

On delicate night hunters: observations of the feeding behaviour of *Imantodes cenchoa* (Linnaeus, 1758) and *Sibon nebulatus* (Linnaeus, 1758) through staged and natural encounters (Serpentes: Dipsadidae: Dipsadinae)

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The food animals eat and the way they obtain that food are central in species ecology (Curio, 1976; Slip and Shine, 1988). Feeding habits of snakes are of particular interest because they show remarkable adaptations for locating, capturing, subduing, and ingesting a wide array of prey (Cundall and Greene, 2000). Snakes' diets vary within and between taxa due to evolutionary history, ontogeny, as well as differences in prey size, prey type, aspects of foraging, and microhabitat use (Greene, 1997; Cundall and Greene, 2000; Alencar et al., 2013). Detailed knowledge on feeding ecology and behaviour of several species is poorly understood, especially for neotropical species (e.g., Marques and Sazima, 1997; Alencar et al., 2013). Most of the data available about feeding behaviour of snakes comes from single observation (e.g., Rojas-Morales et al.,

2017; Guedes et al., 2018a; Mario-da-Rosa et al., 2020), captivity (e.g., Braz et al., 2006; Rojas-Morales, 2013), or by encounters in the wild (e.g., Sazima, 1974, 1989; Gómez-Hoyos et al., 2015).

Among neotropical arboreal snakes, species in general such as *Imantodes* Duméril, 1853 and *Sibon* Fitzinger, 1826 show a compressed body, disproportionately slender neck, big and movable eyes, and a blunt head, making them easy to distinguish from other sympatric snakes. Other than their morphological similarity, arboreal niche, and nocturnal activity pattern (Ray, 2012), these groups have a substantially different diet. *Imantodes* prey mainly upon *Anolis* lizards (Duellman, 1978; Martins and Oliveira, 1998; Savage, 2002; Sousa et al., 2014), with frogs and amphibian eggs also recorded (Zug et al., 1979; Martins and Oliveira, 1998). In contrast, *Sibon* are included among the so-called "goo-eaters" (Cundall and Greene, 2000; Savage, 2002; Zaher et al., 2014), which exhibit a feeding strategy based on the consumption of small, soft-bodied invertebrates, including slugs and land snails. Goo-eaters have a specialized dentition and glandular toxins secreted by the infralabial glands to extract snails from their shells (Sheehy, 2013; Zaher et al., 2014). *Sibon* may also feed on annelids and amphibian eggs (Ray et al., 2012; Ward, 2016).

Imantodes cenchoa (Linnaeus, 1758) and *Sibon nebulatus* (Linnaeus, 1758) share a similar geographical distribution, ranging from southeastern Mexico across Central America into northern South America (Guedes et al., 2018b), inhabiting primary and second-growth forests, shrubs, and crops from sea level to 2300 m in elevation (Myers, 1982; Savage, 2002; Solórzano, 2004; Rojas-Morales et al., 2014, Missassi and Prudente, 2015). Both species are commonly syntopic in forested habitats in Colombia at elevations below 1500 m, where they are also usually one of the most frequently

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encountered species. We here report observations on the feeding behaviour of *I. cenchoa* and *S. nebulatus* from staged (with potential prey) and natural encounters in natural habitat of the northern Andes of Colombia with potential prey.

Materials and Methods

Localities. Our observations were made independently during fieldwork at two sites. Two staged observations were made from 21:30–00:40 h on 12–13 December 2019 at the edge of the Mistrató River, 1 km from the upper Morro-Azul Hydroelectric Dam, Belén de Umbria Municipality, Risaralda Department, Colombia (5.2333°N, 75.8160°W, elevation 1290 m). A third, natural observation was made from 20:45–21:40 h on 18 July 2020 at the “Bolloliso” stream, Berlín Village, Samaná Municipality, Caldas Department, Colombia (5.5897°N, 74.9456°W, elevation 807 m). At these localities, the landscape is a heterogeneous matrix of shade-cultivated coffee, banana and avocado crops, as well as cattle ranches and secondary forest remnants distributed along hill slopes and rivers (Rojas-Morales et al., 2018). Temperature and relative humidity in the region range from 15–20°C and 80–90%, respectively, with 2000–3000 mm of mean annual precipitation (Villada-Bedoya and Cultid-Medina, 2017).

Predatory encounters. At the first locality we found one individual of *S. nebulatus* (snout–vent length, SVL = 577 mm; tail length, TL = 179 mm) and one of *I. cenchoa* (SVL = 734 mm, TL = 312 mm) in secondary forest. Both snakes were captured, measured, photographed, and kept in moistened cloth bags. A day later, and before releasing snakes, we found two potential prey items for both snakes: a veronicellid slug (Gastropoda: Soleolifera: Veronicellidae; total length ca. 30 mm) for *S. nebulatus* and an adult *Anolis antonii* Boulenger, 1908 (Squamata: Polychrotidae) for *I. cenchoa*. The staged – or provoked – encounters consisted of offering a single prey item to each snake and to observe the interaction. To initiate the encounter, one of us held the snake at the posterior part of its body and slowly approached the prey to a distance of 20–30 cm from the snake. The snake was then released gently. Encounters took place in the same microhabitats, where prey was observed to occur during the night. At the second locality, we found a juvenile *I. cenchoa* preying upon a robber frog, *Craugastor metriosistus* Ospina-Sarria et al., 2015, and we describe this as a natural prey-predator encounter.

Images and video. Three feeding sequences were

recorded through video and still photography, which are used to illustrate and support descriptions of predatory behaviour. Videos are available as supplemental material (see Appendix). Video recordings of the prey-predator encounters were recorded with a Nikon D5300 camera in the HD video mode. Behavioural sequences were time-monitored from the point when the snake detected the prey until it began to move away after predation. We classified encounters using four phases (detection, subjugation, manipulation, ingestion) and we quantified the time taken for each with a digital stopwatch while also describing the behaviours displayed. We edited videos using Filmora9 for Windows version 9.3.5.8 (Wondershare Technology, Shenzhen, Guangdong, China; www.wondershare.com).

Results

***Sibon nebulatus*, staged encounter.** The staged encounter of *S. nebulatus* (Fig. 1; Supplementary Material 1) occurred on 13 December 2019 at 21:30 h. During a first attempt, the snake was released near the slug but passed it. We recaptured the snake and re-released it, and the snake was now attracted by the slug, focusing on its movements. The snake slowly approached the slug until it was able to touch it using fast tongue flicks, and then it immediately attacked from a distance of 30 mm by grasping the slug at the middle of its body (Fig. 1A, B). The snake then lifted the slug and manipulated it through synchronized lateral movements of the lower jaws until it swallowed the slug head-first (Fig. 1C, D). The slug was still alive when the snake swallowed it. The encounter with the slug lasted 1:33 min. After ingestion of the slug, the snake gaped its mouth ten times in 1–2 s intervals (Supplementary Material 1), then began to move slowly on the forest floor until it was out of sight. We did not see any mucus layer after the slug had been swallowed (Supplementary Material 1).

***Imantodes cenchoa*, staged encounter.** The encounter between *I. cenchoa* and *A. antonii* was staged on 13 December 2019 starting at 23:01 h (Fig. 2; Supplementary Material 2). We first located *A. antonii* sleeping on grass leaves 0.5 m above the ground along the forest edge. One of us held the snake close to the male lizard, which woke up, noticed the presence of the snake, and quickly fled towards the stem of the grass. The snake remained motionless for 12 min and did not appear to be interested in pursuit. We repeated the staging with a second lizard, a female located only 0.3 m from the escaped male. We placed the snake at a distance of 0.2 m from the lizard. The snake detected



Figure 1. Feeding behaviour during a staged encounter of an adult *Sibon nebulatus* preying upon a veronicellid slug in the central Andes of Colombia. (A) Grasping the slug at midbody. (B) Manipulation to place the slug into a head-first position. (C) Initial swallowing of the slug, head-first. (D) Completion of swallowing. Note the movement of the lower mandibles to ingest prey. Images extracted from Supplementary Material 1. Photo editing by Julián A. Rojas-Morales.

the prey by moving its eyes toward the lizard and by tongue-flicking (Fig. 2A). The snake then retracted the anterior third of its body into a sinusoidal strike position, slowly approached the lizard until it almost touched it, tongue-flicked for 45 s, and then struck the lizard at mid-body (Fig. 2B). The attack allowed the snake to grasp the lizard by the middle of its body, close to the pelvis (Fig. 2C). The lizard tried to save itself by biting the head of the snake several times, but without getting the snake to release it (Fig. 2C). By the force of the interaction, after hanging for 2 min in the vegetation at a height of 0.3 m both snake and lizard fell to the ground. After the participants fell on the ground, the lizard was still alive and continued to bite the snake. However, the snake never released the lizard after the initial strike and repeatedly bit and chewed the posterior area of the dorsum for 43 min (Fig. 2D). Marks of bites with saliva from the snake were noted and 17 min after attack the prey was immobile, likely dead. We assume its demise because it closed its eyes, stopped moving, and her breathing was not noticeable from that moment. After that, the snake began to manipulate the lizard

using jaw movements in a posterior–anterior direction along the prey, which allowed it to locate the lizard’s head (time elapsed: 6 min). At 23:43 h, 42 min after the initial attack, the snake began swallowing the prey head-first (Fig. 2E, F). The total time taken to swallow the lizard was 23 min (Table 1).

***Imantodes cenchoa*, natural encounter.** A juvenile *I. cenchoa* was observed preying upon a robber frog, *Craugastor metriosistus* Ospina-Sarria et al., 2015 (Fig. 3B; Supplementary Material 3). We found both snake and frog after hearing the defensive call of the frog (Köhler et al., 2017). At the beginning of our observation, the snake was holding the frog by the head and forelimbs (Fig. 3A). While issuing its defence call, the frog fought the snake by using its hindlimbs to push against the jaws of the snake, but the snake never released the frog. We observed the encounter for 35 min (20:45–21:20 h). Although the process of swallowing could not be observed until the end, the death of the frog was evident because it stopped moving and, based on the position of its head in the jaws of the snake it is most likely that it was swallowed head-first.

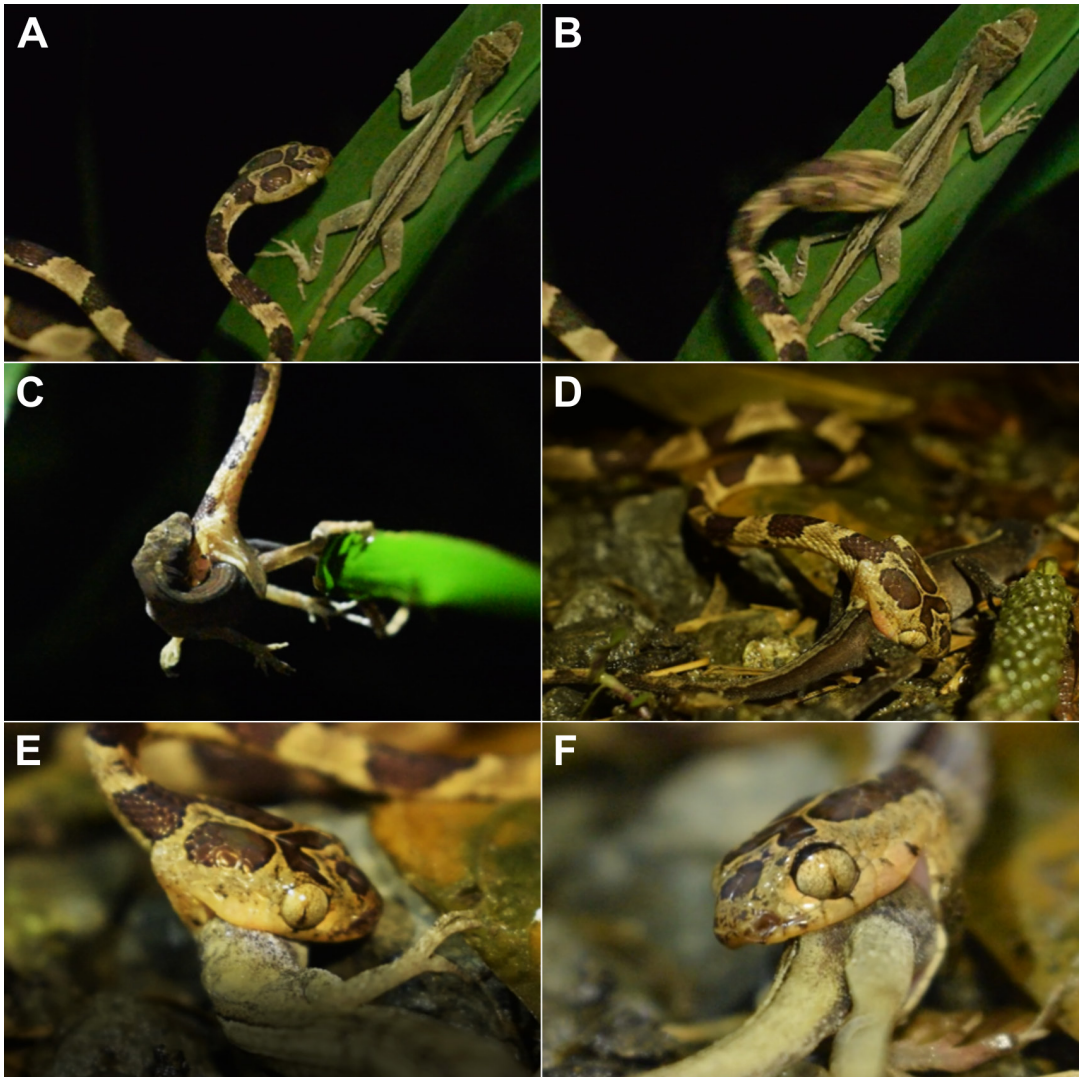




Figure 2. Feeding behaviour during a staged encounter of an adult *Imantodes cenchoa* preying upon a female *Anolis antonii* in the central Andes of Colombia. (A) Approaching and detecting prey. (B) Attacking with a sudden strike. (C) Subjugating prey while hanging off a perch, while receiving defensive bites from the prey. (D) Injecting toxins into the prey using repeated movements of the head. (E) Manipulating the lizard to locate its head. (F) Swallowing the prey by synchronous movements of the lower mandibles and lateral movements of the head. Images extracted from Supplementary Material 2. Photo editing by Julián A. Rojas-Morales.

Discussion

The staged encounter between *S. nebulatus* and the slug allowed us to observe the sequence and timing of feeding activity in this species in detail for the first time in the field. The behaviour we observed is similar to that already reported for captive specimens of *S. nebulatus*

by Sheehy (2013), which consisted of initial visual attraction in the line of sight, followed by scent (fast tongue-flicking), grasping by the head, lifting into the air, and swallowing. Sheehy (2013) also observed that snakes rubbed the side of their mouth on the ground in an effort to rid themselves of the large amount of thick mucus left behind, a behaviour we did not observe. In our encounter, the snake gaped its mouth several times

Table 1. Comparisons between the feeding behaviour of *Sibon nebulatus* and *Imantodes cenchoa*. Prey items were a slug (Gastropoda: Veronicellidae) for *S. nebulatus* and a female *Anolis antonii* (Squamata: Polychrotidae) for *I. cenchoa*. Arrows indicate the feeding behaviour sequence observed. Photo editing by Julián A. Rojas-Morales.

<u>Feeding behaviour phase</u>	 <i>Sibon nebulatus</i>	 <i>Imantodes cenchoa</i>
Detection	Eye fix Tongue flick 30 sec	Eye fix Tongue flick Strong breath 45 sec
↓		
Attacking	Instant attack after detection Strike and bite without releasing prey	Investigate pre-attack Strike and bite without releasing prey
↓		
Subjugation	Holding prey Prey no offers resistance. Lasted few seconds	Holding prey while injecting toxins Prey offers resistance 43 min
↓		
Manipulation	Fast manipulation with lower jaws 50 sec	Repetitive bites in posterior-anterior direction to locate the head of the prey 6 min
↓		
Swallowing	Fast swallow (43 sec) Head-first ingestión. Prey still alive.	Slow swallow (23 min). Head-first ingestion. Dead prey before swallowing

after prey ingestion, which may be a means to deal with mucus or reset the jaw bones. The feeding behaviour observed for *S. nebulatus* is similar to that observed in *Tropidodipsas philippii* (Jan, 1863) and *T. annulifera* Boulenger, 1894 when preying upon slugs. However, it is a completely different feeding behaviour than when these species prey upon snails, which demands greater handling time and energy cost to pull the snail's soft body out of its hard shell (Sheehy, 2013). We did not test the preference of prey (slug or snail) for *S. nebulatus* in this study.

The stage encounter between *I. cenchoa* and the lizard reinforced that the species is an active nocturnal predator that forages mostly on the vegetation and captures prey that is asleep in this type of microhabitat. The main prey of *I. cenchoa* are lizards (Henderson and Nickerson, 1976; Martins and Oliveira, 1998; Sousa et al., 2014). Martins and Oliveira (1998) recorded an adult *I. cenchoa* from Acre, Brazil, ingesting an *A. fuscoauratus* on a tree 1.8 m above the ground. The head-first ingestion corroborates what is known for *I. cenchoa*

(Sousa et al., 2014) as well as for most alethinophidian snakes (e.g., Marques and Sazima, 1997; Cundall and Greene, 2000; Guedes et al., 2018a). Although some of our observations had already been documented in dietary studies of individuals later deposited in scientific collections (e.g., Sousa et al., 2014), our study provides some additional data regarding the feeding behaviour displayed by *I. cenchoa* and allows comparisons with other species of snakes that prey upon lizards.

Additionally, to the best of our knowledge, ours is the first record of predation by *I. cenchoa* on *C. metriosistus* in the wild. Different authors suggest that *I. cenchoa* is a mainly saurophagous snake, with *Anolis* species as its main dietary items. Henderson and Nickerson (1976) indicated that *I. cenchoa* always fed on lizards, and that individuals rejected small frogs under semi-natural conditions. Because this snake species is easily kept in captivity (see Henderson and Nickerson, 1976), it could be assessed whether prey diversification exists in other populations, as in the northern Andes.

Our observations on the behaviour displayed by *S.*

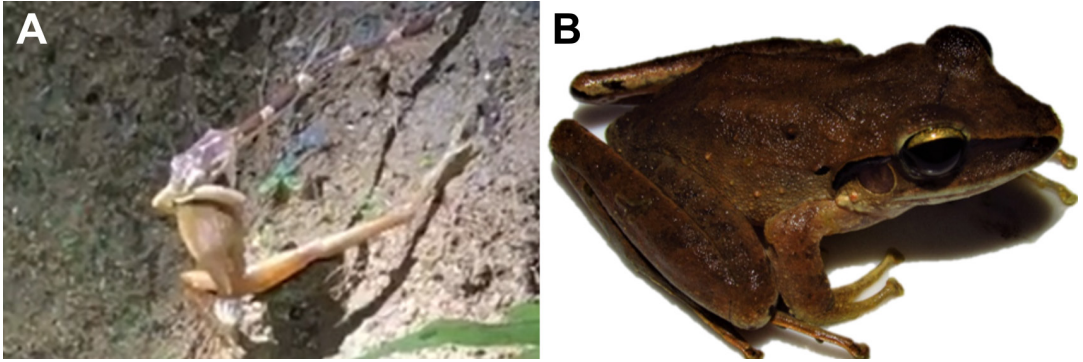


Figure 3. (A) Predation of a *Craugastor metriosistus* (Anura: Craugastoridae) by *Imantodes cenchoa* in Samaná Municipality, Caldas Department, central Andes of Colombia. The image was extracted from Supplementary Material 3. (B) An adult male *C. metriosistus* from the Manso River in the same municipality. Photo by Mateo Marín. Photo editing by Julián A. Rojas-Morales.

nebulatus and *I. cenchoa* show a remarkable difference in the cost and time of predation (Table 1), validating the general suggestion by Cundall and Greene (2000) for these species. Since observations of feeding behaviour in the wild are scarce and generally serendipitous for most snake species (Sazima, 1989; Cundall and Greene, 2000), conducting staged encounters in nature, using potential prey from the same habitat, is a useful strategy to observe feeding behaviour in the wild and better understand the evolution of the foraging mode among the species (e.g., Sazima, 1989; Rojas-Morales et al., 2017). However, staged encounters are not commonly used in observations with snakes, in part because it is more expedient to deduce feeding behaviours from snakes' diets via specimens deposited in scientific collections. We highlight that both data are important and complete knowledge comes when they turn complementary.

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Appendix

The following supplementary materials are available online:

Supplementary Material 1. Video of a staged encounter between an adult *Sibon nebulatus* and a veronicellid slug (Gastropoda: Veronicellidae) to show the details of the snake's feeding behaviour. The video was recorded on the night of 12 December 2019 in Belén de Umbría Municipality, Risaralda Department, Colombia. Available at: <https://www.youtube.com/watch?v=wTZsuGk58r8>.

Supplementary Material 2. Video of a staged encounter between an adult *Imantodes cenchoa* and the lizard *Anolis antonii* to show the details of the snake's feeding behaviour. The video was recorded on the night of 12–13 December 2019 in Belén de Umbría Municipality, Risaralda Department, Colombia. Available at: <https://www.youtube.com/watch?v=TzHMBwPkgss>.

Supplementary Material 3. Video showing the natural encounter of a juvenile *Imantodes cenchoa* preying upon a robber frog, *Craugastor metriosistus*. The video was recorded during the night of 18 July 2020 in Samaná Municipality, Caldas Department, Colombia. Available at: https://www.youtube.com/watch?v=QQZ_NKN4S2w&t=1s&ab_channel=Julio%3%A1nRojas.