat use (Shine 1986; Camilleri and Shine 1990), or by phylogenetic conservatism (Westeen et al. 2020), we believe that filling in gaps in the knowledge of the natural history of *Helicops* spp. through a phylogenetic approach can clarify the morphological evolution of the group. The proportionally larger tails in males may be due to three classic and non-excluding hypotheses: (1) "The Morphological Constraint Hypothesis" — to accommodate the hemipenis (e.g., King 1989; Shine, et al. 1998; Sivan et al. 2020); (2) "The Female Reproductive Output Hypothesis" — females have relatively shorter tails as a secondary result of natural selection for increased reproductive capacity; or (3) "The Mating Ability Hypothesis" — an increased reproductive ability in males (sexual selection) (King 1989; Shine et al. 1999). However, we did not detect significant differences in the allometric coefficient between adults from both sexes for tail length, suggesting that males are born with a proportionally larger tail, or acquire this trait during the juvenile stage, thus both hypotheses should be tested in the future with neonates.

Although head height showed isometric growth in adults and juveniles, the differences in the growth coefficient of this trait (Table 1) and for the allometric coefficient of head length and head width between ages was expected, according to the proportional decrease in relative brain size during development (Gould 1966; Phillips and Shine 2006).

Paradoxically, the area with the highest concentration of *H. danieli* records is also one of the most threatened regions in South America due to the gold mining industry, in addition to other factors such as

Fig. 5. Distribution maps of Daniel's Keelback (*Helicops danieli*), including (A) occurrence in five Colombian ecoregions (ecoregions base map: Dinerstein et al. 2017), (B) anthropic impact index on *H. danieli* range distribution (human footprint base map: Venter et al. 2016*a*), and (C) suitable areas for *H. danieli* potential occurrence in Colombia and Venezuela (elevation base map: Fick and Hijmans 2017). Color version online.



deforestation and river pollution as a result of agricultural practices (Sánchez-Cuervo et al. 2012; Alvarez-Berríos and Aide 2015). Aquatic snakes can act as bioindicators along River Basins (Haskins et al. 2021), as they are susceptible to wastewater and siltation. Conservation strategies for *H. danieli* should be especially directed toward the Atlantic Caribbean region, which is also the region with the highest HFP values. As our records were associated with rivers, we suggest that *H. danieli* populations should be monitored and that physiological studies on this species should be performed, with the aim of contributing to the management of water and bioaccumulation (Fontenot et al. 2000; Haskins et al. 2021).

Finally, we found that *H. danieli* occurrence in the Amazon Basin region was not suitable, even though one record (ICN-R 242) in Mitú, Vaupés, Colombia, was reported by Yuki and Castaño (1998). Rossman (2002*a*) confirmed the identification of this specimen as *H. danieli* and commented that is probably wrong in origin. However, we cannot simply discredit the possibility of the correct origin of the specimen, based on the possibility of human transportation from trans-Andean locations or even the chance that this specimen may represent an unknown species to science with a general phenotype similar to *H. danieli*. Unfortunately, we did not find the specimen in the ICN-R collection, but all our records are from Caribbean drainages and at most ca. 1000 m above sea level. We believe that the Colombian Andes (Cordillera Oriental and the Sierra de Perijá) act as important physical barriers to this species, which may also explain why we identified a high suitability for *H. danieli* around Lake Maracaibo Basin, in association with the absence of records there. A similar endemism pattern is found in other Hydropsini snakes, such as *H. scalaris* and the South American Pond Snake (*Pseudoeryx relictualis* Schargel, Rivas-Fuenmayor, Barros, Péfaur and Navarette, 2007), that are restricted to the Lake Maracaibo Basin (Rossman 2002*b*; Schargel et al. 2007).

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