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Sexual dimorphism and reproductive biology of the cloudy snail-eating snake *Sibon nebulatus* (Linnaeus, 1758) (Serpentes: Dipsadini) from isolated humid forests of Ceará, Brazil

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Resumo

Apresentamos os primeiros dados integrados sobre o dimorfismo sexual de adultos e juvenis e sobre a biologia reprodutiva da serpente malacófaga *Sibon nebulatus*, com base em espécimes provenientes de enclaves florestais úmidos isolados ("Brejos de Altitude") do estado do Ceará, nordeste do Brasil. Esses ambientes montanos, inseridos na diagonal seca neotropical, abrigam populações localmente abundantes, porém pouco estudadas, atualmente sob forte pressão antrópica e intensa fragmentação do habitat. Esse isolamento pode influenciar características ecológicas e de história de vida, reforçando a necessidade de dados biológicos básicos para a conservação. Foram analisados 72 indivíduos, incluindo 53 adultos (26 fêmeas e 27 machos) e 19 juvenis. Machos e fêmeas adultos não diferiram significativamente no comprimento rostro-cloacal, mas machos apresentaram maior tamanho relativo de cauda. Medidas cefálicas exibiram ampla sobreposição entre os sexos. A reprodução apresentou padrão sazonal associado ao regime de chuvas, com desenvolvimento folicular no início da estação chuvosa e ovos no oviduto entre junho e setembro, com ninhadas de dois a seis ovos. Esses resultados ampliam o conhecimento sobre a variação intraespecífica em traços de história de vida e fornecem uma base empírica para comparações futuras ao longo da distribuição de *S. nebulatus*.

Palavras-chave

Brejos de altitude, Dimorfismo sexual, História natural, Reprodução, Serpentes neotropicais.

Abstract

We present the first integrated data on sexual dimorphism based on body measurements of adults and juveniles, together with information on the reproductive biology of the snail-eating snake *Sibon nebulatus*, based on specimens from isolated humid montane forest enclaves ("Brejos de Altitude") in the state of Ceará, northeastern Brazil. These forests are situated within the Neotropical dry diagonal and host locally abundant yet understudied populations that are currently threatened by intense human activity and habitat fragmentation. Such isolation may influence ecological and life-history traits, underscoring the importance of baseline biological data for conservation. We examined 72 individuals, including 53 adults (26 females and 27 males) and 19 juveniles. Adult males and females showed no difference in snout–vent length, but males had relatively longer tails. Cranial measurements were largely overlapping between sexes. Reproductive data reveal a seasonal cycle linked to rainfall, with follicular development occurring at the start of the rainy season and oviductal eggs observed from June to September. Clutch size ranged from two to six eggs. These results expand current knowledge of intraspecific variation in life-history traits and provide an empirical basis for future comparisons across the distribution of *S. nebulatus*.

Key words:

Brejos de Altitude, Neotropical snakes, Natural history, Reproduction, Sexual dimorphism.

Studies of natural history are fundamental for understanding ecological niches, life cycles, and reproductive strategies, as well as for supporting conservation actions, particularly in tropical regions where basic biological data on snakes remain scarce (Greene, 1988; Martins et al., 2021; Maschio et al., 2023). Reproduction, in particular, represents one of the most critical components of life-history strategies and may exhibit strong seasonality in tropical environments, driven by variation in precipitation, temperature, and food availability (Seigel & Ford, 1987; Brown & Shine, 2006). Because reproductive investment and selective pressures often differ between males and females, studies of sexual dimorphism provide important insights into reproductive ecology, mating systems, and life-history evolution. In snakes, sexual dimorphism encompasses a range of traits, including differences in body size and proportions, scale counts and morphology, and the position or size of internal organs and glands. These differences are key to understanding reproductive strategies, sexual selection, and patterns of resource use (Shine, 1993; Keogh & Walach, 1999). Dipsadidae (Bonaparte, 1838) is one of the most diverse snake families in the Neotropical region (Uetz & Hošek, 2026). Within this family, the genus *Sibon* Fitzinger, 1826 includes *S. nebulatus* (Linnaeus, 1758). Recent taxonomic revisions have substantially changed the delimitation of the *Sibon nebulatus* complex. Fouquet et al. (2025) restricted *S. nebulatus* sensu stricto to populations ranging from Colombia to northeastern Brazil, including those from the humid forest enclaves of Ceará. In contrast, the Central American populations previously referred to as *S. nebulatus*, including those examined by Lewis et al. (2013), are now recognized as *Sibon* aff. *nebulatus*. Consequently, much of the published information on the morphology, ecology, and natural history previously attributed to *S. nebulatus* actually refers to a different taxonomic entity. This taxonomic reassessment highlights the need for biological studies focused on populations unequivocally assigned to *S. nebulatus* sensu stricto under the current taxonomic framework. The species is oviparous (Savage, 2002), exhibits generalist habitat use, and is specialized in the consumption of gastropods (Quirino et al., 2024). Nevertheless, information on life-history traits—such as sexual maturity, fecundity, and reproductive cycles—remains lacking across much of its range.

In the state of Ceará, northeastern Brazil, the species occurs in humid forest enclaves at high elevations, known as "Brejos de Altitude," and is found in the Ibiapaba, Baturité, Maranguape, and Aratanha massifs (Roberto & Loebmann, 2016). These forested landscapes are embedded within a semi-arid matrix and are recognized for promoting microendemism and ecological isolation (Borges et al., 2003; Guillory et al., 2025). These forest enclaves are increasingly threatened by habitat loss, wildfires, real estate expansion, and climate change, all of which may severely impact isolated snake populations and underscore the urgent need for baseline biological and reproductive data (Tabarelli et al., 2005; Gibbons et al., 2000; MapBiomas, 2025). In this context, sexual dimorphism and reproductive studies are essential for understanding the ecology of snake populations inhabiting relict forest fragments.

In this study, we investigated sexual dimorphism and reproductive ecology of *Sibon nebulatus* sensu stricto based on specimens from isolated humid montane forest enclaves in Ceará, northeastern Brazil, aiming to provide baseline life-history data and contribute to a broader understanding of the biology of this taxon, particularly in the context of habitat heterogeneity and fragmentation.

MATERIAL AND METHODS

Specimens of *S. nebulatus* (Figure 1) were collected at 10 sampling points across four "Brejos de altitude" in the state of Ceará, northeastern Brazil: Planalto da Ibiapaba, Maciço de Baturité, Serra de Maranguape, and Serra da Aratanha (Figure 2). These areas are relictual highland enclaves (≥600 m elevation) covered by remnants of Atlantic and Amazon rainforests (de Medeiros 2020).



Figure 1. *Sibon nebulatus* from "Brejos de Altitude", Ceará State, northeastern Brazil. (Photo: Átilas Rodrigues).

The Planalto da Ibiapaba, including the municipalities of Ubajara, Ibiapina, and São Benedito, presents the highest annual rainfall in the state (e.g., São Benedito: 2,062.8 mm; Ibiapina: 1,744.6 mm; Ubajara: 1,441 mm) and mean temperatures ranging from 22 to 26°C (Funceme 2014). The Maciço de Baturité, encompassing the municipalities of Baturité, Guaramiranga, Mulungu, Aratuba, and Pacoti, exhibits climatic variation along the elevation gradient, with higher elevations characterized by a mean annual temperature of 22.6°C, a hot sub-humid tropical climate, and mean? annual rainfall of 1,089.7 mm (Funceme 2007). The Serra de Maranguape, located in the Metropolitan Region of Fortaleza, is a pre-littoral residual massif reaching 920 m in elevation and extending across the municipalities of Maranguape, Maracanaú, and Caucaia, approximately 30 km from the coast (Arruda 2001). Annual precipitation exceeds 1,300 mm, with mean temperatures between 23 and 26°C (Ceará 2002), and vegetation composed of Tropical Rain Subcaducifolia Forest (dry forests) and Tropical Pluvio-Nebular Subperennial Forest (wet forests) (Fernandes 1998). The Serra da Aratanha, situated between the municipalities of Pacatuba and Maracanaú, is a residual massif characterized by a humid forest enclave within the semi-arid Caatinga domain, with mean temperatures around 26°C, a hot humid tropical climate, and a rainy season from January to May (ICMBio 2012).

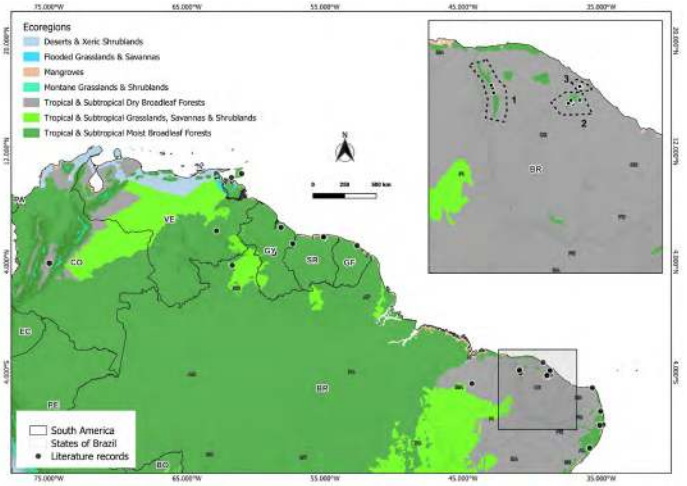


Figure 2. Geographic distribution of *Sibon nebulatus* in South America, highlighting literature records and sampling sites in the "Brejos de Altitude" of Ceará, northeastern Brazil. Numbered localities correspond to: (1) Planalto da Ibiapaba (Ubajara, Ibiapina, and São Benedito), (2) Maciço de Baturité (Baturité, Guaramiranga, Mulungu, Aratuba, and Pacoti), (3) Serra de Maranguape (Maranguape, Maracanaú, and Caucaia), and (4) Serra da Aratanha (Pacatuba and Maracanaú). Country abbreviations: BR = Brazil, CO = Colombia, EC = Ecuador, VE = Venezuela, GY = Guyana, SR = Suriname, and GF = French Guiana. Adapted from Fouquet et al. (2025).

A total of 72 individuals were examined, including 53 adults (26 females and 27 males) and 19 juveniles, primarily from the Herpetological Collection of the Universidade Federal do Ceará (CHUFC). Three additional individuals were obtained through recent field collections conducted under SISBio permit 29613-6 and from secondary collections associated with other research projects (Aratuba and Maranguape). For each specimen, we recorded snout–vent length (SVL), tail length (TL), head length (HL), and head width (HW). Collection month was obtained from specimen labels and field records and used to characterize reproductive seasonality. Sex was determined through gonadal inspection (see Ávila et al., 2006). Males were classified as reproductively active when convoluted epididymides were observed, whereas females were considered reproductive when vitellogenic follicles or eggs were present. Sexual maturity was estimated based on the smallest individual exhibiting these reproductive traits—that is, the smallest female with vitellogenic follicles or eggs

and the smallest male with convoluted epididymides. Juveniles were excluded from all analyses of sexual dimorphism. Differences between males and females in snout–vent length (SVL), tail length (TL), head length (HL), and head width (HW) were evaluated using Student's t-tests after verifying the assumptions of normality and homogeneity of variances. Additionally, separate analyses of variance (ANOVAs) were performed to test for sex differences in each morphological variable. Statistical analyses were conducted in R version 4.4.0 (R Core Team, 2025), and statistical significance was set at $\alpha = 0.05$.All procedures were approved by the Animal Ethics Committee of UFC (CEUA-UFC protocol 6314010321).

RESULTS AND DISCUSSION

Adult females exhibited a SVL of 40.2 ± 6.1 cm (33.0–57.5), whereas males averaged 41.0 ± 6.2 cm (29.6–51.0). No significant difference in SVL was detected between sexes ($t = -0.60$; $p = 0.5485$; Figure 3). In contrast, relative TL was significantly longer in males (14.6 ± 2.9 cm [8.8–18.5]) than in females (13.0 ± 2.6 cm [7.5–18.0]) (ANOVA: $F = 4.709$; $p = 0.0347$), a pattern consistent with sexual dimorphism associated with the male tail base in Neotropical snakes (Greene, 1988; Vitt, 2013). Head length was 1.9 ± 0.3 cm (1.4–2.5) in females and 1.8 ± 0.2 cm (1.4–2.1) in males, whereas head width measured 1.0 ± 0.2 cm (0.6–1.5) in females and 1.0 ± 0.2 cm (0.5–1.3) in males, indicating minor and non-systematic differences between sexes. The morphometric pattern observed for *Sibon nebulatus* is broadly consistent with previous studies on the genus. Lewis et al. (2013) reported that females of *S. aff. nebulatus* tended to be larger than males in SVL, total length, and body mass, although these differences were not statistically significant. Our results corroborate the absence of significant sexual size dimorphism in SVL and further indicate that males exhibit proportionally longer tails than females. The absence of SVL dimorphism aligns with findings for other *Sibon* species (Lewis et al., 2013) but contrasts with other Dipsadini, where females are typically larger (Pizzato et al., 2008b). Conversely, the male-biased TL dimorphism observed here diverges from the pattern reported for other *Sibon* (Lewis et al., 2013) but agrees with data for other Dipsadini species (Pizzato et al., 2008b), in which longer male tails are frequently associated with arboreal or semi-arboreal habits (Pizzato & Marques, 2007). This pattern is further supported by the broader dipsadid literature, where longer tails in males are linked to the presence of hemipenes and associated musculature (Shine, 1993; Kissner et al., 1998; Keogh & Walach, 1999). The lack of pronounced differences in SVL and head dimensions reinforces that sexual dimorphism in *S. nebulatus* is modest and largely confined to reproductive structures. The overall body size recorded for our specimens also falls within the range reported for *S. nebulatus* in Central America. Lewis et al. (2013) found mean adult SVLs ranging from approximately 486–537 mm for *S. nebulatus*, whereas the remaining *Sibon* species (*S. annulatus* (Günther, 1872), *S. argus* (Cope, 1876), and *S. longifrenis* (Stejneger, 1909)) generally exhibited mean SVLs between 322 and 385 mm, reinforcing the relatively large body size of *S. nebulatus* throughout its geographic distribution.

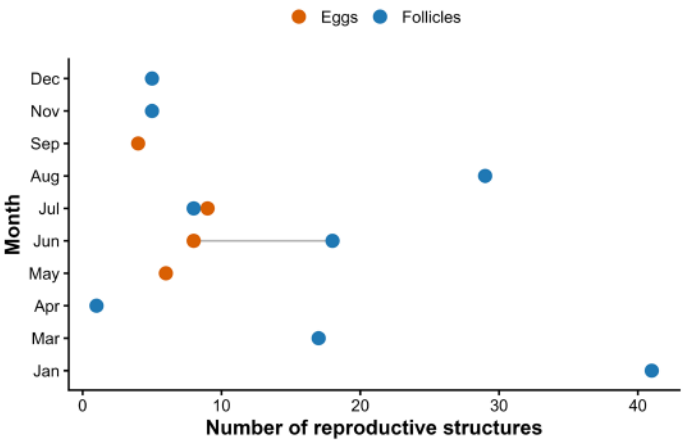


Figure 3. Seasonal variation in the number of follicles and eggs recorded in female specimens throughout the year. Each point represents the total number of reproductive structures observed in females examined during a given month. The gray line connects follicles and eggs recorded within the same month to facilitate comparison between reproductive conditions.

Principal Component Analysis (PCA) revealed extensive morphological overlap between males and females (Figure 4), indicating that the only consistent dimorphic trait is tail length. The first principal component

(PC1) explained 56.8% of the total variance, and the second component (PC2) explained 21.6%. Extensive overlap between sexes indicates weak overall morphological differentiation, with consistent sexual dimorphism restricted to relative TL.

Nineteen juvenile individuals (11 males and 8 females) from different montane forest localities were examined. In juvenile males, SVL ranged from 15.5 to 39.0 cm and TL from 4.9 to 12.0 cm. Juvenile females exhibited SVL ranging from 16.0 to 34.22 cm and TL from 4.5 to 10.1 cm. Head length ranged from 1.0 to 1.6 cm in males and from 1.0 to 1.5 cm in females; head width varied from 0.3 to 0.9 cm in males and from 0.4 to 0.9 cm in females. However, these specimens were excluded from the formal sexual dimorphism analysis because they were sexually immature. The observed variation is consistent with ontogenetic growth rather than sex-related differentiation. These data represent the first organized morphometric dataset for juvenile *S. nebulatus*.

Among the 26 adult females examined, 24 (92.3%) exhibited reproductive activity. Vitellogenic follicles were recorded during most of the year, with the highest frequencies in January, March, and August. Oviductal eggs were observed mainly between March and September, peaking in June. No reproductive females were recorded in May or October (Figure 3).

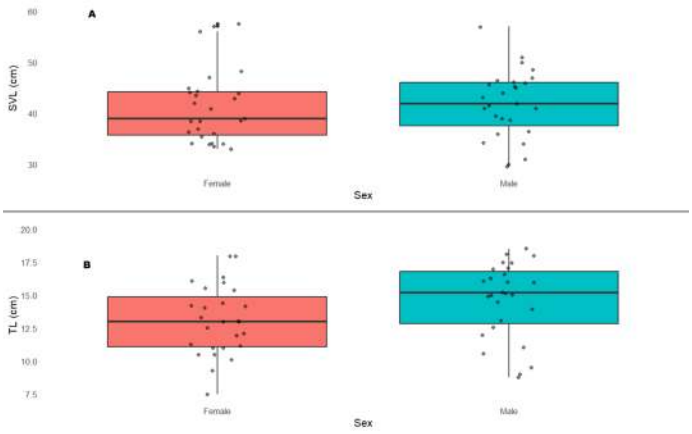


Figure 4. Boxplots of snout–vent length (SVL, in A) and of tail length (TL, in B) for adult female (in coral) and male (in blue) of *Sibon nebulatus* from Ceará, northeastern Brazil. Dots represent individual specimens.

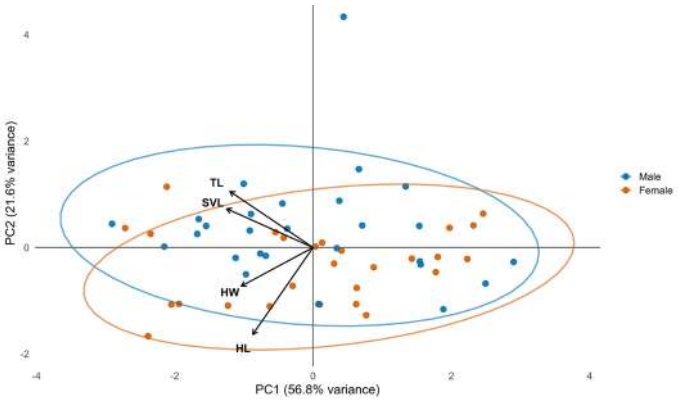


Figure 5. Principal Component Analysis (PCA) of morphological traits based on scaled morphological variables: snout–vent length (SVL), tail length (TL), head length (HL), and head width (HW) of adults of *Sibon nebulatus* from 'Brejos de Altitude' in Ceará. Ellipses represent 95% confidence regions for males (blue) and females (orange).

Clutch size ranged from 2 to 6 eggs (mean = 4.33; N = 6 ovigerous females), values consistent with reproductive patterns documented for other oviparous Neotropical Dipsadini (Pizzato et al., 2008b; Santos-Costa et al., 2015; Marques et al., 2016; França et al., 2020). Although primary and secondary follicles were recorded across multiple months, only females bearing oviductal eggs allowed accurate estimation of clutch size. Overall, these data indicate a seasonal reproductive cycle, with follicular development concentrated at the onset of the rainy season and oviposition occurring from March to September, a pattern likely associated with climatic conditions, prey availability, and suitable microhabitats for egg incubation, as reported for other South American snakes (Brown & Shine, 2004; Loebmann & Haddad, 2010; Pizzato & Marques, 2007; Pizzato et al., 2008a). The populations analyzed here occur in isolated humid forest enclaves surrounded by extensive semiarid Caatinga, a landscape configuration that may restrict gene flow and promote divergence in life-history traits. In light of the genetic differentiation reported for northeastern Brazilian populations by Fouquet et al. (2025), the reproductive traits documented here may represent local ecological adaptations rather than species-wide patterns. Because Fouquet et al. (2025) demonstrated that most previous records assigned to *Sibon nebulatus* actually correspond to distinct evolutionary lineages, the present study provides the first life-history dataset that can be unequivocally

assigned to *S. nebulatus* sensu stricto. Consequently, these data establish the first reliable baseline for future ecological and comparative studies of the species under the current taxonomic framework.

The data presented herein constitute the first integrated dataset on morphometry, sexual dimorphism, and reproductive ecology of *S. nebulatus* strictu sensu, particularly from isolated montane forest enclaves in Ceará, Brazil. These systems harbor more than 50 endemic vertebrate and invertebrate species and represent highly vulnerable environments, where baseline natural history data are essential for informing local conservation strategies (e.g., Gibbons et al., 2000; Marques et al., 2009). Thus, our results expand current knowledge of the species' natural history and provide an important baseline for conservation planning in highly threatened forest habitats.

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Appendix 1. Examined material

Sibon nebulatus (N = 72). **Brazil: Ceará:** specimens deposited in the Herpetological Collection of the Federal University of Ceará (CHUFC). **Maciço de Baturité** (Acarape, Baturité, Guaramiranga, Mulungu, Pacoti, Aratuba): CHUFC 1347, 1379, 1380, 1383, 1516–1519, 1520, 2009, 2175, 2237, 2459, 2460, 2479, 2606, 2608, 2618, 2621, 2771, 2773, 2777–2780, 2785, 2788–2793, 2795–2799, 2800–2801, 2836–2838, 3632, 3715, 3735, 3765, 3818, 4232, 4265, 4424–4425, 4529, 4531, 4533, 4534. **Serra de Maranguape** (Maranguape): CHUFC 2788, 2800, 3287, 3632, 3765, 4507–4508, 4529. **Planalto da Ibiapaba** (Ibiapina, São Benedito, Ubajara): CHUFC 2106, 2124, 2138, 2602, 2776, 2782, 2784, 2797–2798, 4036–4037, 4074.



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