SALAMANDRA **56**(1): 39–47
15 February 2020 | ISSN 0036–3375

SALAMANDRA
German Journal of Herpetology

A fisherman's tale:
Activity, habitat use and the first evidence of lingual lure behavior in a South American snake

Conrado Mario-da-Rosa[1], Arthur Diesel Abegg[2,3], Leandro Malta-Borges[1], Alexandre Ferreira Righi[4], Paulo Sérgio Bernarde[5], Sonia Zanini Cechin[1] & Tiago Gomes dos Santos[1,6]

1) Programa de Pós-Graduação em Biodiversidade Animal, Universidade Federal de Santa Maria, Av. Roraima, 1000, Santa Maria, Rio Grande do Sul, Brazil

2) Laboratório Especial de Coleções Zoológicas, Instituto Butantan, Av. Vital Brasil, 1500, São Paulo, São Paulo, Brazil

3) Programa de Pós-Graduação em Zoologia, Instituto de Biociências, Universidade de São Paulo, Travessa 14, Rua do Matão, 321, 05508-090, São Paulo, São Paulo, Brazil

4) Museu de História Natural e Jardim Botânico da Universidade Federal de Minas Gerais, R. Gustavo da Silveira, 1035, Belo Horizonte, Minas Gerais, Brazil

5) Laboratório de Herpetologia, Centro Multidisciplinar, Campus Floresta, Universidade Federal do Acre, Cruzeiro do Sul, Acre, Brazil

6) Universidade Federal do Pampa, Campus São Gabriel, Av. Antônio Trilha, 1847, São Gabriel, Rio Grande do Sul, Brazil

Corresponding author: Conrado Mario-da-Rosa, e-mail: conradomdr@gmail.com

Manuscript received: 23 August 2019
Accepted: 25 November 2019 by Arne Schulze

Abstract. Literature data suggests that *Thamnodynastes strigatus* (Serpentes, Dipsadidae) is a snake that actively forages for anurans near waterbodies, using several microhabitats for this activity (e.g., shrubs, soil, and water). However, herein we present dissonant data previously known to the species, both concerning type of prey and foraging strategy. A total of 72 observations were performed exclusively at night, when snakes were in vegetation near streams in 93% of the cases. Among these observations, 41 were active snakes, and most of them (97%) were in an ambush position on the vegetation, peering at fishes. On two occasions, the snakes used a lingual lure behavior in order to attract fishes. This is only the sixth species in which this behavior has been observed, and the first in South America. Therefore, we provide additional data on *T. strigatus* habitat activity and habitat use, as well as unpublished data on ambush and lingual lure behavior for the Neotropical genus *Thamnodynastes*.

Key words. *Thamnodynastes strigatus*, nocturnal activity, ambush behavior, sub-arboreal, Uruguayan savannah.

Introduction

Data on the feeding ecology of any species aids in the understanding of its natural history, ecological requirements and the diverse approaches involved in the search for food and habitat use (Al-Sadoon & Parray 2016). In snakes, the most commonly observed criteria for habitat selection and use are the selection of better hibernation sites (Reinert 1993), safer refuges for predator avoidance (Martins 1993, Webb & Whiting 2005), or prey distribution and availability (Madsen & Shine 1996). Notably, the foraging environment is strongly related to the availability and abundance of potential prey (Bernarde et al. 2000a). Concerning basic hunting strategies, snakes may use the ambush method (Glaudas & Alexander 2017), the active search (Bernarde et al. 2000a) or even both, in different situations (Martins & Oliveira 1998). These foraging strategies are evolutionarily plastic and can be shaped by prey abundance and behavior (Vitt & Caldwell 2014). Some snakes, in association to the ambush-hunting method, use attractive exhibitionist displays to maximize prey capture success (Sazima 1991, Welsh & Lind 2000, Hansknecht 2008), also termed mimetic-aggressive behaviors (Glaudas & Alexander 2017). However, although visible growth in recent decades is noted (Bernarde et al. 2000b, Hartmann & Marques 2005), studies on snake feeding ecology are still scarce in the Neotropical region (Andrade et al. 2010, Braz & Marques, 2016), when compared to temperate northern hemisphere regions and the Australian continent (Shine 1988, Welsh & Lind 2000, Gibbons & Dorcas 2004, Hansknecht 2008).

The genus *Thamnodynastes* Wagler, 1830 comprises 20 species distributed throughout South America (Franco et al. 2017). *Thamnodynastes strigatus* (Günther, 1858) is a medium-sized snake that reaches about 800 mm in length (Giraudo 2001) and occurs in Argentina, Paraguay, Uruguay, and southern and southeastern portions of Brazil (Borges-Martins et al. 2007). Its diet consists of fishes, lizards, mammals and, predominantly, anuran amphibians (Bernarde et al. 2000b, Ruffato et al. 2003). The only in situ feeding ecology study concerning *T. strigatus* reported some anuran predation events and concluded that the species is an active forager that exploits different types of substrates at night (ground, vegetation, water body surface and interior) and uses undergrowth vegetation for daytime rest (Bernarde et al. 2000a). However, we found a *T. strigatus* population in the Uruguayan Savannah ecoregion (sensu Olson et al. 2001), southern Brazil, which differs remarkably concerning previously known hunting strategies and food items. Therefore, the aim of the present study is to describe this population's hunting strategies, habitat use and activity.

Material and methods

Study site

The fieldwork was performed in the Serra do Caverá region, in the east portion of the geomorphological unit named Cuesta de Haedo (Pilau 2011). This area is located between the municipalities of Rosário do Sul and Santana do Livramento, in southwestern state of Rio Grande do Sul (Brazil), in the Uruguayan Savannah ecoregion (30°21'41.16" S 55°15'53.15" W). The region is composed of a natural mosaic that includes steep elevations with flat or round ridges and flooded lowlands, both with the predominance of grasslands, besides arboreal-shrub vegetation restricted to stream banks and some hill slopes (Robaina et al. 2015). The climatic seasonality of the region is marked, with the four well defined seasons. The thermal amplitude is accentuated, ranging from -3°C during the winter to 39°C during the hottest months of the year (Wrege et al. 2012). Although the rainfall in the region is high and constant throughout the year (1400–1700 mm; Rossato 2011), a drop-in surface water availability (rainfall-evapotranspiration) is noted in the summer months (Wrege et al. 2012).

Sampling and data collection

Monthly samplings were carried out during one year, from August 2017 to July 2018 (except in June, due to logistical problems), with each field trip lasting 5–6 days. Searches for specimens were performed using the visual search method (McDiarmid et al. 2012). After sighted, the snakes were monitored at a minimum distance of 1.5 m, in order to minimize possible disturbances due to the presence of the field team. The following data were recorded at each encounter: (1) habitat use (macrohabitat = individuals found in an open or forest area; microhabitat = individuals found on soil, in the water surface, or on riparian vegetation; and height (cm) of the specimens perched on the substrate in relation to the water or soil surface, measured with a millimeter measuring tape); (2) activity pattern (active = specimens hanging on branches, perpendicular to the water surface (ambush position) or in motion; inactive = specimens that remained static on a substrate, with no signs of activity for at least 15 minutes) (adapted from Di-Bernardo et al. 2007); (3) air temperature (°C), determined using a digital thermo-hygrometer. Monthly average maximum and minimum temperatures were obtained from the Instituto Nacional de Meteorologia (INMET) (http://www.inmet.gov.br/portal/) for the Alegrete meteorological station, 78 km distant from the study area. These averages were used to test the relationship between the abundance of snake encounters and temperature extremes (minimum and maximum).

In order to describe *T. strigatus* ambush-hunting behavior, we opted for ad libitum observations (Altmann 1974), of active individuals and better observation conditions at each sampling (i.e. allowing for a nearby observation site with the least possible visual obstruction). Video recordings were made in order to document and characterize the duration of the displayed behaviors, using a Nikon Coolpix p510 camera. Additionally, the snout–vent length (SVL, to the nearest mm) and sex of the individuals (determined with eversion of hemipenis) observed in predation events were also recorded.

Statistical analyses

Student's t-test was applied to assess possible differences in the mean values of the behaviors exhibited by the snakes. Linear regressions were used to evaluate the relationship between snake abundance and air temperature (mean monthly minimum and maximum). An alpha < 0.05 was established for all statistical tests. All statistical analyses were carried out with the R software (R Core Team 2015).

Results

Activity and habitat use

A total of 72 *T. strigatus* specimen observations were made throughout the samplings, distributed during the hottest months of the year (November to April). A positive and significant relationship between the number of observations and the average minimum and maximum temperature was observed ($R^2aj = 0.45$; $p < 0.05$; $R^2aj = 0.45$; $p < 0.05$, respectively). A significant difference ($t = 2.49$, $p < 0.05$) regarding temperature and the respective snake activity pattern was noted, since active individuals were found in higher temperatures ($\bar{x} = 22.93 \pm 0.43$; $n = 45$) compared to inactive ones ($\bar{x} = 20.96 \pm 0.64$; $n = 22$) (Fig. 1a).

Individuals were found predominantly perched on riparian vegetation (97.18%, n = 69) compared to ground (1.41%, n = 1), or in streams (1.41%, n = 1). A significant

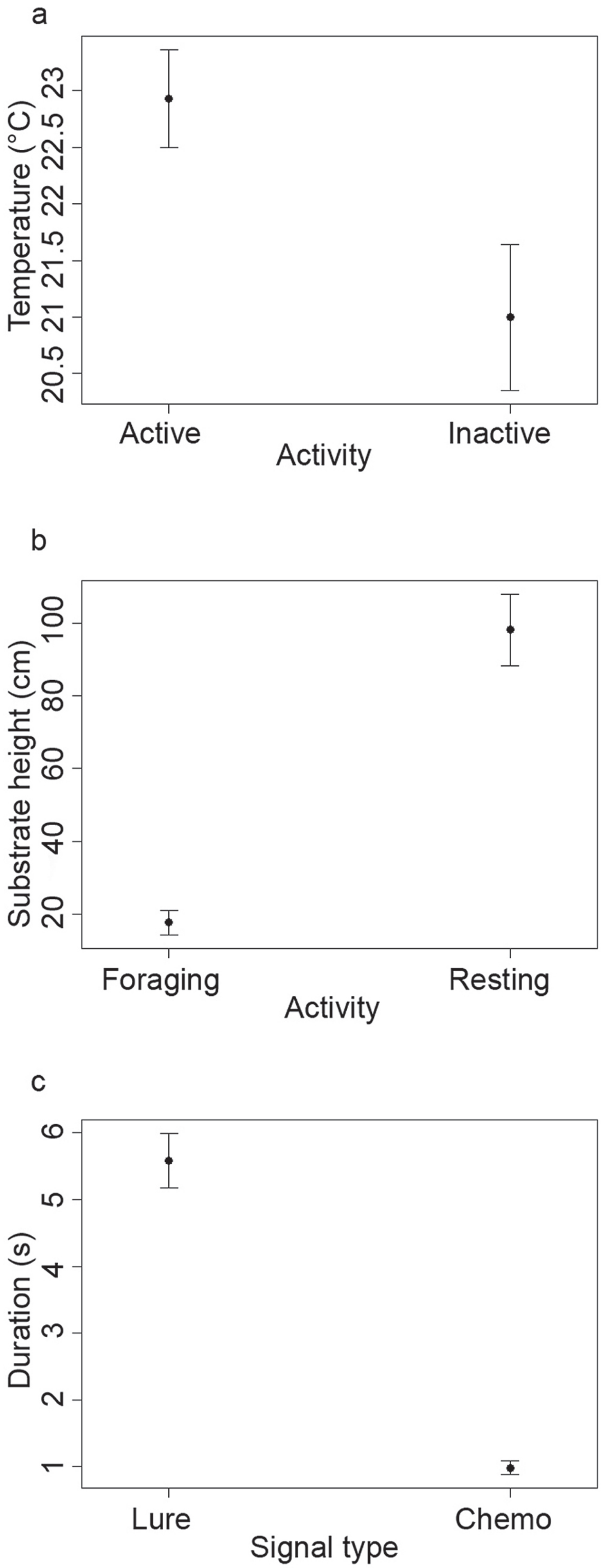

Figure 1. Mean and standard errors for *Thamnodynastes strigatus* activity (a); substrate use (b) and lingual protrusions (lure and chemossensorial) (c).

difference in perch height when the snakes were found on vegetation was observed ($t = -7.74$; $p < 0.05$), with inactive individuals occupying higher substrates ($\bar{x} = 98.12 \pm 9.81$ cm, n = 17) compared to active ones ($\bar{x} = 17.68 \pm 3.39$ cm, n = 11) (Fig. 1b). A total of 41 snakes were observed in hunting activity, always at night, beginning after dusk and extending until dawn (19 h 00 min–03 h 12 min). Of this total, most were found on the edge and interior of forest areas (95.12%, n = 39), rarely foraging in grassy areas (4.88%, n = 2). All environments were associated with streams containing fish. With the exception of one individual, found moving between the rocks of a stream, all other snakes (97.56%, n = 40) were observed in an ambush position, perched on riparian vegetation (Fig. 2c).

Ambush behavior description

Thamnodynastes strigatus ambush behavior can be basically defined as consisting of three phases: i) selection phase – the snakes select a vegetable substrate immediately over the water surface ($\bar{x} = 17.68 \pm 3.39$ cm) (Fig. 2a); ii) establishment phase – the snakes twist the last third of their body onto the vegetation (usually a small branch) and slide the front of the body perpendicularly towards the water surface (Fig. 2b); iii) waiting phase – after setting itself close to the water surface, the specimens open their mouths and position themselves very close to or touching the water surface with the end of their mandible, with the body slightly flexed laterally or even stretched (see Fig. 2c below for an example and online supplementary material 1). The timeframe in which individuals remained in this ambush position ranged from 1 h 47 min to 5 h 30 min ($\bar{x} = 3.6 \pm 1.1$, n = 15).

Although the first two phases were highly conservative within the study population, the last waiting phase varied in two occasions, when two adult individuals displayed prolonged lingual protrusions (different from the slow-motion tongue-flicks proposed by Gove (1979), considered as a lingual lure in the present study. This behavior comprised three basic steps: protrusion, attraction and tongue retraction. The attraction mechanism consisted of maintaining the tongue extended pendularly to the water surface. To perform the attraction display, the snakes hold both ends of the tongue apart, curved down and back, forming a semicircle. Then, the tongue tips assume a m-shaped configuration, and vibrate frantically. This exhibition was concomitantly associated to smooth lateral and anteroposterior movements of the tongue body (see online supplementary materials 2 and 3). A significant difference in protrusion duration was noted ($t = 10.90$; $p < 0.05$, Fig. 1c), with attractive displays lasting longer (1.7–10 seconds, $\bar{x} = 5.57 \pm 0.41$ seconds; n = 32) than typical chemosensory protrusions (0.24–1.9 seconds, $\bar{x} = 0.98 \pm 0.09$ seconds; n = 21). In both prolonged lingual protrusion observations potential prey (little fishes *Hyphessobrycon luetkenii* (Boulenger, 1887); Characidae) were located in the water just below the snake.

Predation records

Three predation events were recorded throughout the study. The first was observed in November, for an adult female (SVL 524 mm) perched on riparian vegetation at 9:00 p.m. The snake started its ambush behavior at 7:45 p.m., with its mouth open and the jaw end touching the water surface. One of the numerous fishes present near the water surface accidentally touched the snake's mouth. Immediately, the snake captured the prey by its head, by a frontal attack. Therefore, the snake slightly flexed its body laterally and, still hanging perpendicularly to the water surface, began ingesting the fish in an anteroposterior direction. After the fish ingestion, which lasted about five minutes, the snake returned to its ambush position. After being ingested, the fish continued to move inside the snake for some seconds. The second predation event also occurred in November, at 8:30 p.m.. When found, the snake was already in an ambush position, beginning at 7:49 p.m.. The way of capture was identical to that of the first record, with the difference that this time the fish (*H. luetkenii*) was caught by its the median dorsal body part. After the capture, the snake remained perched on the vegetation, taking about 15 minutes to position the fish in anteroposterior direc-

Figure 2. *Thamnodynastes strigatus* ambush behavior stages: selection phase (a); establishment phase (b); waiting phase (c).

tion. Only then did the ingestion occur, lasting two and a half minutes, with no visible movements by the prey. After ingestion, the snake descended from its ambush site and swam through the stream, disappearing into the riparian vegetation.

The third predation event was observed with an adult female (SVL 550 mm), in December, at 9:40 p.m.. The snake was in an ambush position on watery riverside vegetation, as previously described. The prey was a catfish (Siluriformes Cuvier, 1817), captured in the same way described previously. The fish was captured at its anterior region and ingested in less than a minute and the snake still hung down from the vegetation above the water.

Discussion

Activity, habitat use and foraging behavior

As expected for reptile species in subtropical South America, the *T. strigatus* population studied herein displayed a markedly seasonal abundance pattern with activity associated to the austral spring and summer period (Di-Bernardo et al. 2007, Winck et al. 2007). A strong literature support indicates that temperature plays an important role in daily activity patterns exhibited by snakes since the physiological and behavioral capacities of these ectotherms are best performed when body temperature is close to the optimum required for each species (Lillywhite 1987, Oishi et al. 2004).

The observations reported herein corroborate the daily activity pattern and microhabitat use previously described for *T. strigatus*, since the population assessed here was also composed of nocturnal foragers, who exhibit microhabitat use plasticity, occupying terrestrial, aquatic and arboreal environments, as well as higher substrates for resting instead of foraging (Bernarde et al. 2000a). The behavior of picking high soil substrates to stand is known for several forest snake species and may represent protection against terrestrial, nocturnal predators (Martins 1993, Bernarde et al. 2000a). A difference, however, in the height of the substrate used for foraging between studies is observed (0–100 cm in Bernarde et al. 2000a; 0–40 cm in our study). This may be related to the different hunting strategies applied by *T. strigatus* populations, since the population monitored by Bernarde et al. (2000a) was composed of active predators, and the act of searching for the prey requires greater snake mobility, exploring different vegetation strata. On the other hand, in the present study the specimens occupied an ambush position near the water surface, which naturally limits the height of the vegetation being explored and depending on the respective snakes' body length and distance from the water surface.

Differences in foraging strategies among the *T. strigatus* population observed by Bernarde et al. (2000a) and herein are particularly interesting, since drastic geographic variations in diet composition and/or foraging strategies are hardly observed in snakes (Alencar & Nascimento 2014). Geographic differences in diet composition have been observed for *Crotalus oreganus* Holbrook, 1840 and *Vipera latastei* Bosca, 1878 (Glaudas et al. 2008), respectively, and were associated with differences in prey availability throughout the distribution of these species. However, if these differences triggered different foraging sites or types is still an open question. On the other hand, Arnold (1977), when comparing insular and continental *Thamnophis elegans* specimens, perceived that observed morphological and behavioral differences coincided with dietary variations. Individuals from islands foraged longer in the water and fed on anurans, while individuals on the continent foraged both on land and in water and fed on both slugs and anurans. In these cases, islands represent extreme scenarios, as allopatry is often accompanied by resource constraints for some populations, which in turn, suffer from strong adaptive pressure, and display marked phenotypic and genotypic differences. Although *T. strigatus* presents a continuous distribution in southern South America (Giraudo 2001), it is important to emphasize that the population assessed herein inhabits hill formations at a mountain formation in the Uruguayan Savannah ecoregion, which may be associated to a continuous continental insularization process (Pilau 2011), eventually leading to allopatric processes and different interpopulational selective pressures.

As an alternative to the possibility of variations in foraging strategies, the behavioral and dietary differences in the *T. strigatus* population assessed here may be the result of taxonomic incongruence. For example, Trevine (2017) did not recover *T. strigatus* as a monophyletic species, pointing out *T. strigatus* as being a cryptic species complex. In general, the meristic, morphometric and color data of the study population (CMR pers. obs.) are compatible with those described for *T. strigatus* (Franco et al. 2017). However, the white coloration at the end of the tongue in the *T. strigatus* population studied herein is worth mentioning, which seems to be an exception for the species (CMR pers. obs.). Bearing in mind that the name *T. strigatus* possibly represents a species complex, and that the assessed population studied presents morphological and behavioral differences, integrative taxonomic studies (including morphological, behavioral and molecular data) are strongly desirable to elucidate this issue.

When comparing the ambush fishing behavior adopted by *T. strigatus* population of this study with that reported for other piscivorous snakes, notable differences in strategies were again noted. *Thamnophis rufipunctatus* (Cope, 1875), a specialized aquatic species, performs a subaqueous ambush with its mouth closed, with visual prey detection and capture through frontal attacks (Alfaro 2002). In contrast, *Nerodia rhombifer* (Hallowell, 1852), another aquatic specialist, also performs ambush fishing, with its body submerged but with the head out of the water and the mouth wide open, capturing its prey through lateral attacks (Alfaro 2002), and sometimes using its tongue to attract fish (Czaplicki & Porter 1974). The terrestrial generalist species *Thamnophis sirtalis* (Linnaeus, 1758) and *Thamnophis atratus* (Kennicott, 1860) (juveniles) perform ambushes and capture prey from ground perches with frontal or lateral attacks (Lind & Welsh 1994, Alfaro 2002). On some occasions, *T. atratus* juveniles exhibit this hunting repertoire in conjunction with lingual lure behavior (Welsh & Lind 1994). The ambush-fishing behavior of *T. strigatus*, which exhibits mainly terrestrial and arboreal habitats, is usually performed from an arboreal position, with a vertical positioning on the water surface waiting with an open mouth touching the water. Similar to *T. sirtalis* and *T. atratus*, no visual detection of prey is observed, and capture occurs through a frontal attack, after a fish touches the snake's mouth. As noted by Alfaro (2002), specialized aquatic snakes present a series of fish capture adaptations, which involve greater visual orientation, lower cranial rotation during jaw opening, and less time to perform the latter procedure. However, the species studied by Alfaro (2002) are diurnal foragers. In contrast, *T. strigatus* is a nocturnal hunter, although its optical anatomy is more similar to that of diurnal species (Hauzman 2014). This apparent anatomical and behavioral incongruity may have played an important role in the evolution of the ambush-hunting repertoire observed in the *T. strigatus* population assessed in the present study.

Evidence of lingual lure behavior

Possibly the most surprising observation of this study is that of prolonged lingual protrusions in *T. strigatus*, which may be associated with prey attraction mechanisms. Historically, the interpretation of this behavior has generated controversial conclusions among researchers, demanding explanations. Observations concerning prolonged lingual protrusions in snakes have been mentioned since the end of the 19th century by Fischer (1882), especially in relation to observations of South American snakes belonging to the genus *Oxybelis* (Wagler, 1830), but hypotheses for its function were proposed only in the following century. Procter (1924), and Hediger (1955) proposed that prolonged protrusions could act as a mechanism to "fascinate" potential prey. Curran & Kauffeld (1937), on the other hand, raise the possibility that the tongue could act like a lizard lure, which would confuse it with a worm or insect larvae. Ardrey (1970) proposed that the prolonged protrusions recorded for *Oxybelis*, coupled to snake throat expansion and contraction movements, could both attract and confuse potential prey. However, Keiser (1975), after monitoring the feeding behavior of *Oxybelis aeneus* (Wagler, 1824) in captivity for seven years, contested all the aforementioned authors and their respective hypotheses, providing solid evidence that the tongue was not used to fascinate prey, nor to deceive them concerning the presence of potential prey. Instead, this author proposed two new hypotheses to explain the prolonged protrusions: the "Disruptive Morphology Hypothesis" and the "Olfactory Threshold Hypothesis". However, the *T. strigatus* protrusion behavior is apparently not reflected by any of the hypotheses proposed by Keiser (1975).

The "Disruptive Morphology Hypothesis" proposes that the tongue, when extended for a long time and in the absence of movement, would act as a confounding effect for the prey, making it difficult to spot the snake (i.e., the prey would not form the image of an approaching snake); while the "Olfactory Threshold Hypothesis" states that extended tongue immobility would maintain continuous olfactory contact with the environment, without attracting undue prey attention, maximizing particle capture and, consequently, an environment reading by snake. Both hypotheses present a very important premise: tongue immobility during prolonged protrusion. Thus, snakes would remain undetectable as they approach already detected prey (first hypothesis) or remain undetectable while still harvesting accurate information on prey location (second hypothesis). However, this is not the case for the *T. strigatus* population observed in this study. On the contrary, when prolonged protrusions were observed in this species, they were accompanied by frantic vibrations of both ends of the tongue, accompanied by slight lingual body movements. At the same time, as an addendum to the main objective supported by the stated hypotheses – i.e., the undetectability of the snake by prey – Keiser (1975) reports that *Oxybelys* species tongues display a uniform coloration, similar to that of the anterior region of the lingual body, and that for the tongue to function as a prey fascination or attraction mechanism, it would necessarily have to be conspicuous in order to be effective. This is the exact opposite of what was observed found in the *T. strigatus* population studied herein, whose tongue displays a bicolor pattern, with a black lingual body and whitish ends.

Some authors consider that the striking bicolor pattern found in the tongue of some snake species does not necessarily evolve to attract prey, since it may be associated to defensive displays (against predators) or social iterations (against rivals or in favor of mating) (Gove 1979, Gove & Burghardt 1983). However, again, these possibilities do not seem to fit the observations reported here for *T. strigatus*, since prolonged protrusion behavior was observed only in ambushed prey situations, and never in the presence of a potential sexual partner, rival or predator. Another relevant issue is that the North American species *T. atratus* and *Nerodia sipedon* (Linnaeus, 1758), for which there is convincing evidence of lingual lure (Czaplicki & Porter 1974, Welsh & Lind 2000), also present a bicolored tongue. However, unlike *T. strigatus*, the lingual body in those species is red, with black ends. This difference in coloration is interesting since, considering that *T. atratus* and *N. sipedon* forage during the day, a tongue with a light-colored end would not be potentially attractive for visually oriented prey. At the same time, for *T. strigatus* – a nocturnal forager – it seems useful that the tip of its tongue is light-colored, standing out in darkness, even more so if we consider that one of the food items consumed by this snake, the fish *H. luetkenii*, is a visually-oriented species (Gelós et al. 2010)

In addition, differences between the lingual lure mechanisms of *T. strigatus* and that of other species for which

Table 1. Lingual lure records for snake species worldwide.

Taxon	Distribution	Habitat	Prey	Source
Colubridae				
Nerodia clarkii	North and Central America	Aquatic, terrestrial	Fish	Hansknecht (2008)
Nerodia rhombifer	North America	Aquatic	Fish	Czaplicki & Porter (1974)
Nerodia sipedon	North America	Aquatic	Fish	Czaplicki & Porter (1974)
Thamnophis atratus	North America	Aquatic, terrestrial	Fish	Welsh & Lind (2000)
Dipsadidae				
Thamnodynastes strigatus	South America	Aquatic, terrestrial, arboreal	Fish	This study
Viperidae				
Bitis arietans	Africa	Terrestrial	Amphibians	Glaudas & Alexander (2017)

this behavior is already known, are not limited to tongue color. The basic *T. strigatus* lingual lure movements were similar to those described for *Nerodia clarkii* (Baird & Girard, 1853) and *T. atratus*, comprising three phases, respectively: protrusion, lure and retraction (Welsh & lind 2000, Hansknecht 2008). However, important differences regarding the execution of the second stage are noted, i.e. concerning prey attraction. While *N. clarkii* displays a lingual lure with its body in the water and practically in a horizontal position, wrapping the tongue up and back, in or out of the water, and stretching it until at its tip forms a terminal handle (Hansknecht 2008), *T. atratus* performs a lingual lure with its body almost vertical or oblique to the water, from rocks above the surface, stretching the entire tongue and keeping its ends fluttering on the water surface (Welsh & Lind 2000). *Thamnodynastes strigatus* obtains attraction in a similar way to *T. atratus*. However, it assumes an even more perpendicular position to the water, hanging from branches, stretching its tongue and keeping its tips diametrically separated, each one forming a terminal handle, that flutters close to the water, without touching it. The behavior exhibited by *T. strigatus*, of fluttering the tips of the tongue on the water surface, resembles the beating of an insect's wings. This hypothesis is quite plausible, since the fish *H. luetkenii* is abundant at the studied site (CMR pers. obs.), explores the water surface (Lima et al. 2008) and presents a generalist diet—including the adults of some insects (e.g., Diptera and Ephemeroptera) (Graciolli et al. 2003), which commonly fly over the water surface at night to perform oviposition.

As with ambush behavior, prey attraction mechanisms also seem to be associated with species primary habits. While *N. clarkii* is an aquatic specialist species (Mullin & Mushinsky 1995), *Thamnophis atratus* forages on both land and water (Welsh & lind 2000). The lingual lure method performed by *T. strigatus* is more similar to that exhibited by *T. atratus*, which also shares greater plasticity in foraging environments, although *T. strigatus* also exhibits arboreal habits (Bernarde et al. 2000a).

The observation of a lingual lure in *T. strigatus* deserves special mention, since this is a very rare behavior in snakes, described only five other species worldwide, and the first description for a South America species (Table 1). However, despite our extensive field observation effort, we were not able to verify the effectiveness of the lingual lure in *T. strigatus*; in other words, it was not possible to verify whether the fish were really attracted to the tongue. Likewise, due to the low number of specimens observed performing lingual lure (n = 2) it was not possible to establish which factors influence the display of this behavior (e.g., high or low prey availability, prey type, luminosity, etc.). Some possibilities can be raised to explain these issues. First, because it is naturally difficult to observe predation events in the field, and throughout our whole sample we only observed such events on three occasions (where all snakes were in an ambush position, with their mouths open and jaws touching the water, and captured their prey when the fish touched their jaws). Second, lingual lure behavior does not appear to be a frequent behavior in this *T. strigatus* population, since it was observed only for two individuals, which makes it even more difficult to evaluate its effectiveness in the field. However, lingual lure behavior is difficult to also observe for other snakes. Glaudas & Alexander (2017), after recording 4,634 hours of *Bitis arietans* (Merrem, 1820), activity recorded lingual lure behavior only for adult individuals on nine occasions, while Welsh & Lind (2000), registered the behavior only in four *T. atratus* juveniles of 24 observed individuals. Thus, this behavior, in addition to being difficult to observe in situ, may not be exhibited by all age groups (Hansknecht 2008), which poses a real challenge for field monitoring. In this sense, studies performed in the laboratory controlling a series of variables may provide important clues concerning the evolution and function of lingual lure behavior in *T. strigatus*.

Final remarks

Our ability to understand predator-prey systems is limited by a lack of detailed information on fundamental natural history aspects, and it is particularly difficult to gather quantitative data on the behavior of ambush predators, who are usually secretive and feed infrequently (Clark 2006). The present study provides additional data on habitat activity and use, as well as the first contribution concerning ambush hunting for the Neotropical genus *Thamnodynastes*. However, our findings suggest the need for further research to (1) elucidate the phylogenetic position of the population assessed in the present study within the *T. strigatus* complex; (2) evaluate the effects of *T. strigatus* lingual lure behavior on fish, and identify which factors influence the performance of this behavior; (3) determine if fish capture by *T. strigatus* population of this study, in the absence of lingual lure behavior, occurs due to accidental or purposeful prey approach; and finally (4) to understand if *T. strigatus* fishing strategies are shared by other phylogenetically close species. Certainly, fishermen always have incredible new tales to tell.

Acknowledgments

The authors are grateful to the Instituto Chico Mendes de Conservação da Biodiversidade (ICMBIO) for the collection permit (SISBIO 58966–1), Érica Fonseca for the suggestions to the manuscript, and to Everton Rodolfo Behr for valuable help in identifying the preyed fish. ADA, CMR, and LMB would like to thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for master's fellowships (ADA – 130115/ 2019–3; CMR – 131574/ 2017–5; LMB – 131572/2017–2). TGS and SZC thank CNPq research fellowships (TGS – process 308687/2016–7, and SZC – process 309095/2016–6).

References

Alencar, L. R. V. & L. B. Nascimento (2014): Natural history data of a common snake suggest interpopulational variation and conservatism in life history traits: the case of *Erythrolamprus poecilogyrus*. – The Herpetological Journal, **24**: 79–85.

Alfaro, M. E. (2002): Forward attack modes of aquatic feeding garter snakes. – Functional Ecology, **16**: 204–215.

Al-Sadoon, M. K. & B. A. Paray (2016): Ecological aspects of the horned viper, *Cerastes cerastes gasperettii* in the central region of Saudi Arabia. – Saudi journal of biological sciences, **23**: 135–138.

Altmann, J. (1974): Observational study of behavior: sampling methods. – Behaviour, **49**: 227–267.

Andrade, D. V., O. A. Marques, R. S. Gavira, F. E. Barbo, R. L. Zacariotti & I. Sazima (2010): Tail luring by the golden lancehead (*Bothrops insularis*), an island endemic snake from south-eastern Brazil. South American Journal of Herpetology, **5**: 175–181.

Ardrey, R. (1970): The social contract. – Atheneum Press, New York.

Arnold, S. J. (1977): Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. – Science, **19**: 676–678.

Bernarde, P. S., M. N. C. Kokubum & O. A. V. Marques (2000a): Utilização de hábitat e atividade em *Thamnodynastes strigatus* (Günther, 1858) no sul do Brasil (Serpentes, Colubridae). – Boletim do Museu Nacional, **428**: 1–8.

Bernarde, P. S., J. C. Moura-Leite, R. A. Machado & M. C. N. Kokubum (2000b): Diet of the colubrid snake, *Thamnodynastes strigatus* (Günther, 1858) from Paraná state, Brazil, with field notes on anuran predation. – Revista Brasileira de Biologia, **60**: 695–699.

Borges-Martins, M., M. L. M. Alves, M. L. Araujo, R. B. Oliveira & A.C. Anés (2007): Répteis. – pp. 292–315 in: Becker, F. G., R. A. Ramos & L. A. Moura (eds): Biodiversidade: Regiões da Lagoa do Casamento e dos Butiazais de Tapes, Planície Costeira do Rio Grande do Sul. Brasília, DF. – Ministério do Meio Ambiente, Secretaria de Biodiversidade e Florestas.

Braz, H. B. & O. A. V. Marques (2016): Tail-first ingestion of prey by the false coral snake, *Erythrolamprus aesculapii*: Does it know where the tail is? – Salamandra, **52**: 211–214.

Clark, R. W. (2006): Fixed Videography to Study Predation Behavior of an Ambush Foraging Snake, *Crotalus horridus*. – Copeia, **2006**: 181–187.

Curran, C. H. & C. Kauffeld (1937): Snakes and their ways. – Harper and Bros, New York.

Czaplicki, J. A. & R. H. Porter (1974): Visual cues mediating the selection of goldfish (*Carassius auratus*) by two species of *Natrix*. – Journal of Herpetology, **8**: 129–134.

Di-Bernardo, M., M. Borges-Martins, R. B. Oliveira & G. M. P. Pontes (2007): Taxocenoses de serpentes de regiões temperadas do Brasil. – pp. 222–263 in: Nascimento, L. B. & M. E. Oliveira (eds): Herpetologia no Brasil II. – Sociedade Brasileira de Herpetologia, Belo Horizonte.

Fischer, J. F. (1882): Die Braune Peitschen- oder Baumschlange (*Oxybelis aeneus* Wagler) in der Gefangenschaft. – Der Zoologische Garten, **23**: 331–336.

Franco, F. L., V. C. Trevine, G. G. Montingelli & H. Zaher (2017): A new species of *Thamnodynastes* from the open areas of central and northeastern Brazil (Serpentes: Dipsadidae: Tachymenini). – Salamandra, **53**: 339–350.

Gelós, M., F. Teixeira-de-Mello, G. Goyenola, C. Iglesias, C. Fosalba, F. García-Rodríguez & M. Meerhoff (2010): Seasonal and diel changes in fish activity and potential cascading effects in subtropical shallow lakes with different water transparency. – Hydrobiology, **646**: 173–185.

Gibbons, J. W. & M. E. Dorcas (2004): North American watersnakes: a natural history. – University of Oklahoma Press, Norman, 438 pp.

Giraudo, A. (2001): Serpientes de la Selva Paranaense y del Chaco Húmedo. – Buenos Aires, L. O. L. A., 328 pp.

Glaudas, X. & G. J. Alexander (2017): A lure at both ends: aggressive visual mimicry signals and prey-specific luring behaviour in an ambush-foraging snake. – Behavioral Ecology and Sociobiology, **71**: 1–7.

Glaudas, X., T. Jezkova & J. A. Rodríguez-Robles (2008): Feeding ecology of the great basin rattlesnake (*Crotalus lutosus*, Viperidae). – Canadian Journal of Zoology, **86**: 723–734.

Gove, D. (1979): A comparative study of snake and lizard tongue-flicking, with an evolutionary hypothesis. – Zeitschrift für Tierpsychologie, **51**: 58–76.

Gove, D. & G. M. Burghardt (1983): Context-correlated parameters of snake and lizard tongue-flicking. – Animal Behaviour, **31**: 718–723.

Graciolli, G., M. A. Azevedo & F. A. Melo (2003): Comparative study of the diet of Glandulocaudinae and Tetragonopterinae (Ostariophysi: Characidae) in a small stream in southern Brazil. – Studies on Neotropical fauna and environment, **38**: 95–103.

Hansknecht, K. A. (2008): Lingual luring by mangrove saltmarsh snakes (*Nerodia clarkii compressicauda*). – Journal of Herpetology, **42**: 9–15.

Hartmann, P. A. & O. A. V. Marques (2005): Diet and habitat use of two sympatric species of Philodryas (Colubridae), in South Brazil. – Amphibia-Reptilia, **26**: 25–31.

Hauzman, E. (2014): Ecologia e evolução do sistema visual de serpentes Caenophidia: estudos comparativos da morfologia retiniana e genética de opsinas. – Ph.D. Dissertation, Universidade de São Paulo, São Paulo.

Hediger, H. (1955): Studies on the Psychology and behaviour of captive animals in zoos and circuses. – Butterworths Scientific Publications, London.

Keiser Jr, E. D. (1975): Observations on tongue extension of vine snakes (Genus *Oxybelis*) with suggested behavioral hypotheses. – Herpetologica, **31**: 131–133.

Lillywhite, H. B. (1987): Temperature, energetics, and physiological ecology. – in: Seigel, R. A., J. T. Collins & S. S. Novak (eds): Snakes: ecology and evolutionary biology. – McGraw-Hill, New York.

Lima, S. M., A. A. Cunha, J. I. Sánchez-Botero & É. P. Caramaschi (2008): Vertical segregation of two species of *Hyphessobrycon* (Characiformes: Characidae) in the Cabiúnas coastal lagoon, southeastern Brazil. – Neotropical Ichthyology, **6**: 683–688.

Lind, A. J. & H. H. Welsh Jr (1994): Ontogenetic changes in foraging behaviour and habitat use by the Oregon garter snake, *Thamnophis atratus hydrophilus*. – Animal Behaviour, **48**: 1261–1273.

Madsen, T. R. L & R. Shine (1996): Seasonal migration of predators and prey–A study of pythons and rats in tropical Australia. – Ecology **77**: 149–156.

Martins, M. (1993): Why do snakes sleep on the vegetation in Central Amazonia? – Herpetological Review, **24**: 83–84.

Martins, M. & M. E. Oliveira (1998): Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. – Herpetological Natural History, **6**: 78–150.

McDiarmid, R. W., M. S. Foster, C. Guyer, J. W. Gibbons & N. Chernoff (2012): Reptile biodiversity: standard methods for inventory and monitoring. – University of California Press, London.

Mullin, S. J. & H. R. Mushinsky (1995): Foraging ecology of the mangrove salt marsh snake, *Nerodia clarkii compressicauda*: effects of vegetational density. – Amphibia-Reptilia. **16**: 167–175.

Oishi, T., K. Nagai, Y. Harada, M. Naruse, M. Ohtani, E. Kawano & S. Tamotsu (2004): Circadian rhythms in amphibians and reptiles: ecological implications. – Biological Rhythm Research, **35**: 105–120.

Olson, D. M., E. Dinerstein, E. D. Wikramanayake et al. (2001): Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. – BioSciences, **51**: 933–938.

Pilau, E. M. (2011): Perspectivas geográficas pertinentes para uma análise integrada da Cuesta do Haedo Brasil-Uruguai. – Graduate thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Procter, J. B. (1924): Unrecorded characters seen in living snakes, and a description of a new tree-frog. – Proceedings of the Zoological Society of London, **4**: 1125–1129.

R Core Team (2015): R: A language and environment for statistical computing. R Foundation for Statistical Computing. – Available from http://www.R-project.org/, accessed 12 October 2018.

Reinert H. K. (1993): Habitat selection in snakes. – pp. 201–240 in: Seigel R. A. & J. T. Collins (eds): Snakes: Ecology and Behavior. – The Blackburn Press, Caldwell, New Jersey.

Robaina, L. E. S., R. Trentin, F. Laurent & A. A. V. Sccoti (2015): Zoneamento morfolitológico da bacia hidrográfica do Rio Ibicuí e sua relação com processos superficiais e o uso do solo. – Revista Brasileira de Geomorfologia, **16**: 63–77.

Rossato, M. S. (2011): Os climas do Rio Grande do Sul: variabilidade, tendências e tipologia. – Ph.D. thesis, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Ruffato, R., M. Di-Bernardo & G. F. Maschio (2003): Dieta de *Thamnodynastes strigatus* (Serpentes, Colubridae) no sul do Brasil. – Phyllomedusa, **2**: 27–34.

Sazima, I. (1991): Caudal luring in two Neotropical pitvipers, *Bothrops jararaca* and *B. jararacussu*. – Copeia, **1**: 245–248.

Shine, R. (1988): Food habits and reproductive biology of small Australian snakes of the genera *Unechis* and *Suta* (Elapidae). – Journal of Herpetology, **22**: 307–315.

Trevine, V. C. (2017): Sistemática da tribo Tachymenini Bailey, 1967 (Serpentes, Dipsadidae, Xenodontinae). – Ph.D thesis, Universidade de São Paulo, São Paulo.

Vitt L. J. & J. P. Caldwell (2014): Herpetology: an introductory biology of amphibians and reptiles. – Academic Press, San Diego.

Webb, J. K. & M. J. Whiting (2005): Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. – Oikos, **110**: 515–522.

Welsh Jr., H. H. & A. J. Lind (2000): Evidence of lingual-luring by an aquatic snake. – Journal of Herpetology, **34**: 67–74.

Winck, G. R., T. G. Santos & S. Z. Cechin (2007): Snake assemblage in a disturbed grassland denvironment in Rio Grande do Sul State, southern Brazil: population fluctuations of *Liophis poecilogyrus* and *Pseudablabes agassizii*. – Annales Zoologici Fennici, **44**: 321–332.

Wrege, M. S., S. Steinmetz, C. Reisser-Júnior & I. D. Almeida (2012): Atlas climático da região sul do Brasil: estados do Paraná, Santa Catarina e Rio Grande do Sul. – Embrapa Clima Temperado, Pelotas.

Supplementary data

The following data are available online:

Supplementary document 1. Adult *Thamnodynastes strigatus* initiating the waiting phase. Available at: www.salamandra-journal.com/SuppData/Mario-da-Rosa_et_al-1354-Supp_file 1

Supplementary document 2. First record of an adult *Thamnodynastes strigatus* executing the lingual lure for fish attraction. Available at: www.salamandra-journal.com/SuppData/Mario-da-Rosa_et_al-1354-Supp_file 2

Supplementary document 3. Second record of an adult *Thamnodynastes strigatus* executing the lingual lure for fish attraction. Available at: www.salamandra-journal.com/SuppData/Mario-da-Rosa_et_al-1354-Supp_file 3