THAMNODYNASTES STRIGATUS (GÜNTHER, 1858) (SERPENTES, DIPSADIDAE): FORAGING SITE FIDELITY

Ana Helena Pagotto, Daniel Rodrigues Stuginski, Edelcio Muscat*

Projeto Dacnis, Estrada do Rio Escuro, 4754, Sertão das Cotias, 11680-000, Ubatuba, SP, Brazil.
* Corresponding author: edelciomuscat@terra.com.br

Like many other taxa, snakes have home ranges where they perform daily activities like foraging, breeding, thermoregulating and resting (Macartney *et al.*, 1988; Powell *et al.*, 2000). Although home ranges can differ seasonally and/or depend on the species and sex (Hyslop *et al.*, 2009; Breininger *et al.*, 2011), snakes generally remain within their home ranges, and even philopatry has already been reported for some species (Brischoux *et al.*, 2009). In recent decades, long-term mark-recapture studies and the use of radio-telemetry have provided an increasing amount of data about home ranges, movement and habitat use (Webb & Shine, 1997; Dorcas & Willson, 2009), and there is now a much more fine-scale comprehension of how snakes use their habitats. It is now known that they exhibit site fidelity, using the same spots within their home range repeatedly to perform various activities (Madsen & Shine, 1996; Moore & Gillingham, 2006). Site fidelity can occur for short periods or for years, restricted to small areas (e.g., a burrow used as shelter) or large (e.g., extensive hunting grounds) within a snake's home range (Madsen & Shine, 1996; Webb & Shine, 1997). Site fidelity was reported for some species in the Northern Hemisphere that use the same den site for hibernation, sometimes travelling great distances (Burger & Zappalorti, 1992; Gomez *et al.*, 2015). Sea snakes, such as *Laticauda colubrina* (Schneider, 1799), have long-term egg-laying site fidelity (Brischoux *et al.*, 2009). Whitaker & Shine (2003) reported the daily use of a shelter site by the same individual of *Pseudonaja textilis* (Duméril, Bibron & Duméril, 1854). These authors reported snakes traveling more than 800 m from their hunting grounds to the same retreat site daily. One explanation for site fidelity is linked to the fact that habitats are complex and heterogeneous, with some sites offering better feeding opportunities, protection against predators, and more favorable thermal and hydric microenvironments (Du *et al.*, 2009). It is expected that snakes use some sites within their home range more frequently because of the need of a particular resource.

Food is a resource that can be highly variable across the landscape. Such variability may also be seasonal, and prey abundance can differ spatially and temporally (Madsen & Shine, 1996; Cundall & Pattishall, 2011). The Foraging Theory predicts that animals increase their energetic gain by decreasing the time and energy spent searching for food (Stephens & Krebs, 1986). Thus, if a site presents food abundance or any hunting advantage, some degree of site fidelity by predators is expected. Foraging site fidelity has been reported for snakes, and they used specific hunting grounds repeatedly, in both foraging modes (sit-and-wait ambushers and active searching) (Puente-Rolón & Bird-Picó, 2004; Sazima & Marques, 2007). The ambush-hunting snake *Chilabothrus inornatus* (Reinhardt, 1843), in Puerto Rico, used the entrance of one cave to hunt bats, returning to the same point regularly (Puente-Rolón & Bird-Picó, 2004). Sazima & Marques (2007) observed a specimen of the active-searching *Philodryas olfersii* (Lichtenstein, 1823) revisiting a successful bird-hunting site for nine months. The authors recorded the same snake hunting birds in the same tree five times (three of which were successful) and suggested that this foraging site fidelity could be linked to a snake's learning process. In the present manuscript, we report similar foraging site fidelity during two consecutive years, by *Thamnodynastes strigatus* (Günther, 1858), a snake species that usually hunts by active searching (Bernarde *et al.*, 2000b; but see Mario-da-Rosa *et al.* [2020], who monitored specimens relying exclusively on ambush hunting).

Thamnodynastes strigatus is a nocturnal, viviparous and opisthoglyphous xenodontine (Marques *et al.*, 2001; Zaher *et al.*, 2019). The species occurs in Argentina, Paraguay, Uruguay, and Brazil. In Brazil, *T. strigatus* occurs in the southeastern and southern Atlantic Forest, the Pampa and the Cerrado (Nogueira *et al.*, 2019). The species can be locally abundant: Zanella & Cechin (2006) found *T. strigatus* to be the most common snake in the Planalto Médio of the state of Rio Grande do Sul. Specimens seem to use swampy areas frequently, searching for food on the ground and in vegetation (Bernarde *et al.*, 2000a,b).

The diet of *T. strigatus* consists of anurans, fish, mammals, and reptiles. Anurans of the families Leptodactylidae, Odontophrynidae, Bufonidae and Hylidae represent the major part of the diet in some populations of *T. strigatus* (Bernarde *et al.*, 2000a; Ruffato *et al.*, 2003). The species may be considered an anuran specialist that occasionally feeds on other prey, although some populations seem to be highly specialized in eating fish (Mario-da-Rosa *et al.*, 2020).

On 12 November 2018, we recorded a specimen of *T. strigatus*, SVL 390 mm, foraging on the lower branches of a tree in the Projeto Dacnis private reserve (22°53′44.7″ S, 45°56′29.4″ W), São Francisco Xavier subdistrict, municipality of São José dos Campos, state of São Paulo, Brazil. Identification was based on the following morphological features: dorsal scales smooth, in 19 rows at midbody, and infralabial scales with dark markings that taper ventrally (Franco & Ferreira, 2003). The tree stands on the edge of a swamp area and near an artificial pond. Approximately 20 frog species use the pond and swamp area as breeding sites, and at least five treefrog species use this tree as a calling site: *Boana faber* (Wied, 1821), *Dendropsophus minutus* (Peters, 1872), *Scinax eurydice* (Bokermann, 1968), *Scinax* aff. *perereca*, and *Scinax crospedospilus* (Lutz, 1925). During this first encounter, we observed the snake hunting for one hour, without success in capturing prey. We returned to the same tree ten times over the next 17 nights.

During eight of these nights we identified the same individual of *T. strigatus* foraging for frogs on low tree branches. We recognized this individual by the following characters: the third and fourth brown bars of the left supralabial scales in contact on the upper edge; the fifth and sixth brown bars on the distal portion of the fifth and sixth supralabials not reaching the upper margin of those scales; the fourth left supralabial brownish bar with an inverted "L" shape; the lower portion of the left postocular dark stripe narrows markedly at the distal margin of the last supralabial scale; prefrontal and internasal scales have a V-shaped brownish blotch; a dark-bordered circular mark on the left supraocular and frontal scale forms a complete circle, in contrast with the right side, where the circle is interrupted on the rostral part of the frontal scale (Figure 1).

In our sixth encounter, we inadvertently surprised a specimen of *S.* aff. *perereca* (SVL approximately 40 mm) that jumped near the *T. strigatus*. The snake grasped the frog and started eating it immediately (Figure 2). The frog appeared to have been envenomated because it did not react vigorously, but remained motionless for most of the ingestion process, similar to the findings of Bernarde *et al.* (2000a). The feeding event lasted at most five minutes, and after that the snake moved along the branches to the trunk of the tree. The last date on which we found the snake on the tree, 29 November 2018, was coincident with a decrease in the calling activity of *Scinax*.

During the monitoring period, we found four more specimens of *T. strigatus* foraging at the swamp area, and also other snake species (*Bothrops*

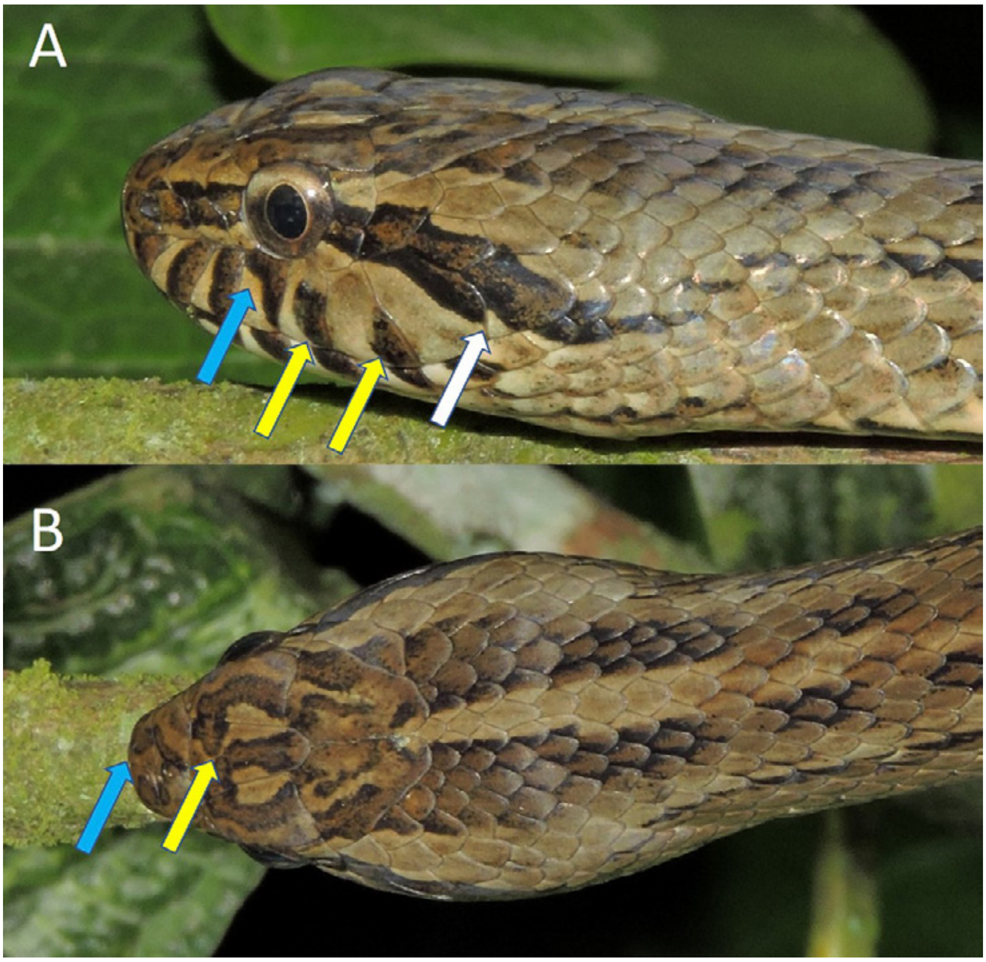

Figura 1. Morphological features used to recognize the *Thamnodynastes strigatus* individual. (A) Third and fourth brownish bars on the left supralabial scales in contact at the upper edge of the scales. The fourth left supralabial brownish bar forms an inverted "L" shape (blue arrow). Fifth and sixth brownish labial bars are short, not reaching the upper edge of the scales and are only at the distal portion of the scale (yellow arrows). Lower portion of the left postocular dark stripe narrows at the distal margin of the last supralabial scale (white arrow). (B) Prefrontal and internasal scales have a V-shaped brownish blotch (blue arrow). On the portion formed by the frontal and scales there is a pair of dark-bordered ocelli, but the border of the right ocellus is interrupted at the rostral portion of the frontal scale (yellow arrow). Both pictures were taken in 2019.

Figura 2. Thamnodynastes strigatus feeding on *Scinax* aff. *perereca*, on 22 November 2018.

jararaca (Wied, 1824), *Oxyrhopus guibei* (Hoge & Romano, 1977), and *Dipsas neuwiedi* (Ihering, 1911), but no snake other than this specimen of *T. strigatus* on this particular tree. We kept monitoring the area, searching the tree thoroughly, twice a week for 12 months, but found no more snakes.

In early November 2019 we detected a number of *S.* aff. *perereca* and *S. crospedospilus* using the same tree as a calling site. On 20 November 2019, during one of our regular field surveys, we found a specimen of *T. strigatus* on the tree. A comparison of photos taken in 2018 and on this night showed that it was the same individual we had monitored in the previous year. The snake was resting on tree branches approximately 1 m above ground. During the encounter we noticed that the stomach area was distended, suggesting recent ingestion of prey.

This is the first report of foraging site fidelity for a *Thamnodynastes* species and the second long-term foraging site fidelity reported for a Brazilian species (Sazima & Marques, 2007). The relationship between snake presence on that tree and anuran calling activity, especially *Scinax* spp. suggests a resource-based foraging site fidelity instead of random use of the space. It is clear to us that this snake used the same foraging site while prey abundance was high, but when resources decreased it moved from this area, returning after 12 months, when resources were abundant again.

Frogs were abundant in all swamp areas and we also found other snakes, including more specimens of *T. strigatus*, foraging in the swamp and around the pond. Despite searching the swamp area thoroughly, we only saw this individual when it was on the tree, never elsewhere. Foraging site fidelity by active-hunting snakes was previously reported in *P. olfersii*, a semi-arboreal and diurnal Xenodontine species (Sazima & Marques, 2007). Similarly to *P. olfersii*, *T. strigatus* feeds on a wide range of taxa, although some populations show a strong predilection for frogs (Bernarde *et al.*, 2000a; Ruffato *et al.*, 2003) or even fish (Mario-da-Rosa *et al.*, 2020). Based on the analysis of the stomach contents of 44 *T. strigatus*, Bernarde *et al.* (2000a) hypothesized that most foraging activity occurred on the ground and at water level, but they also suggested the use of the arboreal stratum as a foraging site for the species. These authors noted that *Scinax* was the most frequent frog genus in the stomach contents, accounting for over 40% of the preyed frogs.

In our sampled area, frogs were present in the entire swamp, but we do not know if frog abundance was greater near the tree than in other areas. Some *Scinax* used this tree as a calling site but not as a breeding site, since all *Scinax* species observed in our field surveys breed in flooded areas (Haddad & Prado, 2005). The choice of a specific tree as the snake's main foraging area seems to be directly related to the abundance of prey on it. It is relevant that there were other frog species that are regularly consumed by *T. strigatus* in the studied area (Ruffato *et al.*, 2003). So, it is possible that the site fidelity we report is related not only to frog abundance but specifically to *Scinax* abundance on that tree. Furthermore, Bernarde *et al.* (2000b) suggested that *T. strigatus* hunts by visual orientation based on frog movement, and that the snake is less prone to detect frogs that remain quiet and motionless. As most frogs on the tree were males in high calling activity and its branches were diffuse and easily accessible, the snake could gain some advantage by performing a visually oriented search at this foraging site.

The snake's return to the same hunting spot after one year is surprising and reinforces that snakes may exhibit strong site fidelity related to their feeding grounds (Sazima & Marques, 2007). Long-term site fidelity was also reported for other snake activities, e.g., breeding or hibernating (Brischoux *et al.* 2009, Gomez *et al.*, 2015), but less frequently for foraging. We still do not know if this foraging site fidelity occurs in different snake species and how they maintain this fidelity. It is possible that such long-term foraging site fidelity is guided exclusively by chemical cues of prey congregating seasonally at the same site but learning and memory processes cannot be discarded as leading forces in foraging site fidelity by snakes (Sazima & Marques, 2007).

Acknowledgments

We thank Matheus de Toledo Moroti for the 2019 photographs and Elsie Laura Rotenberg for all the help with this manuscript.

References

Bernarde P.S., Moura-Leite J.C., Machado R.A., Kokobum M.N.C. 2000a. 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.

Bernarde P.S., Kokubum M.N.C., Marques O.A.V. 2000b. Atividade e uso de habitat em *Thamnodynastes strigatus* (Günther, 1858), no sul do Brasil (Serpentes, Colubridae). *Boletim do Museu Nacional (N.S.) Zoologia* 428:1–8.

Breininger D.R., Bolt M.R., Legare M.L., Drese J.H., Stolen E.D. 2011. Factors Influencing Home Range Sizes of Eastern Indigo Snakes in Central Florida. *Journal of Herpetology* 45:484–490.

Brischoux F., Bonnet X., Pinaud D. 2009. Fine-scale site fidelity in sea kraits: Implications for conservation. *Biodiversity and Conservation* 18:2473–2481.

Burger J., Zappalorti R.T. 1992. Philopatry and nesting phenology of pine snakes *Pituophis melanoleucus* in the New Jersey Pine Barrens. *Behavioral Ecology and Sociobiology* 30:331–336.

Cundall D., Pattishall A. 2011. Foraging Time Investment in an Urban Population of Watersnakes (*Nerodia sipedon*). *Journal of Herpetology* 45:174–177.

Dorcas M.E., Willson J.D. 2009. Innovative methods for studies of snake ecology and conservation. Pp. 5–37, in: Mullin S.J., Seigel R.A. (Eds.), Snakes: Ecology and conservation. Comstock, Ithaca.

Du W., Webb J.K., Shine R. 2009. Heat, sight and scent: multiple cues influence foraging site selection by an ambush-foraging snake *Hoplocephalus bungaroides* (Elapidae). *Current Zoology* 55:266–271.

Franco F.L., Ferreira T. 2002. Descrição de uma nova espécie de *Thamnodynastes* Wagler, 1830 (Serpentes, Colubridae) do nordeste brasileiro, com comentários sobre o gênero. *Phyllomedusa* 1:57–74.

Gomez L., Larsen K.W., Gregory P.T. 2015. Contrasting patterns of migration and habitat use in neighboring Rattlesnake populations. *Journal of Herpetology* 49:371–376.

Haddad C.F.B., Prado, C.P.A. 2005. Reproductive Modes in Frogs and Their Unexpected Diversity in the Atlantic Forest of Brazil. *BioScience* 55:207–217.

Hyslop N.L., Cooper R.J., Meyers J.M. 2009. Seasonal Shifts in Shelter and Microhabitat Use of *Drymarchon couperi* (Eastern Indigo Snake) in Georgia. *Copeia* 2009:458–464.

Macartney J.M., Gregory P.T., Larsen K.W. 1988. A tabular survey of data on movement and home ranges of snakes. *Journal of Herpetology* 22:61–73.

Madsen T., Shine R. 1996. Seasonal migration of predators and prey: pythons and rats in tropical Australia. *Ecology* 77:149–56.

Mario-da-Rosa C., Abegg A.D., Malta-Borges L., Righi A.F., Bernarde P.S., Cechin S.Z., Santos T.G. 2020. A fisherman's tale: Activity, habitat use and the first evidence of lingual lure behavior in a South American snake. *Salamandra* 56:39–47.

Marques O.A.V., Eterovic A., Sazima I. 2001. Serpentes da Mata Atlântica - Guia Ilustrado para a Serra do Mar. Holos, Ribeirão Preto.

Moore J.A., Gillingham J.C. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the Eastern Massasauga (*Sistrurus catenatus catenatus*). *Copeia* 2006:742–51.

Nogueira C.C., Argôlo A.J.S., Arzamendia V., Azevedo J.A., Barbo F.E., Bérnils R.S., ..., Martins M.M. 2019. Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South American Journal of Herpetology* 14:1–274. doi:10.2994/SAJH-D-19-00120.1.

Pattishall A., Cundall D. 2008. Spatial Biology of Northern Watersnakes (*Nerodia sipedon*) Living along an Urban Stream. *Copeia* 2008:752–762.

Powell R.A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-100, in Boitani L., Fuller T.K. (Eds.). Research Techniques in Animal Ecology. Columbia University Press, New York.

Puente-Rolón A.R., Bird-Picó F.J. 2004. Foraging behavior, home range, movements and activity patterns of *Epicrates inornatus* (Boidae) at Mata de Platano Reserve in Arecibo, Puerto Rico. *Caribbean Journal of Science* 40:343–352.

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

Sazima I., Marques O.A.V. 2007. A reliable customer: hunting site fidelity by an actively foraging neotropical colubrid snake. *Herpetological Bulletin* 99:36–38.

Stephens D.W., Krebs J.R. 1986. Foraging Theory. Princeton, Princeton University Press.

Webb J.K., Shine R. 1997. A field study of the spatial ecology and movements of a threatened snake species, *Hoplocephalus bungaroides*. *Biological Conservation* 82:203–217.

Whitaker P.B., Shine R. 2003. A radiotelemetric study of movements and shelter-site selection by free ranging brownsnakes (*Pseudonaja textilis*, Elapidae). *Herpetological Monographs* 17:130–144.

Zaher H., Murphy R.W., Arredondo J.A.C., Graboski R., Machado-Filho P.R., Mahlow K., ..., Grazziotin F.G. 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE* 14:e0216148.

Zanella N., Cechin S.Z. 2006. Taxocenosis of snakes in the middle plateau region of Rio Grande do Sul, Brazil. *Revista Brasileira de Zoologia* 23:211–217.

Editor: Henrique C. Costa