Ecology of *Philodryas nattereri* in the Brazilian semi-arid region

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We describe, through hypothesis testing and observations on life-history traits, the ecology of the snake *Philodryas nattereri* in a semi-arid region in north-east Brazil, where it is widespread and occurs at high abundance. We document sexual dimorphism in snout–vent length and relative tail length. The species is diurnal and semi-arboreal, and most active during the warmest periods of the day. It is active year-round, with peaks of activity during periods of maximum precipitation and temperature. Adults feed on a variety of prey types, whereas juveniles are lizard specialists. The reproductive season extends over at least nine months of the year. We conclude that, due to its high abundance, foraging skills and fecundity, *P. nattereri* is a major predator in the Brazilian semi-arid region.

Key words: activity, caatinga, diet, Dipsadidae, reproduction, Serpentes, snake

INTRODUCTION

Information on the natural history of snakes is important in understanding the wide variety of habits adopted by many species (Greene, 1997), and the widespread current declines in snakes (Reading et al., 2010). *Philodryas nattereri* is a member of the Dipsadidae, Xenodontinae, Philodryadini (Zaher et al., 2009; Vidal et al., 2010; Ferrarezzi, 1994; Uetz, 2009), and a medium-sized, active forager (Vitt, 1980). The species occurs in arid and semi-arid regions of Brazil, Paraguay and Colombia (Uetz, 2009), and is one of the most common snake species in northeastern Brazil (Amaral, 1936).

Activity patterns of snakes can vary at different temporal scales under the influence of biotic and abiotic factors. Seasonal activity has been the focus of many studies in both temperate and tropical climates, and, in general, depends on climatic variables such as rainfall, humidity and temperature. Short-term activity patterns such as daily activity, on the other hand, have been rather poorly studied in neotropical snakes such as *P. nattereri*, and our knowledge is usually limited to characterizing species as diurnal or nocturnal (Vitt & Vangilder, 1983; Martins & Oliveira, 1999). The available information on habitat use by *P. nattereri* is also very general, characterizing the species as mainly ground dwelling (Vanzolini et al., 1980; Vitt, 1980; Vitt & Vangilder, 1983). Members of the genus *Philodryas* usually consume a wide array of vertebrate prey (Vitt, 1980; Hartmann & Marques, 2005; López & Giraudo, 2008; Leite et al., 2009; but see Marques et al., 2006 for *P. agassizi*). *Philodryas nattereri*, like most other congeners, can be classified as a generalist, including amphibians, reptiles, birds and mammals in its diet (Marques et al., 2005; Vitt, 1980; Lima-Verde, 1991).

Sex differences in body measurements are widespread across the animal kingdom, and reflect the different se-lective pressures acting on males and females. In snakes, sexual dimorphism in snout–vent length, tail length, size and shape of the head and coloration is common (Rivas & Burghardt, 2001; Shine, 1991, 1994; for *Philodryas* see Fowler & Salomão, 1994). Information on reproductive biology is important in understanding the life history of snakes, yet it is still poorly studied for most neotropical species (Pizzato et al., 2008a). Tropical snakes exhibit a variety of reproductive strategies depending on climate seasonality, prey availability and phylogeny, amongst other factors (Marques, 1996a,b; Pizzato & Marques, 2002; Pinto & Fernandes, 2004; Alves et al., 2005; Pizzatto et al., 2008a,b). The information available for the genus *Philodryas* suggests that reproduction throughout the year is common, to some degree representing phylogenetic conservatism (Fowler et al., 1998; Vitt & Vangilder, 1983). Here we present new information on sexual dimorphism, daily and seasonal activity, feeding habits and female reproductive biology of *P. nattereri* in northeastern Brazil.

MATERIALS AND METHODS

The study area was located in the Fazenda Experimental Vale do Curu (3º49'06.1"S, 39º20'14.8"W, GPS datum: WGS 84) in Pentecoste municipality, Ceará state, and covers 823 ha, including 142 ha of relicts of the caatinga biome. The climate is semi-arid, with an annual mean temperature of 26.8 ºC, 73% relative humidity and 723.3 mm rainfall. Seasonality is marked, with a wet period from February to July and a dry period during the reminder of the year (Barros et al., 2002; Leão et al., 2004).

We searched the study area for *P. nattereri* on four days in each month from July 2008 through June 2010. For each individual recorded in the field, we noted the date, time of day, and use of substrate at the time of the encounter. For each individual captured, we noted the sex,

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and induced regurgitation by gentle abdominal palpation in order to gather dietary data (Tuttle & Gregory, 2009). Additionally, we analysed individuals deposited in the Collection of Herpetology of the Universidade Federal do Ceará (CHUFC) from the study area and its surroundings. For each preserved specimen, we measured snout–vent length (SVL), relative tail length (TL), head length (HL) and mass after draining the preservation liquids. We examined the contents of the digestive tract through a ventral incision, measured the gonads of females to the nearest mm, and counted the number of follicles in secondary vitellogenesis (if present). We considered females to be mature when they contained yellowish and enlarged follicles (> 10 mm) or eggs in the oviduct (Shine 1993, 1994), and the presence of a loosened oviduct as evidence of recent oviposition.

To compare SVL data between the sexes, we used an analysis of variance (ANOVA) and the sexual size-dimorphism index proposed by Shine (1994). To compare TL and HL we used an analysis of covariance (ANCOVA) with SVL as the covariate. Similarly, we applied an AN-COVA to detect differences in mass using total length (SVL + TL) as the covariate of the cubic root of the mass. Individuals with partly or totally amputated tails were excluded from analyses involving tail length, and road-killed specimens or those kept in captivity before euthanasia were excluded from analyses involving mass. Individuals that were not sexed were excluded from all analyses of sexual dimorphism, and specimens that were kept in captivity before euthanasia were excluded from the analysis of sexual dimorphism and diet.

To test for monthly variation in abundance we applied a chi-square test. To examine seasonal activity we used a multiple regression model of monthly abundance against rainfall, maximum (T_{max}), minimum (T_{min}) and mean (T_{mean}) temperature obtained from a meteorological station in the study area. To assess the lag period of response to the significant variables, we used a cross-correlation test using PAST software (Hammer et al., 2001). To detect possible ontogenetic and sexual segregation in diet composition, we used G tests (Sokal & Rohlf, 1995). To evaluate the association of female reproductive season and climate
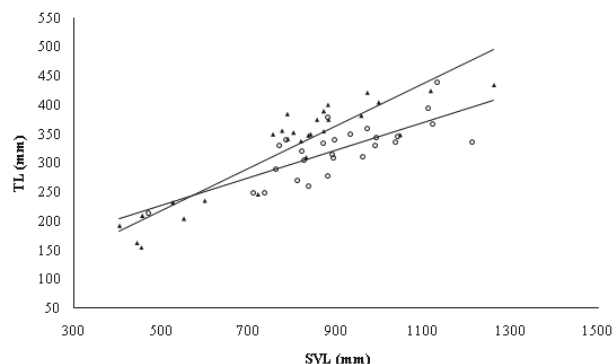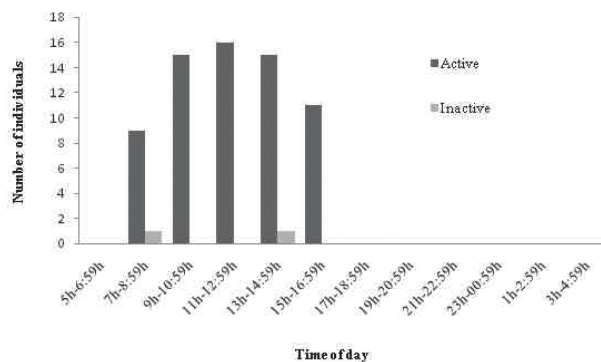
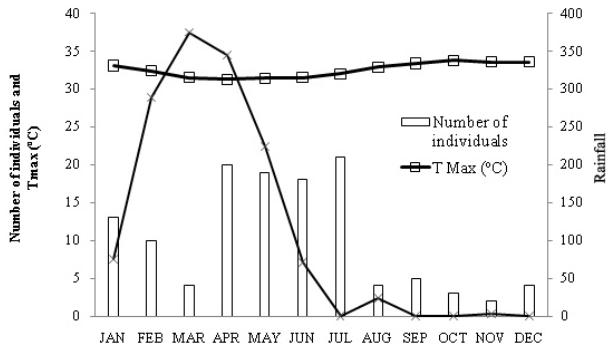**Fig. 2.** Number of *Philodryas nattereri* found across the day.

seasonality we used a multiple regression model of the natural log of monthly mean ovarian follicle size against rainfall, T_{max}, T_{min} and T_{mean}. A one-way ANOVA was used to determine if there was monthly variation in the size of ovarian follicles. All tests except the cross-correlation were conducted with Statistica 7.0 (Statsoft, 2004).

RESULTS

Of 58 sexed individuals, 27 were females and 31 were males. SVL of females ranged from 470 to 1210 mm (mean = 900.3±155.4; n=27), and SVL of males from 403 to 1260 mm (mean = 788.32±210.9; n=31); females had a higher SVL than males ($F_{1,55}$=4.992; P=0.030), corresponding with an SSD index of 0.142. There were no sex differences in HL ($F_{1,61}$=0.442; P=0.509) or mass ($F_{1,55}$=1.29; P=0.263); males, however, had longer tails ($F_{1,55}$=15.847; P<0.001; see Fig. 1).
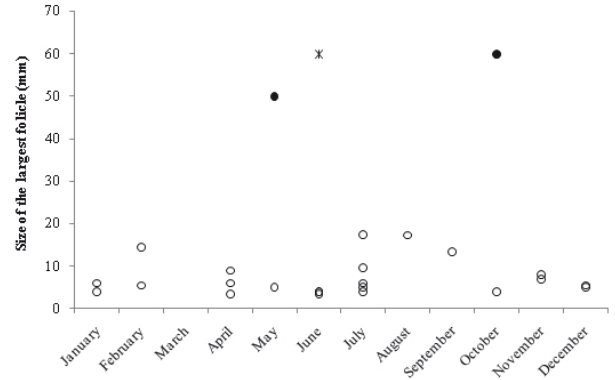
We obtained information on daily activity from 68 field encounters. *Philodryas nattereri* was exclusively diurnal, and most active during the warmest period of the day (between 1100 and 1259, see Fig. 2). We recorded information on substrate use for 74 individuals. Of these, 73% (n=54) were found on the ground (including road killed individuals), 21.6% (n=16) were above the ground (including rooftops), and 5.4% (n=4) were underground. At least four of the individuals on the ground attempted to flee to underground shelter.

We also obtained seasonal records for 51 individuals deposited in the CHUFC, totalling 125 records. Recording rates differed between months (chi-square =60.51; P<0.001, df=11). The multiple regression model (R^2=0.645; P=0.007) indicated that rainfall (t= –2.56; P=0.031) and maximum temperature (t= –2.67; P=0.037) were the best predictors of snake abundance, whereas minimum and mean temperatures did not explain any variation. The cross-correlation test indicated that *P. nattereri* reduced its activity almost immediately after temperature changes (Lag=0, R^2= –0.738, P=0.006) and around two months after the end of the rainy season (Lag= –2, R^2=0.926, P>0.001; Fig. 3).

Fig. 1. Sexual dimorphism in relative tail length in *Philodryas nattereri.* Triangles: males, circles: females.

Fig. 3. Number of individual *Philodryas nattereri* found in relation to maximum temperature and rainfall.

Fig. 4. Female reproductive cycle of *Philodryas nattereri.* Black circles: eggs; asterisk: evidence of recent oviposition; white circles: vitellogenic follicles.

We investigated the digestive tract of 39 individuals, 66.67% of which (*n*=26) contained dietary items (*n*=32 items). Lizards were the most common prey (68.75%), followed by mammals (18.75%), an amphibians, snake, and a squamate egg (3.125% each, Table 1). The most frequent prey item was the whip-tail lizard *Cnemidophorus ocellifer*, which comprised 28.12% of the total food items. There was a pronounced ontogenetic shift in feed-

ing habits (G=5.145; *P*=0.023); juveniles fed exclusively on lizards, whilst adults were generalists, consuming a variety of prey types. There was no difference between the feeding habits of males and females (G=6.666, *P*=0.246).

Females contained between eight and 21 follicles in secondary vitellogenesis or eggs in the oviduct from February through October, indicating an extended repro-

Table 1. Contents of the digestive tract of *Philodryas nattereri*. *N1* = number of *P. nattereri* containing the prey item; *N2* = number of times the prey item was found; *RF* = relative frequency of the prey item.

Prey taxon	Item	*N1*	*N2*	*RF* (%)
Lizards				68.75
Teiidae	*Ameiva ameiva*	2	3	9.375
	Cnemidophorus ocellifer	8	9	28.125
	Unidentified Teiidae	1	1	3.125
Tropiduridae	*Tropidurus hispidus*	3	3	9.375
Gekkonidae	*Hemidactylus mabouia*	1	1	3.125
Phyllodactylidae	*Phyllopezus pollicaris*	1	1	3.125
Unidentified	Unidentified lizard	4	4	12.5
Snakes				3.125
Colubridae	*Oxybelis aeneus*	1	1	3.125
Eggs				3.125
Squamata	Squamate egg	1	1	3.125
Amphibians				3.125
Leptodactylidae	*Leptodactylus macrosternum*	1	1	3.125
Mammals				18.75
Cricetidae	*Necromys lasiurus*	1	1	3.125
	Wiedomys pyrrhorhinos	2	2	6.25
Didelphidae	*Monodelphis domestica*	1	1	3.125
Vespertilionidae	*Myotis nigricans*	1	1	3.125
Unidentified	(fur and bones)	1	1	3.125
Birds				3.125
Unidentified	Passeriformes	1	1	3.125
Total			32	100

Table 2. Prey items previously reported for *Philodryas nattereri* in northeastern Brazil. *Previously published in Mesquita & Borges-Nojosa (2009). **Previously published in Mesquita et al. (2010).

Taxon	Species	Registered in	
		Vitt (1980)	This study
Lizards			
Teiidae	*Ameiva ameiva*	X	X
	Cnemidophorus ocellifer	X	X
	Tupinambis merianae	X	
	Unidentified Teiidae		X
Tropiduridae	*Tropidurus hispidus*	X	X
Gekkonidae	*Hemidactylus mabouia*		X
Phyllodactylidae	*Phyllopezus policaris*	X	X
Gymnophthalmidae	*Vanzosaura rubricauda*	X	
Scincidae	*Mabuya heathi*	X	
Unidentified	Unidentified lizard		X
Snakes			
Colubridae	*Oxybelis aeneus**		X
Eggs			
Squamata	Squamate egg		X
Amphibians			
Leptodactylidae	*Leptodactylus macrosternum*		X
Mammals			
Cricetidae	*Necromys lasiurus*	X	X
	Wiedomys pyrrhorhinos		X
Muridae	*Rattus rattus*	X	
Didelphidae	*Monodelphis domestica*		X
Vespertilionidae	*Myotis nigricans***		X
Unidentified	Unidentified		X
Birds			
Passeriformes	Unidentified	X	X

ductive season that was not influenced by seasonality (R^2=0.249; P=0.145; Fig. 4). There was no variation in the size of ovarian follicles ($F_{9,21}$=0.938; P=0.531) during the year. Two ovigerous females also had follicles in secondary vitellogenesis.

DISCUSSION

Sexual dimorphism, which can be influenced by reproductive pressures or dietary differences between sexes (Shine, 1991, 1993, 1994; Pizzatto et al., 2007), was previously reported for adult *P. nattereri* by Fowler & Salomão (1994). We found that juveniles and small adults have similar size and body proportions, and that sex differences emerge after sexual maturity and increase with SVL (Fig. 1). However, we found no dietary difference between males and females, indicating that the sexual dimorphism observed for *P. nattereri* is due to reproductive traits rather than dietary pressures. This result is consistent with observations by López & Giraudo (2008) for the congener *P. patagoniensis*.

Body size and the high level of foraging activity may explain the pattern of daily activity, which peaks during the warmest times of the day. The main prey of *P. nattereri*, the whip-tail lizard *C. ocellifer*, is also mainly active during the warmer hours (Mesquita & Colli, 2003). When ambient temperatures remained high for longer periods, snakes reduced their activity, probably because of physiological traits that evolved from ectothermy. We observed increased activity in the rainy season, when prey is presumably more abundant, and environmental heterogeneity increases with the growth of vegetation.

Our study revealed that *P. nattereri* is semi-arboreal. This is not in line with Vitt (1980) and Vanzolini et al. (1980), who described the species as terrestrial. We observed individuals up to 7 m above ground, and the presence of typically arboreal prey, such as bats, birds, arboreal snakes and rodents, indicates that *P. nattereri* is an efficient arboreal forager (Table 2). *Philodryas nattereri* is thought to subdue its prey by constriction. Although this is the most common behaviour, we observed an individual subduing an adult *C. ocellifer* by poisoning with the rear fangs. We also found one ingested squamate egg. Queiroz & Rodriguez-Robles (2006) suggested that feeding on squamate eggs is most likely to occur among snakes that also feed on adult squamates. As most snakes

use chemical cues prior to predation, this might aid in the recognition of eggs as suitable food because of chemical similarities between eggs and corresponding juveniles or adults.

Seasonal reproduction is common among snakes in temperate regions (Seigel & Ford, 1987). However, in tropical regions we might expect longer and possibly continuous reproductive cycles despite dry periods that can restrict reproductive activity (Saint-Girons, 1982; Brown & Shine, 2002). Our results are complementary to those presented by Vitt & Vangilder (1983), who inferred a rather short reproductive season. The presence of follicles in secondary vitellogenesis in ovigerous females suggests the possibility of multiple clutches during one reproductive season. This is rare in snakes, although it has been observed in other Brazilian species of Xenodontinae (Pinto & Fernandes, 2004).

Taking into consideration its high abundance, ability to forage in arboreal, terrestrial, and underground substrates, wide variety of suitable prey, extended reproductive cycle and high fecundity, we suggest that *P. nattereri* is a major snake predator in our study area. It may be a keystone species in most biological communities of the Brazilian semi-arid region (Pain, 1969; Underwood, 1986).

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APPENDIX 1

List of museum specimens used in this study

BRAZIL: CEARÁ: Pentecoste: CHUFC 714, CHUFC 2959, CHUFC 3008, CHUFC 3048, CHUFC 3085, CHUFC 3086, CHUFC 3087, CHUFC 3088, CHUFC 3113, CHUFC 3139, CHUFC 3143, CHUFC 3144, CHUFC 3171, CHUFC 3173, CHUFC 3193, CHUFC 3194, CHUFC 3195, CHUFC 3196, CHUFC 3197, CHUFC 3198, CHUFC 3212, CHUFC 3213, CHUFC 3506, CHUFC 3343, CHUFC 3344, CHUFC 3345, CHUFC 2803, CHUFC 2942, CHUFC2972, CHUFC 2943, CHUFC 3268; Boa Viagem: CHUFC 1249; Caucaia: CHUFC 2267; Caridade: CHUFC 1214; Catuana: CHUFC 1767; Cedro: CHUFC 1097; Crateús: CHUFC 2521; Fortaleza: CHUFC 1568, CHUFC 1632, CHUFC 2279, CHUFC 1352, CHUFC 2292; Guaiuba: CHUFC 1920; Limoeiro do Norte: CHUFC 13, CHUFC 91, CHUFC 98, CHUFC 103, CHUFC 125, CHUFC 215; Quixadá: CHUFC 722; Quixeramobim: CHUFC 1096.