

New dietary records and geographic variation in the diet composition of the snake *Philodryas nattereri* in Brazil

Raul Fernandes Dantas Sales¹, Juliana Delfino Sousa², Carolina Maria Cardoso Aires Lisboa³, Paulo Henrique Marinho³, Eliza Maria Xavier Freire¹, Marcelo Nogueira de Carvalho Kokubum^{2,4,5}

¹ Laboratório de Herpetologia, Departamento de Botânica e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Campus Universitário Lagoa Nova, 59072-970, Natal, RN, Brazil.

² Laboratório de Herpetologia, Unidade Acadêmica de Ciências Biológicas, Centro de Saúde e Tecnologia Rural, Universidade Federal de Campina Grande, Jatobá, 58708-110, Patos, PB, Brazil.

³ Programa de Pós-graduação em Ecologia, Departamento de Ecologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, 59072-970, Natal, RN, Brazil.

⁴ Programa de Pós-graduação em Ciências Florestais, Centro de Saúde e Tecnologia Rural, Universidade Federal de Campina Grande, Jatobá, 58708-110, Patos, PB, Brazil.

⁵ Programa de Pós-graduação em Ecologia e Conservação, Universidade Estadual da Paraíba, 58429-500, Campina Grande, PB, Brazil.

Recibida: 14 Abril 2020

Revisada: 02 Julio 2020

Acceptada: 21 Agosto 2020

Editor Asociado: V. Arzamendia

doi: 10.31017/CdH.2020.(2020-015)

ABSTRACT

In this study, we report new dietary data about the South American dipsadine snake *Philodryas nattereri* in the Caatinga ecoregion of northeastern Brazil. Our observations in the wild include predation on a large-sized lizard, an adult bird, venomous toads, a snake, bird chicks inside nests, and a mammal. Besides that, we compared the diet composition of *P. nattereri* between the Caatinga and the Cerrado ecoregions of Brazil, by pooling our original data with all available literature records. We found a significant difference in the diet of *P. nattereri* between these two regions: lizards comprise the predominant prey category for *P. nattereri* in the Caatinga, whereas mammals stand out as the most reported prey in the Cerrado. Our results evidence generalist and opportunistic feeding habits of *P. nattereri*, one of the most common snake species in Brazil.

Key Words: Caatinga; Cerrado; Dipsadinae; Feeding habits; Semi-arboreal habits.

Data on the natural history of snakes are important for studies on evolutionary biology and ecology (Greene, 1997; Martins and Oliveira, 1998). Furthermore, regional life-history data can contribute to an understanding of the patterns of ecological geographic variation of widely distributed snake species (Coelho *et al.*, 2019). Some snakes are known to show geographic variations in morphology (King, 1989; How *et al.*, 1996), habitat use (Shine, 1987), reproductive tactics (Seigel and Ford, 2001), defensive behavior (Sweet, 1985), foraging behavior and diet composition (Arnold, 1977; Luiselli *et al.*, 2005; Coelho *et al.*, 2019). However, detailed knowledge on feeding ecology and behavior of many snakes are still poorly understood, particularly for neotropical species (Guedes *et al.*, 2018).

The Paraguay Green Racer, *Philodryas nattereri* Steindachner, 1870, is a dipsadine snake widely distributed in the South American dry diagonal, from northeastern (NE) Brazil to Paraguay, occurring in the Caatinga, Cerrado and Pantanal ecoregions (Guedes *et al.*, 2014). It has diurnal activity and is considered a primarily terrestrial snake, but may also perch on trees and shrubs (Mesquita *et al.*, 2011, 2013). In the semiarid Caatinga of NE Brazil, *P. nattereri* is among the most common and abundant species of local snake assemblages, both in natural and in disturbed environments (Mesquita *et al.*, 2013; Guedes *et al.*, 2014). Like with most of its congeners, its diet can be classified as generalist and includes several small vertebrates such as lizards, birds, mammals and anurans (Vitt and Vangilder,

1983; França *et al.*, 2008; Mesquita *et al.*, 2011). Moreover, natural episodes of ophiophagy have also been reported in this species (Mesquita *et al.*, 2011; Guedes, 2017; Coelho-Lima *et al.*, 2019).

In this study, our goals were: (1) to report a compilation of predation events recorded by us in the Caatinga of northeastern Brazil involving different vertebrates species, most of them previously not reported as prey of *P. nattereri*; and (2) to present a literature review of all prey items reported for *P. nattereri* throughout its geographic distribution in Brazil. The combination of our original data with data from literature allowed us to test for geographic differences in the diet composition of *P. nattereri* between the Caatinga and the Cerrado, the two largest non-strictly forest ecoregions of Brazil.

The predation events described in this study were opportunistically recorded in the states of Rio Grande do Norte (RN) and Pernambuco (PE), between 2017 and 2020. One predation event was recorded by RFDS in João Câmara municipality, RN state (municipality's central coordinates: 5.5344° S; 35.8131° W), and eight predation events were recorded by JDS in Brejinho Municipality, PE state (municipality's central coordinates: 7.3473° S; 37.2868° W). We also present a predation event registered by an external collaborator (Cícero Lajes) in Angicos municipality, RN state (municipality's central coordinates: 5.6582° S; 36.6097° W), who kindly provided the photos and videos, together with the information about the observation. All these sites are in the Caatinga ecoregion of northeastern Brazil, where the climate is semiarid (BSh according to Köppen), hot and dry, with annual precipitation between 500 and 800 mm (Velloso *et al.*, 2002). None of the specimens (predators and prey) were collected, and the records were based on natural observations and photographs/videos.

In order to compile the available data about diet composition of *P. nattereri*, we made an extensive search in the literature in on-line bibliographic databases (Web of Science JSTOR, Scielo, Scopus, and Google Scholar), looking for dietary records of the species using a combination of the keywords "Paraguay Green Racer" or "*Philodryas nattereri*" plus "diet" or "feeding habits" or "prey". We also used a "snowball" method, searching for records in the "References" section of found articles. Unpublished predation records from dissertations, theses, and works published in congresses were not considered in the review. We split the records in relation to the

ecoregion of Brazil where they were made (Caatinga versus Cerrado). We present data on prey types by the taxonomic level of species when provided by the author. Higher taxonomic levels (e.g. genus, family) were pooled in the "unidentified" subcategory of each defined prey category (amphibians, lizards, snakes, mammals, birds, and vertebrate eggs). We considered in the review only studies where authors provided the number of prey items ingested by *P. nattereri*. To test for geographic differences in the diet composition between the Caatinga and the Cerrado, we used the Kolmogorov-Smirnov two-group test, considering the numeric proportions of prey categories (Fialho *et al.*, 2000).

The predation episodes are described below in chronological order. The first observation was recorded by JDS on 14 October 2017, at 09:40, in "Sítio Degredo" (7.3164° S; 37.2794° W, 755 m a.s.l.), Brejinho municipality, PE state. The vegetation physiognomy in this site is arboreal caatinga, with some disturbed areas due to cattle and agricultural activities. An adult individual of *P. nattereri* (sex not determined; total length around 150 cm) was observed on the ground below a tree subduing an adult individual (probably a female; total length around 50 cm) of the Common Green Iguana, *Iguana iguana* (Linnaeus, 1758). When spotted, the snake was already constricting and adjusting the lizard in the mouth (Fig. 1A). Ingestion process lasted about 20 minutes, and the snake stayed motionless for several minutes in the same place after completing swallowing.

The second observation was recorded by JDS on 31 January 2018, at 13:38, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. Similar to "Sítio Degredo", the vegetation physiognomy in this site is arboreal caatinga, with some disturbed areas due to cattle and agricultural activities. An adult individual of *P. nattereri* (sex not determined; total length around 100 cm) was observed on bare soil below a tree subduing an adult individual of the Picui ground-dove, *Columbina picui* (Temminck, 1813). When spotted, the snake was biting and holding the bird's neck on its mouth (Fig. 1B) but released the prey and quickly fled after human approximation. The observer checked the bird on the ground and confirmed that it was already dead. The snake would clearly succeed in the predation without the human interference.

The third observation was recorded by RFDS on 02 May 2018, at 16:18, in "Maria da Paz" com-

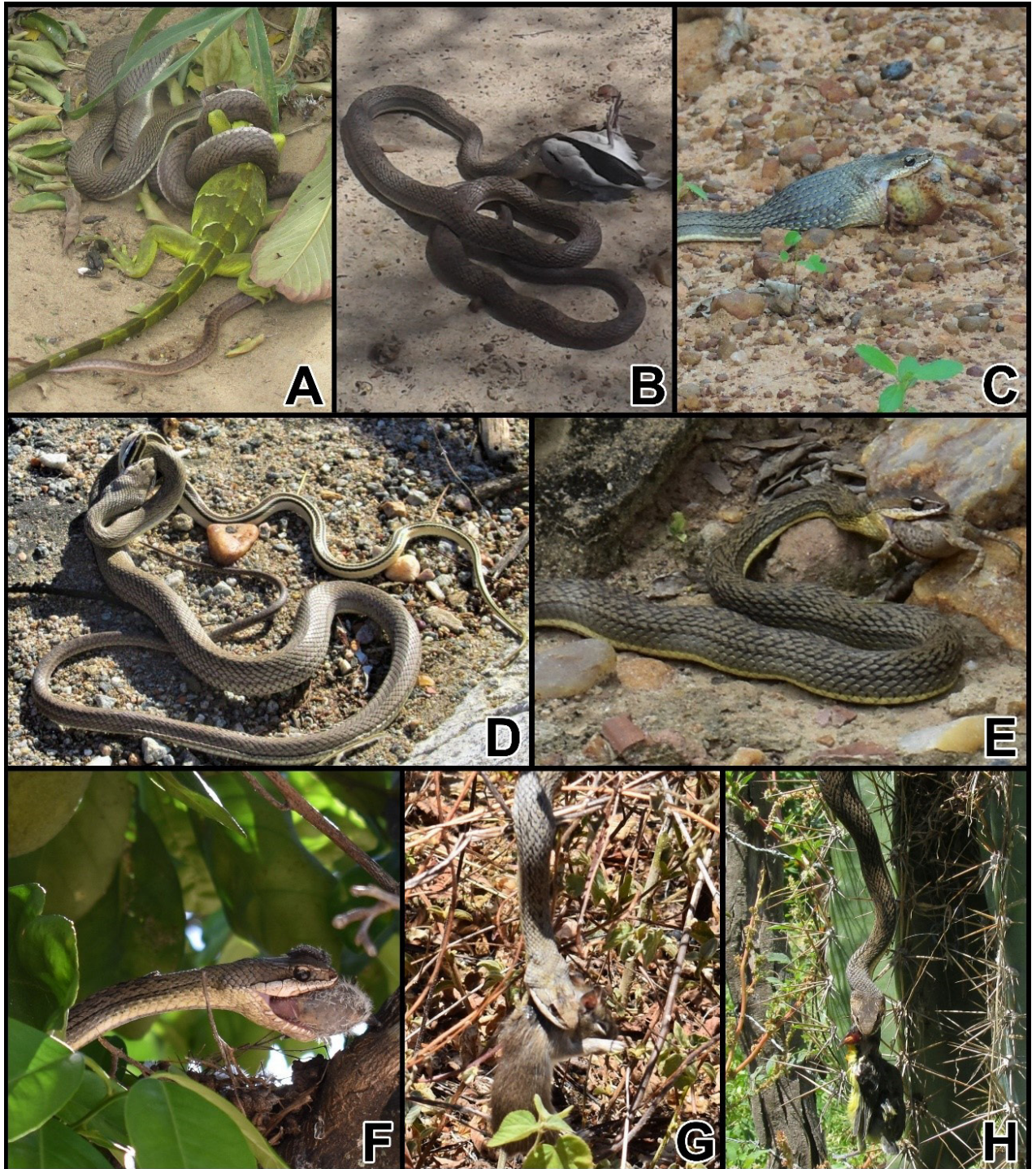


Figure 1. Prey items of the snake *Philodryas nattereri* reported in this study: A) *Iguana iguana*; B) *Columbina picui*; C) *Rhinella jimi*; D) *Lygophis dilepis*; E) *Rhinella granulosa*; F) chicks of *Columbina picui*; G) *Galea spixii*; H) *Coereba flaveola*.

munity (5.4570° S; 35.8905° W, 195 m a.s.l.), João Câmara municipality, RN state. The vegetation physiognomy in this site is shrubby caatinga, with some disturbed areas due to wind farms, cattle and agricultural activities. An adult individual of *P. nattereri* (sex not determined; total length around 150 cm) was observed on bare soil in the margins

of dense shrubby vegetation ingesting a juvenile individual (total length around 10 cm) of the Cururu toad, *Rhinella jimi* (Stevaux, 2002). When spotted, the snake was already adjusting the puffed-up toad in the mouth. The toad was swallowed belly up and head first (Fig. 1C), and the ingestion process lasted 15 min; after that, the snake remained motionless for

about three minutes, and then entered the shrubby vegetation and disappeared from the observer's sight.

The fourth observation was recorded by a group of cyclists on 09 September 2018, at 08:30, in the roadside of the highway BR 304 (5.6894° S; 36.3500° W, 153 m a.s.l.), Angicos municipality, RN state. The vegetation physiognomy in this site is disturbed shrubby caatinga due to cattle and agricultural activities, and the proximity of the highway facilitates anthropogenic disturbance. An adult individual of *P. nattereri* (sex not determined; total length around 100 cm) was spotted trying to subdue and swallow an adult individual of the Lema's striped snake, *Lygophis dilepis* Cope, 1862 (Fig. 1D). Although the *L. dilepis* was thinner than the *P. nattereri*, the two snakes had similar sizes, with the predator slightly larger than the prey. The *P. nattereri* kept a bite on the head region of the *L. dilepis*, presumably poisoning the prey with the rear fangs. After about five minutes, the two snakes were in the same position, but the observers left the site, so we cannot be sure if the attempted predation was successful or not.

The fifth observation was recorded by JDS on 20 March 2019, at 11:40, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex not determined; total length around 150 cm) was observed on bare rocky soil ingesting a juvenile individual (total length around 5 cm) of the Cururu toad, *Rhinella granulosa* (Spix, 1824). The observer located the individuals (predator and prey) because the toad emitted distress calls after being captured by the snake. When spotted, the snake was already adjusting the puffed-up toad in the mouth, which was swallowed belly down and head first (Fig. 1E). Ingestion lasted about 3 min, and the snake left the site immediately after swallowing the toad.

The sixth observation was recorded by JDS on 22 March 2019, at 11:36, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex not determined; total length around 150 cm) was observed perched on a tree (*Anacardium occidentale* L.) attempting to reach a nest of the Sayaca tanager, *Tangara sayaca* (Linnaeus, 1766). The bird parents mobbed the snake continuously, flying towards it and emitting alarm calls, which made the snake to withdraw approximation to the nest and move to the upper branches of the tree. During the snake's approach to the nest, two chicks fell to the ground

and were immediately assisted by the parents. The predation attempt was thereby unsuccessful.

The seventh observation was recorded by JDS on 16 September 2019, at 14:15, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex not determined; snout-vent length around 180 cm) was observed perched on a tree (*Citrus × sinensis* Macfad.), moving up to the higher branches. After 15 min, at 14:30, the snake moved down towards a nest of the Picui ground-dove, *Columbina picui* (Temminck, 1813). The snake stopped right above the nest, when an adult individual of *C. picui* (probably one of the parents) flew towards it but quickly moved away. The *P. nattereri* then captured a chick in the nest (Fig. 1F), which was swallowed in just 30 seconds; 22 seconds after ingestion, the snake captured another chick in the nest and swallowed it in 32 seconds. After the predation of the two chicks, the snake came down from the tree; the entire observation lasted 32 min.

The eighth observation was recorded by JDS on 16 October 2019, at 10:09, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex not determined; snout-vent length around 140 cm) was observed on the ground over some dry branches, preying upon a juvenile individual (total length around 8 cm) of the Spix's cavy, *Galea spixii* (Wagler, 1831). When spotted, the snake was biting and holding the prey's neck on its mouth, presumably poisoning it with the rear fangs (Fig. 1G); the juvenile *G. spixii* was still alive and emitting loud and pitched whistles. An adult individual of *G. spixii* (presumably the mother) was seen close to the snake, but ran away after the human approximation. The snake kept the juvenile on its mouth for 6 min, but the noise caused by the observer trying to get closer to take pictures disturbed the snake, leading it to release the prey and flee. The mammal was already dead when released by the snake, which would clearly succeed in the predation if there was no human interference.

The ninth observation was recorded by JDS on 5 April 2020, at 13:55, in "Sítio Fechado" (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex and snout-vent length not determined) was observed perched on a guava tree (*Psidium guajava* L.), at a height of about 2 m, being mobbed by two individuals of the Tropical Wren, *Troglodytes mus-*

culus Naumann, 1823. The birds mobbed the snake continuously, flying towards it and emitting alarm calls. A hole in the tree trunk, about 1 m below the location where the snake was, allowed the researcher to confirm the existence of a nest with three chicks. The *P. nattereri* entered another hole in the tree trunk near the site where it was first seen, then moved down inside the trunk and reached the nest; then snake ingested all three chicks in sequence (duration of ingestion: 32, 48 and 72 seconds). Fourteen minutes after ingestion of the last chick, the snake appeared in the hole entrance where the nest was positioned, but entered the trunk again. The bird parents continued to emit alarm calls during the entire observation, which lasted 72 minutes, when the researcher left the site.

The tenth observation was recorded by JDS on

14 May 2020, at 09:32, in “Sítio Fechado” (7.2992° S; 37.2978° W, 791 m a.s.l.), Brejinho municipality, PE state. An adult individual of *P. nattereri* (sex and snout-vent length not determined) was observed perched on a “mandacaru” cactus (*Cereus jamacuru* DC.) next to a bird nest preying upon a chick of the Bananaquit, *Coereba flaveola* (Linnaeus, 1758). When spotted, the snake was moving down the cactus, biting and holding the bird’s head on its mouth (Fig. 1H). Ingestion of the prey was completed in the ground and lasted 55 seconds.

We compiled a total of 93 prey items of *P. nattereri* combining the ones reported in this study with those of the literature; 67 records are from the Caatinga ecoregion (Table 1) and 26 records are from the Cerrado (Table 2). Lizards (N= 38) comprised the predominant prey category for *P. nattereri* in

Table 1. Summary of prey items of *Philodryas nattereri* in the Caatinga ecoregion of Brazil based on literature data and new observations.

Prey category	N	Source
Amphibians (N= 6)		
<i>Leptodactylus macrosternum</i> Miranda-Ribeiro, 1926	1	Mesquita <i>et al.</i> , 2011
<i>Rhinella granulosa</i> (Spix, 1824)	1	This study
<i>Rhinella jimi</i> (Stevaux, 2002)	3	Guedes <i>et al.</i> , 2018; this study
Unidentified	1	Vitt and Vangilder, 1983
Lizards (N= 38)		
<i>Ameivula ocellifera</i> (Spix, 1825)	11	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011
<i>Ameiva ameiva</i> (Linnaeus, 1758)	9	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011
<i>Tropidurus hispidus</i> (Spix, 1825)	5	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011; Menezes <i>et al.</i> , 2013
<i>Brasiliscincus heathi</i> (Schmidt & Inger, 1951)	2	Vitt and Vangilder, 1983
<i>Phyllopezus pollicaris</i> (Spix, 1825)	2	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011
<i>Hemidactylus mabouia</i> (Moreau de Jonnès, 1818)	1	Mesquita <i>et al.</i> , 2011
<i>Iguana iguana</i> (Linnaeus, 1758)	1	This study
<i>Salvator merianae</i> Duméril & Bibron, 1839	1	Vitt and Vangilder, 1983
<i>Vanzosaura multiscutata</i> (Amaral, 1933)	1	Vitt and Vangilder, 1983
Unidentified	5	Mesquita <i>et al.</i> , 2011
Snakes (N= 4)		
<i>Leptodeira annulata</i> (Linnaeus, 1758)	1	Guedes, 2017
<i>Oxybelis aeneus</i> (Wagler, 1824)	1	Mesquita <i>et al.</i> , 2011
<i>Oxyrhopus trigeminus</i> Duméril, Bibron & Duméril, 1854	1	Coelho-Lima <i>et al.</i> , 2019
<i>Lygophis dilepis</i> Cope, 1862	1	This study
Birds (N= 9)		
<i>Coereba flaveola</i> (Linnaeus, 1758)	1	This study
<i>Columbina picui</i> (Temminck, 1813)	3	This study
<i>Tangara sayaca</i> (Linnaeus, 1766)	*	This study
<i>Troglodytes musculus</i> Naumann, 1823	3	This study
Unidentified	2	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011

Mammals (N= 9)

<i>Necomys lasiurus</i> (Lund, 1841)	2	Vitt and Vangilder, 1983; Mesquita <i>et al.</i> , 2011
<i>Wiedomys pyrrhorhinos</i> (Wied-Neuwied, 1821)	2	Mesquita <i>et al.</i> , 2011
<i>Galea spixii</i> (Wagler, 1831)	1	This study
<i>Myotis nigricans</i> (Schinz, 1821)	1	Mesquita <i>et al.</i> , 2011
<i>Monodelphis domestica</i> (Wagner, 1842)	1	Mesquita <i>et al.</i> , 2011
<i>Rattus rattus</i> Linnaeus, 1758	1	Vitt and Vangilder, 1983
Unidentified	1	Mesquita <i>et al.</i> , 2011

Eggs (N= 1)

Unidentified (Squamata)	1	Mesquita <i>et al.</i> , 2011
-------------------------	---	-------------------------------

* Unsuccessful attempted predation

the Caatinga (56.7% of reported prey items; Table 1; Fig. 2), followed by mammals (N= 9; 13.4 %), birds (N= 9; 13.4%), anuran amphibians (N= 6; 9.0 %), snakes (N= 4; 6.0%), and vertebrate eggs (N= 1; 1.5 %). In the Cerrado ecoregion, mammals (N= 13) stand out as the most reported prey category (50.0% of reported prey items; Table 2; Fig. 2), followed by lizards (N= 7; 26.9%), anuran amphibians (N= 4; 15.4%), and birds (N= 2; 7.7%). Based on these data, the diet composition of *P. nattereri* is significantly different between the Caatinga and Cerrado ecoregions (Kolmogorov-Smirnov two-group test, $D_{\max} = 0.351$, $p < 0.001$).

In this study, we report ten predation events by the snake *Philodryas nattereri* in northeastern Brazil, bringing new data about its feeding habits. Our ob-

servations include predation on a large-sized lizard, one adult bird, two venomous toads, one snake, bird chicks, and one mammal. Our field observations, together with previous studies in the Caatinga (Vitt and Vangilder, 1983; Mesquita *et al.*, 2011) and in the Cerrado (França *et al.*, 2008) evidence that *P. nattereri* is a generalist and opportunistic snake predator in these ecoregions of Brazil. Mesquita *et al.* (2011) studied the autecology of *P. nattereri* in a Caatinga site in Ceará state, and argued that this snake may be a keystone species in the Caatinga, taking into consideration its high abundance, ability to forage in different substrates (e.g. ground, rocky outcrops, trees), wide variety of suitable prey, extended reproductive cycle and high fecundity. Thus, like other generalist and widely distributed snakes, *P. nattereri*

Table 2. Summary of prey items of *Philodryas nattereri* in the Cerrado ecoregion of Brazil based on literature data.

Prey category	N	Source
Amphibians (N= 4)		
<i>Leptodactylus vastus</i> A. Lutz, 1930	1	Araújo <i>et al.</i> , 2013
<i>Physalaemus cuvieri</i> Fitzinger, 1826	1	Gambale <i>et al.</i> , 2014
<i>Scinax x-signatus</i> (Spix, 1824)	1	Godinho <i>et al.</i> , 2012
Unidentified	1	França <i>et al.</i> , 2008
Lizards (N= 7)		
<i>Hemidactylus mabouia</i> (Moreau de Jonnés, 1818)	1	Godinho <i>et al.</i> , 2012
<i>Tropidurus itambere</i> Rodrigues, 1987	1	França <i>et al.</i> , 2008
<i>Tropidurus torquatus</i> (Wied-Neuwied, 1820)	4	França <i>et al.</i> , 2008
Unidentified	1	França <i>et al.</i> , 2008
Birds (N= 2)		
<i>Volatinia jacarina</i> (Linnaeus, 1766)	1	França <i>et al.</i> , 2008
Unidentified	1	França <i>et al.</i> , 2008
Mammals (N= 13)		
Unidentified	13	França <i>et al.</i> , 2008

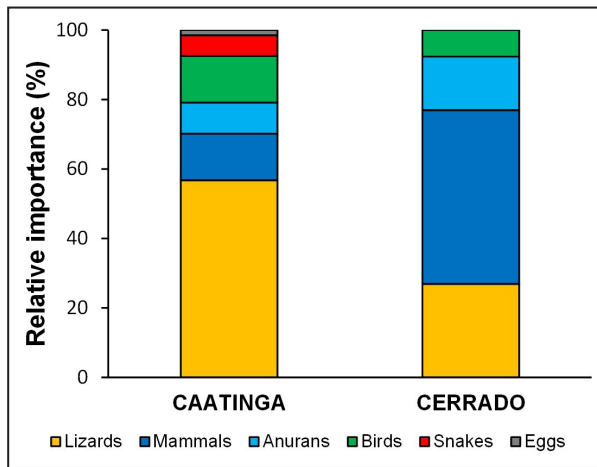


Figure 2. Relative contribution of different prey categories in the diet of *Philodryas nattereri* in the Caatinga and Cerrado ecoregions of Brazil.

can play an important ecological role in controlling prey populations (Cabral *et al.*, 2019), especially in altered environments where top predators have been locally extinct.

In agreement with Mesquita *et al.* (2011), our observations confirm the semi-arboreal habits of *P. nattereri*, which was previously thought to be terrestrial (Vitt, 1980; Vanzolini *et al.* 1980). This snake is able not only to perch on trees, but is also an efficient arboreal forager, feeding on adult birds (França *et al.*, 2008; Mesquita *et al.*, 2011), bird chicks inside nests (this study), arboreal snakes (Mesquita *et al.*, 2011) and bats, presumably in their shelters (Mesquita *et al.*, 2011). Our data also evidence that some flying and/or arboreal prey can be captured by *P. nattereri* in the ground. Many birds forage in the ground (Sick, 1997), and thus can be ambushed by *P. nattereri*, such as the dove *Columbina picui* reported in this study, which was captured by *P. nattereri* in the ground (Fig. 1B). The predation of the arboreal lizard *Iguana iguana* in the ground by *P. nattereri* (Fig. 1A) can be defined as highly opportunistic, since this lizard spends most of the time perched on trees, but can eventually go down to the soil to bask (Sales *et al.*, 2009).

Our data also revealed different feeding tactics of *P. nattereri* depending on the type, size and vitality of prey. This species can use constriction (e.g. large-sized lizards, Fig. 1A) and/or poisoning to subdue the preys (e.g. adult birds, Fig. 1B; rodents, Fig. 1G), or simply catch and swallow defenseless prey (e.g. bird chicks, Figs. 1D and 1H). *Philodryas nattereri* is also able to feed on toads of the genus *Rhinella* (Figs.

1C and 1E), which are stocky, inflate their bodies in defense, and have parotoid macroglands behind the eyes that secrete powerful venom (Jared *et al.*, 2009). Guedes *et al.* (2018) suggest that this way of ingestion of *P. nattereri* enables the snake's post-diastemal teeth to puncture the puffed-up bodies of toads, deflating them and facilitating ingestion. Moreover, this position may prevent the toad from grasping on the substrate, or may reduce the compression of parotoid glands against the palate of the snake, avoiding venom liberation in the oral mucosa (Guedes *et al.* 2018). Nevertheless, in the predation episode on *R. granulosa* (Fig. 1E), a smaller *Rhinella* species, the toad was ingested belly down and did not deflate during swallowing, which indicates that *P. nattereri* may vary the way of ingestion of toads depending on their sizes. Since toads are nocturnal and *P. nattereri* is diurnal, it is highly likely that *P. nattereri* actively searches for them in their shelters. This same hunting strategy is probably adopted by *P. nattereri* towards bats (Mesquita *et al.*, 2011).

Several authors report birds as part of the diet of snakes of the genus *Philodryas* (Vitt, 1980; Hartmann and Marques, 2005; Leite *et al.*, 2009; Mesquita *et al.*, 2011), but few literature records (e.g. Sazima and Marques, 2007; Sazima, 2015) specify how snakes catch these highly evasive preys. For instance, the Lichtenstein's Green Racer, *Philodryas olfersii* (Lichtenstein, 1823) chooses profitable hunting spots in trees to ambush birds (Sazima, 2015). The new field observations reported in this study show that *P. nattereri* can both ambush adult birds and actively search for bird chicks in their nests. Bird chicks are defenseless, and can be quickly swallowed without any resistance. However, if the snake is detected by adult birds, they can promptly perform mobbing to avoid predation of chicks, as in the episode of approximation of *P. nattereri* to nests of the birds *Tangara sayaca* and *Troglodytes musculus*. Mobbing is a type of harassing behavior employed by birds in the presence of potential predators, in which they emit alarm calls, display visual signals (which may attract additional birds to the mobbing group), and may fly towards the potential predator, disturbing it by pecking (Sick, 1997; Sazima and Marques, 2007; Sazima, 2015). In some instances, the mobbing behavior may be successful in discouraging the predator, as in the attempted predation event upon chicks of *T. sayaca* reported in this study.

Many genera of snakes have members that include snakes as part or all of their diet (Greene,

1997). Observations both in natural conditions and simulated in the lab confirm that some snakes are even able to ingest other snakes that equal or exceed their own body length (Jackson *et al.*, 2004). In the Caatinga of NE Brazil, a few snakes are known by their ophiophagous feeding habits, such as the Sertão Muçurana snake, *Boiruna sertaneja* Zaher, 1996, that despite being characterized as a snake specialist (Alencar *et al.*, 2013), also feeds on lizards, mammals and birds (Sales *et al.*, 2019). Our observation of predation of *Lygophis dilepis* (Fig. 1D) constitutes the fourth record of ophiophagous behavior for *P. nattereri* (Table 1). As suggested by Coelho-Lima *et al.* (2019), the consumption of snakes by *P. nattereri* may be more frequent than previously assumed.

The dietary data of *P. nattereri* yielded from our field observations and literature records revealed geographic variations in diet composition (Fig. 2). Lizards comprised the most reported prey in the Caatinga, whereas mammals are the most reported prey in the Cerrado. These results agree with the geographic variation reported for the Brazilian false coral snake, *Oxyrhopus trigeminus* Duméril, Bibron & Duméril, 1854, in which lizards are massively consumed by Caatinga populations, accounting for ~90% of the diet (Vitt and Valgilder, 1983; Coelho *et al.*, 2019), whereas mammals are the predominant prey in the Cerrado (França *et al.*, 2008), and these prey categories are more equitably consumed in the Atlantic Forest (Alencar *et al.*, 2012). Prey availability is the main discussed cause for geographic variations in diet composition of squamates (e.g. Vitt and Colli, 1994). Thus, given the generalist and opportunistic feeding habits of *P. nattereri*, the differences in diet composition between Caatinga and Cerrado ecoregions are likely related to prey availability. For small non-flying mammals, for example, in the Cerrado there is a greater species richness and abundance than in the Caatinga (Freitas *et al.*, 2005). However, the low sampling effort on the feeding ecology of *P. nattereri* in both ecoregions makes it difficult to establish large generalizations and should be considered when interpreting the results presented here. Other evoked causes for geographic variation in diets of snakes, such as presence/absence of potential competitors (Luiselli *et al.*, 2005) and interpopulational differences in behaviors that influence resource utilization (Arnold, 1977), may also be applicable to *P. nattereri*. Future studies should address these questions to improve knowledge about this abundant and widely distributed snake that plays an important

ecological role as a predator in both natural and disturbed environments of Brazil.

Acknowledgements

We are grateful to Cícero Lajes for kindly provide us the photos and videos, together with the information about the predation events. Raul Sales and Paulo Marinho thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the post-doctoral and PhD (Finance Code 001) scholarships, respectively. Eliza Freire thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research scholarship (process 142961/2019-1).

Literature cited

- Alencar, L.R.V., Galdino, C.A.B. & Nascimento, L.B. 2012. Life history aspects of *Oxyrhopus trigeminus* (Serpentes: Dipsadidae) from two sites in southeastern Brazil. *Journal of Herpetology* 46: 9-13.
- Alencar, L.R., Gaiarsa, M.P. & Martins, M. 2013. The evolution of diet and microhabitat use in Pseudoboine snakes. *South American Journal of Herpetology* 8: 60-67.
- Araújo, S.C.M., Sousam G.D.L. & Andrade, E.B. 2013. *Philodryas nattereri* (Paraguay Green Racer). Diet. *Herpetological Review* 44: 526.
- Arnold, S.J. 1977. Polymorphism and geographic variation in the feeding behavior of the Garter Snake *Thamnophis elegans*. *Science* 197: 676-678.
- Cabral, S.O., Freitas, I.S., Morlanes, V., Katzenberger, M. & Calabuig, C. 2019. Potential seed dispersers: a new facet of the ecological role of *Boa constrictor constrictor* Linnaeus 1758. *Biota Neotropica* 19: e20180626.
- Coelho, R.D.F., Sales, R.F.D. & Ribeiro, L.B. 2019. Sexual dimorphism, diet, and notes on reproduction in *Oxyrhopus trigeminus* (Serpentes: Colubridae) in the semiarid Caatinga of northeastern Brazil. *Phyllomedusa* 18: 89-96.
- Coelho-Lima, A.D., Oliveira-Filho, J.M. & Passos, D.C. 2019. *Philodryas nattereri* (Paraguay Green Racer). Diet. *Herpetological Review* 50: 601.
- Fialho, R.F., Rocha, C.F.D. & Vrcibradic, D. 2000. Feeding ecology of *Tropidurus torquatus*: ontogenetic shift in plant consumption and seasonal trends in diet. *Journal of Herpetology* 34: 325-330.
- França, F.G.R., Mesquita, D.O., Nogueira, C.C. & Araújo, A.F.B. 2008. Phylogeny and ecology determine morphological structure in a snake assemblage in the central Brazilian Cerrado. *Copeia* 2008: 23-28.
- Freitas, R.R., Rocha, P.L.B. & Simões-Lopes, P.C. 2005. Habitat structure and small mammals abundances in one semiarid landscape in the Brazilian Caatinga. *Revista Brasileira de Zoologia* 22: 119-129.
- Gambale, P.G., Batista, V.G., Vieira, R.R., Dias, T.M., Morais, A.R. & Bastos, R.P. 2014. *Physalaemus cuvieri* (Barker Frog). Predation. *Herpetological Review* 45: 682-683.
- Godinho, L.B., Moura, M.R., Peixoto, M.A. & Feio, R.N. 2012. Notes on the diet of *Philodryas nattereri* (Squamata:

- Colubridae) in southeastern Brazil. *Salamandra* 48: 233-234.
- Greene, H.W. 1997. *Snakes: The Evolution of Mystery in Nature*. University of California Press. Berkeley and Los Angeles.
- Guedes, T.B. 2017. *Philodryas nattereri* (Paraguay Green Racer). Diet. *Herpetological Review* 48: 679-680.
- Guedes, T.B., Nogueira, C. & Marques, O.A.V. 2014. Diversity, natural history, and geographic distribution of snakes in the Caatinga, Northeastern Brazil. *Zootaxa* 3863: 1-93.
- Guedes, T.B., Sazima, I. & Marques, O.A.V. 2018. Does swallowing a toad require any specialisation? Feeding behaviour of the dipsadid snake *Philodryas nattereri* on the bufonid toad *Rhinella jimi*. *Herpetology Notes* 11: 825-828.
- Hartmann, P.A. & Marques, O.A.V. 2005. Diet and habitat use of two sympatric species of *Philodryas* (Colubridae), in South Brazil. *Amphibia-Reptilia* 26: 25-31.
- How, R.A., Schmitt L.H. & Suyanto, A. 1996. Geographical variation in the morphology of four snake species from the Lesser Sunda Islands, eastern Indonesia. *Biological Journal of the Linnean Society* 59: 439-456.
- Jackson, K., Kley, N.J. & Brainerd, E.L. 2004. How snakes eat snakes: the biomechanical challenges of ophiophagy for the California kingsnake, *Lampropeltis getula californica* (Serpentes: Colubridae). *Zoology* 107: 191-200.
- Jared, C., Antoniazzi, M.M., Jordão, A.E.C., Silva, J.R.M.C., Greven H. & Rodrigues, M.T. 2009. Parotoid macroglands in toad (*Rhinella jimi*): their structure and functioning in passive defence. *Toxicon* 54: 197-207.
- King, R.B. 1989. Body size variation among island and mainland snake populations. *Herpetologica* 45: 84-88.
- Leite, P.T., Kaefer, I.L. & Cechin, S.Z. 2009. Diet of *Philodryas olfersii* (Serpentes, Colubridae) during hydroelectric dam flooding in southern Brazil. *North-Western Journal of Zoology* 5: 53-60.
- Luiselli, L., Filippi, E. & Capula, M. 2005. Geographic variation in diet composition of the grass snake (*Natrix natrix*) along the mainland and an island of Italy: the effects of habitat type and interference with potential competitors. *The Herpetological Journal* 15: 221-230.
- Martins, M. & Oliveira, M.E. 1998. Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* 6: 78-150.
- Menezes, L.M.N., Reis, P.M.A.G., Souza, K., Urias, I.C., Walker, F.M. & Ribeiro, L.B. 2013. Death of a snake *Philodryas nattereri* (Squamata: Dipsadidae) after predation on a large-sized lizard *Tropidurus hispidus* (Squamata: Tropiduridae). *Herpetology Notes* 6: 55-57.
- Mesquita, P.C.M.D., Borges-Nojosa, D. M., Passos, D.C. & Bezerra, C.H. 2011. Ecology of *Philodryas nattereri* in the Brazilian semi-arid region. *Herpetological Journal* 21: 193-198.
- Mesquita, P.C.M.D., Passos, D.C., Borges-Nojosa, D.M. & Cechin, S.Z. 2013. Ecologia e história natural das serpentes de uma área de Caatinga no nordeste brasileiro. *Papéis Avulsos de Zoologia* 53: 99-113.
- Sales, R.F.D., Lisboa, C.M.C.A. & Freire, E.M.X. 2009. Répteis Squamata de remanescentes florestais do campus da Universidade Federal do Rio Grande do Norte, Natal-RN, Brasil. *Cuadernos de Herpetología* 23: 77-88.
- Sales, R.F.D., Lima, M.L.S. & França, B.R.A. 2019. Dead but delicious: an unusual feeding event by the Sertão Muçurana snake (*Boiruna sertaneja*) on a bird carcass. *Herpetology Notes* 12: 941-943.
- Sazima I. 2015. Predation attempts on birds by the snake *Philodryas olfersii* prevented by mobbing mockingbirds. *Herpetology Notes* 8: 231-233.
- 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.
- Seigel, R.A. & Ford, N.B. 2001. Phenotypic plasticity in reproductive traits: geographical variation in plasticity in a viviparous snake. *Functional Ecology* 15: 36-42.
- Shine, R. 1987. Intraspecific variation in thermoregulation, movements and habitat use by Australian blacksnakes, *Pseudechis porphyriacus* (Elapidae). *Journal of Herpetology* 21: 165-177.
- Sick, H. 1997. *Ornitologia Brasileira*. Nova Fronteira. Rio de Janeiro, Brazil.
- Sweet, S.S. 1985. Geographic variation, convergent crypsis and mimicry in Gopher snakes (*Pituophis melanoleucus*) and Western rattlesnakes (*Crotalus viridis*). *Journal of Herpetology* 19: 55-67.
- Vanzolini, P.E., Ramos-Costa, A. & Vitt, L.J. 1980. Répteis das Caatingas. Academia Brasileira de Ciências. Rio de Janeiro, Brazil.
- Velloso, A.L., Sampaio, E.V.S.B. & Pareyn, F.G.C. 2002. Ecorregiões: Propostas para o Bioma Caatinga. Instituto de Conservação Ambiental. The Nature Conservancy do Brasil. Recife, Brazil.
- Vitt, L.J. 1980. Ecological observation on sympatric *Philodryas* (Colubridae) in northeastern Brazil. *Papéis Avulsos de Zoologia* 34: 87-98.
- Vitt, L.J. & Vangilder, L.D. 1983. Ecology of a snake community in Northeastern Brazil. *Amphibia-Reptilia* 4: 273-296.
- Vitt, L.J. & Colli, G.R. 1994. Geographical ecology of a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. *Canadian Journal of Zoology* 72: 1986-2008.

