Ecology of the Colubrid Snake *Spilotes pullatus* from the Atlantic Forest of Southeastern Brazil

Author(s): Otavio A. V. Marques, Diego F. Muniz-Da-Silva, Fausto E. Barbo, Silvia R. Travaglia Cardoso, Danusa C. Maia, and Selma M. Almeida-Santos

Source: Herpetologica, 70(4):407-416. 2014.

Published By: The Herpetologists' League

DOI: http://dx.doi.org/10.1655/HERPETOLOGICA-D-14-00012

URL: http://www.bioone.org/doi/full/10.1655/HERPETOLOGICA-D-14-00012

Herpetologica, 70(4), 2014, 407–416

ECOLOGY OF THE COLUBRID SNAKE *SPILOTES PULLATUS* FROM THE ATLANTIC FOREST OF SOUTHEASTERN BRAZIL

Otavio A. V. Marques[1,5], Diego F. Muniz-Da-Silva[2], Fausto E. Barbo[3], Silvia R. Travaglia Cardoso[4], Danusa C. Maia[4], and Selma M. Almeida-Santos[1]

[1] *Instituto Butantan, Laboratório de Ecologia e Evolução, Av. Dr. Vital Brazil, 1500, São Paulo, 05503-900, SP, Brazil*
[2] *Setor de Anatomia, Departamento de Cirurgia, Faculdade de Medicina Veterinária e Zootecnia, Universidade São Paulo, Av. Orlando Marques de Paiva 87, 05508-270 Cidade Universitária, São Paulo, SP, Brazil*
[3] *Museu de Zoologia, Universidade de São Paulo (MZUSP), P.B. 42494, 04218-970, São Paulo, SP, Brazil*
[4] *Instituto Butantan, Museu Biológico, Av. Dr. Vital Brazil, 1500, São Paulo, 05503-900, SP, Brazil*

Abstract: Few extensive studies have addressed the ecology of South American colubrids. *Spilotes pullatus* is a large and conspicuous colubrid snake with a broad distribution in South America. We analyzed the morphology, habitat use, diet, feeding behavior, and reproductive biology of *S. pullatus* in a subtropical area of distribution, specifically in the Atlantic Forest of southeastern Brazil. We compared its ecological traits with those of other South American colubrids to identify common characteristics and differences among these snakes. *Spilotes pullatus* inhabits primarily lowland areas and readily occurs in altered habitats. Male and female snakes were similar in median snout–vent length, but the largest known individuals of the species are males. This snake forages actively by day, searching primarily for small mammals and nestling birds (usually 0.36–7.37% of snake mass) on the ground or in vegetation. Observations of captive snakes showed that small prey are quickly swallowed alive, whereas large prey are constricted or pressed against the substrate and die before swallowing. The reproductive cycle of the females appears to be seasonal, with vitellogenesis occurring from the middle of the dry season to the onset of the rainy season. Mating was recorded at the end of the dry season and the onset of the rainy season and coincided with the onset of male–male combat. Such combat behavior includes partial entwining of the anterior portions of the body and a consistent, upright position of the trunk. Recruitment of newborns occurs at the end of the rainy season and during the dry season. *Spilotes pullatus* shows unique characteristics but also shares several ecological traits with other South American colubrids.

Key words: Diet ecology; Habitat use; Reproduction; Subtropical region; Yellow Ratsnakes

The cosmopolitan family Colubridae is diverse in North and Central America but few representatives are found in South America (Greene, 1997). However, certain colubrids are conspicuous elements of the snake fauna in most portions of this region. *Spilotes pullatus* is the most widely distributed colubrid in South America and is abundant in habitats such as the Brazilian Atlantic Forest (Peters and Orejas-Miranda, 1970; Marques, 1998; Hartmann et al., 2009). Despite its conspicuousness and wide distribution, *S. pullatus* has never been the subject of a detailed study covering the principal aspects of its ecology.

Spilotes pullatus grows to a snout–vent length (SVL) of >1500 mm. This snake may be exclusively diurnal and is usually described as arboreal (Amaral, 1978; Dixon et al., 1993; Martins and Oliveira, 1998). The species is reported to feed on a wide range of vertebrates (cf. Beebe, 1946; Cunha and Nascimento, 1978; Murphy, 1997; Martins and Oliveira, 1998), although several researchers have stated that its prey consists primarily of birds and their eggs (e.g., Amaral, 1978; Loiselle and Hoppes, 1983). Subsequent studies found that this snake feeds on smaller-sized prey such as juvenile mammals and nestling birds (Marques and Sazima, 2004). Data on reproduction are scarce and anecdotal, rarely documented (e.g., Hauzman et al., 2005), and insufficient to characterize the reproductive cycle or fecundity of the species. Defensive behaviors have been previously described (Rossman and Williams, 1966; Sazima and Haddad, 1992), but other behavioral characteristics, including feeding and reproduction, are virtually unknown. In this paper we provide information on the habitat use, daily activity, body size, reproductive behavior, reproductive cycles, fecundity, diet, and feeding behavior of *S. pullatus*

---

[5] Correspondence: email, otavio.marques@butantan.gov.br

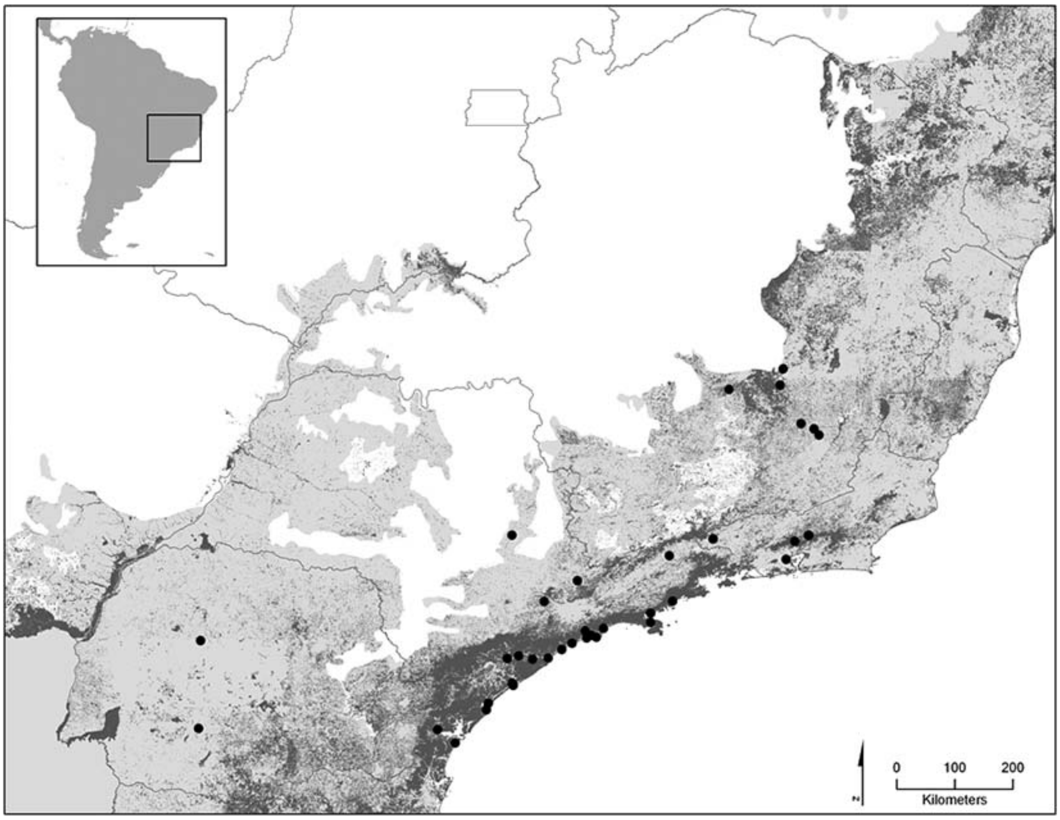

FIG. 1.—Specimen localities of individual *Spilotes pullatus* used in this study. Gray area represents the Atlantic Forest biome within South America (inset). Darker gray areas indicate forest remnants.

in the subtropical Atlantic Forest, where it is locally abundant.

MATERIALS AND METHODS

Specimens and Life-history Data

Our study is based on the dissection of preserved specimens from herpetological collections and on observations in the field and in captivity. We examined 178 preserved specimens from the following museum collections: Fundação Nacional Ezequiel Dias (FUNED), Instituto Butantan (IBSP), Museu de Ciências e Tecnologia da Pontifícia Universidade Católica de Porto Alegre (MCT), Museu de História Natural Capão da Imbuia (MHNCI), Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Museu de Zoologia João Moojen da Universidade Federal de Viçosa (MZUFV), Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (PUC-MG), Centro Universitário Serra dos Órgãos de Teresópolis (UNIFESO), and Museu de História Natural da Universidade Estadual de Campinas (ZUEC). The examined samples included only specimens collected in southeastern Brazil, from Minas Gerais (20°S) to Paraná (25°S). This area lies within the Atlantic Forest domain, with an elevational range of 0–2000 m above sea level (asl; Fig. 1). This portion of the Atlantic Forest has two seasons: rainy, with higher rainfall and temperatures, and dry, with less rainfall and lower temperatures. The rainy season comprises austral spring (October–December) and summer (January–March) whereas the dry season comprises autumn (April–June) and winter (July–September; Nimer, 1989).

We collected the following data for each specimen: (1) SVL; (2) tail length (TL); (3)

sex; (4) juvenile or adult—males were adult if they had enlarged testes and opaque deferent ducts (Shine, 1982), and females were adult if they had either ovarian follicles in vitellogenesis or oviductal eggs (Shine, 1980); (5) for females, diameter of the largest ovarian follicles, diameter of the largest egg, number of ovarian follicles in vitellogenesis (>10 mm), and number of oviductal eggs; and (6) stomach or intestinal contents (or both). All food items in the stomach were removed, identified to the lowest possible taxonomic level, and measured when intact or nearly undigested. Following Shine (1994), the degree of sexual size dimorphism (SSD) was calculated as:

$$\mathrm{SSD} = \frac{1 - (\text{mean adult SVL of the larger sex})}{(\text{mean adult SVL of the smaller sex})}$$

Behavioral Data

Captive individuals (15 adults: SVL > 1280 mm, 13 juveniles: SVL < 950 mm) were housed individually in terraria lined with either 2 cm of soil or corrugated paperboard (minimum terrarium size = 30 × 36 × 56 cm and 32 × 32 × 47 cm for adults and juveniles, respectively). All captive snakes were maintained at room temperature (24–27°C). Prior to their use in feeding trials, subjects were offered gerbils (*Meriones unguiculatus*), house mice (*Mus musculus*), and rats (*Rattus norvegicus*); all snakes accepted prey (each being ~15% of snake body mass). The mass of prey used in the trials ranged from 2–80 g (2.5–30% of subject body mass). After each snake had swallowed its prey, we offered another prey item having a different mass. We recorded the number of mandibular protractions and time (in seconds) from the initiation of swallowing until the prey disappeared into the snake's throat. All feeding sequences were recorded with VHS video, or photographed, or both.

We obtained data on courtship, copulation, and male–male combat for *S. pullatus* in the field (between 2000 and 2012) from observations by fellow researchers, from our own observations, and from documented records (photos and videotapes) furnished by lay people. From these sources, we recorded habitat of occurrence and specific body postures during combat. All behavioral observations from feeding trials and field encounters are archived on a DVD housed at Laboratoìrio de Ecologia e Evolução of Instituto Butantan.

Reproductive Data

We obtained data on oviposition from four gravid females received by Instituto Butantan. The eggs were incubated in moist vermiculite at room temperature (24–27°C). Within 12 h of oviposition, we measured both females and their eggs and calculated relative clutch mass (RCM = clutch mass/maternal body mass; Seigel and Ford, 1987). We measured hatchlings within 24 h of emergence from their eggs. We defined clutch size as the number of oviductal eggs or large vitellogenic ovarian follicles (>10 mm) in preserved females (n = 13) as well as the number of eggs laid by live females ($n = 4$). We used linear regression to examine the relationship between maternal SVL and clutch size (Zar, 1996). All statistical analyses were performed using Statistica (StatSoft, 2003), and differences were considered significant at $\alpha = 0.05$.

Ecological Data

We collected data on habitat use at the Estação Ecológica Jureia-Itatins (EEJI; ~80,000 ha, 24°23′25″S, 47°01′05′W, elevation 0–1240 m asl; GPS datum = SAD69), a preserved portion of Atlantic Forest in southeastern Brazil. The fieldwork at EEJI was part of a study of the natural history of the local snake assemblage (Marques, 1998; Marques and Sazima, 2004). In that study, snakes were sampled in preserved forest and in a disturbed region adjacent to EEJI dominated by banana plantations. Snake surveys at the EEJI were conducted from 1993–1998. One researcher (OAVM) searched for snakes along forest trails every month. The total survey time was 900 h during the day (effort uniform from 0800 to 1800 h) and 300 h at night (effort uniform from 1800 to 2200 h). Snakes were also collected with the aid of local collectors. The local collectors were active in the field throughout the day and less frequently after sunset (effort in each hour was not quantified). To evaluate whether *S. pullatus* is a forest-dependent snake, we compared its

Table 1.—Prey items recovered from *Spilotes pullatus* collected in southeastern Brazil. Forty-two prey items were found in 37 snakes containing prey. The number of prey items (*n*) is provided with the frequency in parenthesis.

Prey category	*n* (%)
Birds	
Trogon sp.	2 (4.8)
Turdus sp.	1 (2.4)
Unidentified	2 (4.8)
Mammals	
Rodentia	
Muridae	
Oligoryzomys sp.	1 (2.4)
Nectomys sp.	1 (2.4)
Unidentified	17 (40.4)
Didelphimorpha	1 (2.4)
Chiroptera	
Molossidae	1 (2.4)
Unidentified	1 (2.4)
Unidentified	15 (35.8)

frequency of occurrence in a disturbed area (a banana plantation near EEJI) with the frequency of occurrence in this area of *Chironius* spp., a genus of forest-dependent arboreal colubrid (Marques and Sazima, 2004). In EEJI, members of *Chironius* include *Chironius bicarinatus*, *Chironius exoletus*, *Chironius foveatus*, and *Chironius fuscus*, which are all ecologically similar (Marques and Sazima, 2004).

Results

Life-history Data

Body size.—Adult male (mean SVL = 1481 ± 171 mm, range 1150–1910 mm, *n* = 112) and adult female snakes (mean SVL = 1413 ± 172 mm, range 1280–1610 mm, *n* = 52) were similar in body size (*F* = 0.13; *P* = 0.722). Adult males had relatively longer tails than the adult females (*F* = 5.96; *P* = 0.015). The largest male specimen measured 2540 mm in total length (SVL + TL) whereas the largest female measured 2295 mm. The degree of SSD equaled –0.032 (cf. Shine, 1994).

Food habits.—Small mammals were the most-common prey, representing approximately 90% of the 42 items recorded (Table 1). At least seven of these items (~17%, including nestlings and bats) are usually positioned in arboreal habitats within the landscape. Prey mass was not correlated with snake mass (r^2 = 0.10, *P* = 0.34, *n* = 11) and ranged from 0.36–7.37% of snake mass ($\bar{X}$ = 3.68 ± 2.34, *n* = 11). Three snakes had more than one neonatal rodent (either 2 or 3) in their stomachs.

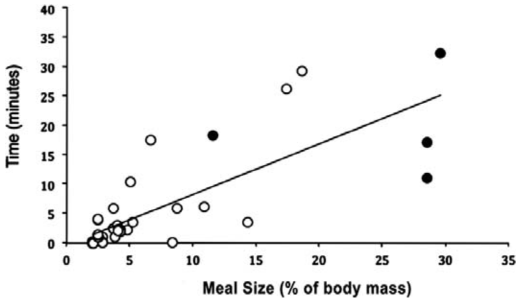

Fig. 2.—Relationship between meal size (% of snake body mass) and ingestion time by specimens of *Spilotes pullatus* (r^2 = 0.61, *P* = 0.003; based on a sample size of 40 feeding episodes involving 28 subjects). Filled circles represent snakes that died after ingestion of meal.

Behavioral Data

Feeding behavior.—Up to five prey items were consumed by each subject in the lab trials. Small rodents were grasped and swallowed alive. However, the mode of handling differed for larger rodents (>10% of the mass of the snake); upon introduction of the rodent, the snake moved toward the rodent, then struck it and subdued it with body coils. During coiling, the snake pushed the prey against the coil or the substrate. The snake then swallowed the prey while moving the right and left mandibles in alternate sequence. The number of mandibular movements required to swallow the rodents varied from 3–54, and the swallowing time ranged from 4.2–1935.6 s. For small rodents (<5% of snake mass), the number of mandibular protractions was always <17, and the swallowing time usually did not exceed 300 sec (Fig. 2). For heavier rodents (>15% of snake mass), the number of mandibular protractions was >30, and swallowing time was usually much longer (Fig. 2). Approximately 30% of the subjects that ate heavy rats regurgitated the prey item; additionally, three subjects (all of which swallowed prey of approximately 30% of their mass) died.

Mating and male–male combat.—Mating and copulation in the field were recorded in

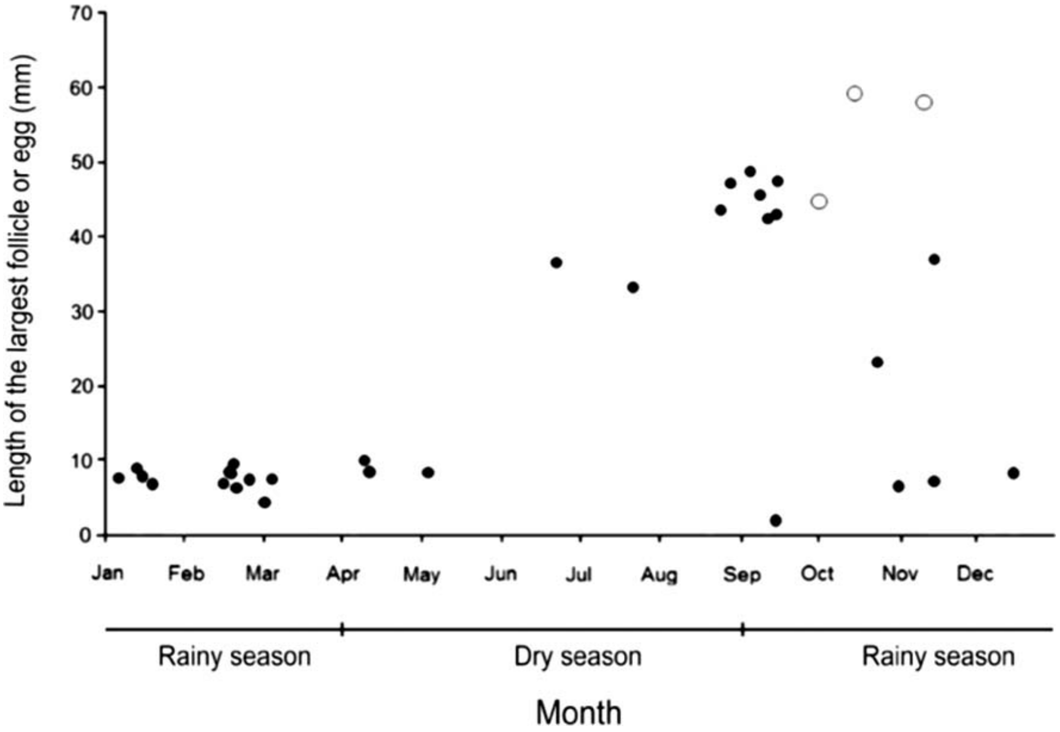

FIG. 3.—Seasonal variation in diameter of the largest ovarian follicle or oviductal eggs in females of *Spilotes pullatus* ($n = 32$) from southeastern Atlantic Forest. Solid circles = ovarian follicles; open circles = oviductal eggs.

the Atlantic Forest of southeastern Brazil on the ground ($n = 4$) and on the vegetation ($n = 1$) in August ($n = 1$), September ($n = 2$), and October ($n = 2$). A sequence of male–male combat behavior (which lasted for at least 1 h) was videotaped on the ground in the Ibiocara municipality, Bahia (18°32′S, 53°07′W; a locality 600 km north of our study site in the southeastern Atlantic Forest) on 19 August 2012. The postures observed included partial entwining of the posterior portions of the body, with the head and anterior portion of the trunk always upright. Each male attempted to obtain a position higher than its adversary by displaying its anterior portion of body as high as possible.

Reproductive Data

Reproductive cycle.—Analyses of follicle sizes indicated a seasonal reproductive cycle in *S. pullatus* (Fig. 3). The follicles were small (diameter <10 mm) for approximately 6 mo (December–May), vitellogenesis occurred from the dry season (June) to the onset of the rainy season (November), and ovulation and oviposition were restricted to the onset of the rainy season (October–November; Fig. 3). Oviposition by the four captive females occurred during the rainy season (November and December; Table 2). The period of egg incubation for two of the captive clutches ranged between 101–117 d. Hatchlings emerged from the eggs in March (middle to late rainy season; Table 2). Preserved hatchlings (SVL < 400 mm, $n = 23$) accessioned in the museum collections were most-often collected in the second half of the rainy season (January–April; Fig. 4).

Fecundity.—Clutch size ranged from 5 to 11 ($\bar{X} = 8.6 \pm 1.5$, $n = 17$) and was positively correlated with maternal SVL ($r^2 = 0.29$, $P = 0.008$; Fig. 5). The RCM ranged from 0.31–0.48. Upon emergence from eggs maintained in captivity, hatchlings averaged 376 ± 32.5 mm in SVL (320–415, $n = 13$) and 18.5 ± 3.1 g in mass (14.3–23.5 g, $n = 13$; Table 2).

Table 2.—Morphometric and reproductive data for four adult female *Spilotes pullatus* collected in southeastern Brazil. Values are reported as means ±1 SD, with range and sample size in parentheses where appropriate. SVL = snout–vent length; RCM = relative clutch mass.

Female		Eggs			Hatchlings		
SVL (mm)	mass (g)	Oviposition date	Number	RCM	Hatching date	SVL (mm)	Mass (g)
1405	610	3 November 2007	9	0.48	—	—	—
1500	539	20 December 2010	10	0.39	31 March 2011	351 ± 21 (320–380, *n* = 7)	15.9 ± 1.1 (14.3–17.3, *n* = 7)
1450	565	16 November 2011	7	0.31	13 March 2012	405 ± 12 (390–415, *n* = 6)	21.4 ± 1.6 (18.6–23.5, *n* = 6)
1440	532	16 November 2011	9	0.44	—	—	—

Ecological Data

We gathered a total of 178 collection records in the Atlantic Forest. The altitudinal distribution of specimens ranged from 0–930 m asl. Most specimens (79%) were collected in low areas (<200 m asl). A total of 40 specimens of *S. pullatus* were found in EEJI (10 by OAVM and 30 by local collectors). Five of these snakes were found on the vegetation (12.5%), with one individual resting and four moving on branches (one of them was observed on a tree approximately 10 m high ingesting two nestlings of a *Trogon* sp.). Specimens on the ground were moving or were observed with the body stretched (possibly pausing or basking). All snakes were found between 0700 to 1700 h (daylight hours). The likelihood of *S. pullatus* occurring in disturbed habitats (8.5% of 130 encounters of all snake species) and preserved areas (12.5% of 204 encounters) was similar (χ^2 = 1.69, df = 1, $P > 0.10$). In contrast, other

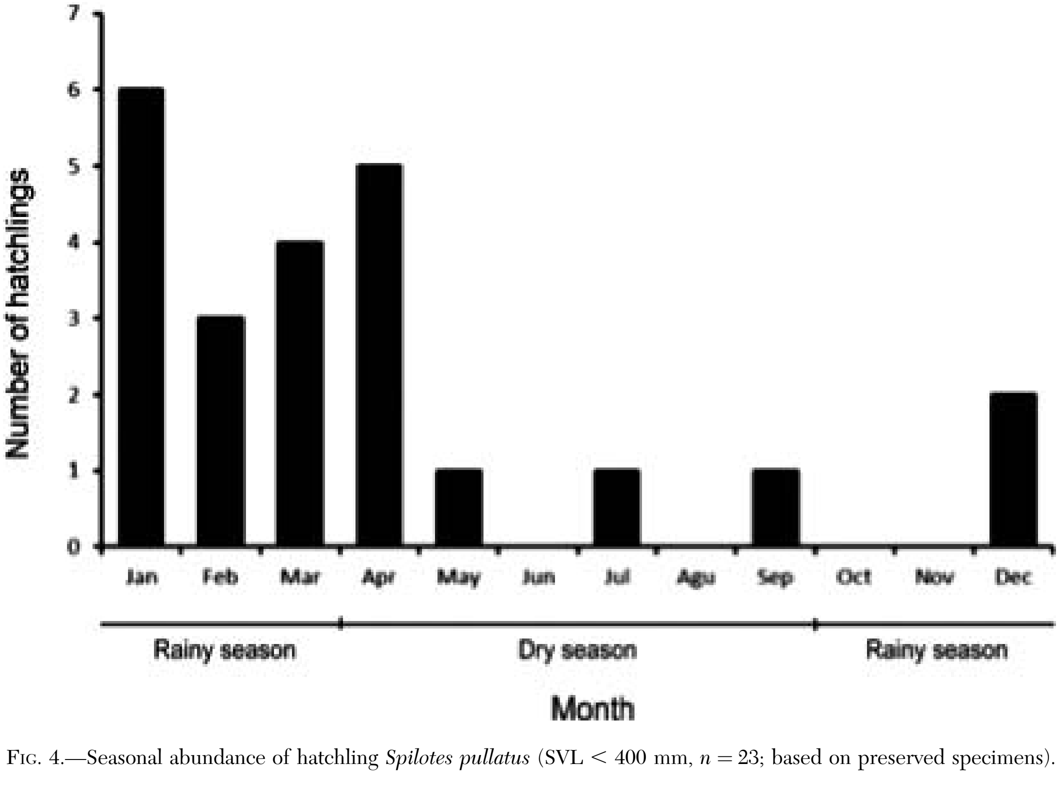

Fig. 4.—Seasonal abundance of hatchling *Spilotes pullatus* (SVL < 400 mm, $n = 23$; based on preserved specimens).

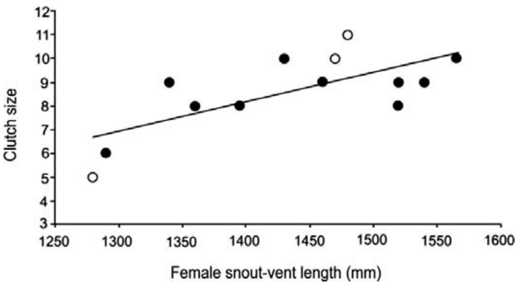

FIG. 5.—Relationship between female snout–vent length (mm) and clutch size in *Spilotes pullatus* from southeastern Atlantic Forest ($r^2 = 0.29$, $P = 0.008$, $n = 13$). Solid circles = vitellogenic follicles; open circles = eggs.

arboreal colubrids (*Chironius* spp.) were less likely to occur in disturbed habitats (1.5% of 130 snake encounters) than in the preserved area (9.3% of 204 encounters; $\chi^2 = 8.42$, df = 1, $P < 0.01$).

DISCUSSION

Spilotes pullatus is among the largest of the South American colubrids, ranging up to 2500 mm in total length (Cunha and Nascimento, 1978; Nickerson et al., 1978). Our data on activity patterns confirm previous reports that *S. pullatus* is diurnal in habit, frequently found in the morning basking on the ground or foraging by day (Sazima and Haddad, 1992; Martins and Oliveira, 1998). *Spilotes pullatus* possesses a round pupil and, while this does not preclude nocturnal activity (Brischoux et al., 2010), the retina is composed primarily of cones that facilitate color vision at high light intensities. Indeed, the co-occurring traits of diurnal activity, circular pupils, and active foraging found in *S. pullatus* represent a common pattern among other South American colubrids (cf. Martins and Oliveira, 1998).

Several previous studies cite birds as an important prey item for *S. pullatus* (e.g., Amaral, 1978; Cunha and Nascimento, 1978), whereas other researchers describe this snake as a generalist that includes frogs, lizards, and mammals in its diet (Martins and Oliveira, 1998). We found only endothermic prey (rodents, marsupials, bats, and birds) in the guts of preserved specimens. Predation on bird nests by *S. pullatus* (observed here and by Robinson and Robinson, 2001), as well as the frequency of neonatal rodents in the diet, indicate that *S. pullatus* forages equally well on the ground or in vegetation (where it usually consumes nest contents). The predominance of nonvolant small mammals, such as terrestrial rodents, suggests that *S. pullatus* forages primarily on the ground. The predominance of terrestrial prey might also explain the occurrence of this species in disturbed habitats. Predation on smaller prey sizes (relative to snake mass) could also facilitate this species' use of arboreal habitat (including locations high in the canopy) where heavy objects in the stomach might impede efficient movement through the vegetation.

Ingestion of relatively small prey sizes has been reported for other terrestrial colubrids in Central America (*Drymobius chloroticus*, *D. margaritiferus*, and *Mastigodryas melanolomus*); the mass of such prey ranges from 4.1–12.9% of snake body mass (Seib, 1984). Other colubrid snakes occurring in South America (*Chironius* spp., *M. bifossatus*, and *Simophis rhinostoma*) also eat small prey (<20% of snake body mass; Bizerra et al., 1994; Marques and Muriel, 2007; Pinto et al., 2008; OAVM, personal observation). Thus, the tendency to eat relatively small prey may be a common trait among these colubrid snakes (Marques and Sazima, 2004; Marques and Muriel, 2007).

Values for time taken, and the number of mandibular protractions required, to swallow small prey (<5% of snake body size) were both low for *Spilotes pullatus*. If this finding applies to other colubrids, then consuming small prey might represent an advantage to these snakes because they can minimize handling time (and potential susceptibility to predators). *Spilotes pullatus* is a large snake and can subdue large prey by constriction (Sazima and Haddad, 1992). In spite of this, the ingestion of larger prey (>15% of snake mass) appears to be difficult for this species as evidenced by the frequency of regurgitation, or even the death of the snake, when offered large prey items. Thus, this snake is potentially strong enough to subdue large prey but likely faces a morphological (functional) constraint on swallowing prey of this size.

Male–male combat behavior has been recorded in *S. pullatus* as well as in South American members of *Chironius* (Almeida-

Santos and Marques, 2002; Muniz-Da-Silva and Almeida-Santos, 2013). Other South American colubrids also show similar patterns of SSD (e.g., *Drymoluber*, *Leptophis*, *Mastigodryas*, and *Pseustes*) and might exhibit male–male combat behavior. The phylogeny proposed by Hollis (2006) indicates that these genera belong to the same clade, and male–male combat may be a trait shared by these snakes. The posture adopted by combating male *S. pullatus* and that described for *Chironius* both include the continuous vertical orientation of the anterior bodies as well as the entwining of the posterior portions (Almeida-Santos and Marques, 2002; Muniz-Da-Silva and Almeida-Santos, 2013). In contrast, other colubrids rarely elevate their head above the ground (Bogert and Roth, 1966; Capula and Luiselli, 1997). We propose that the type of combat posture adopted by males (always raising the anterior portion of their bodies) might be a characteristic common to the South American colubrids. Further detailed observations of combat in these snakes are necessary to confirm this hypothesis.

Tropical and subtropical snakes exhibit relatively high variability in the length of their reproductive cycles, a pattern that is generally viewed as a consequence of seasonal variation in climate, prey availability, or both (Vitt, 1987; Mathies, 2011). Given that prey species of *Spilotes pullatus* are relatively abundant throughout the year (Bergallo, 1994), climate variation is the more-likely explanation for the reproductive seasonality of female *S. pullatus* in this region. Our data indicate a relatively restricted reproductive cycle in *S. pullatus*. A similar cycle was reported in another South American colubrid, *Chironius bicarinatus* (Marques et al., 2009a). Given our limited sample, however, we cannot exclude the possibility that the reproductive cycle of *S. pullatus* is more extended, as in other colubrids from southeastern Brazil (*Chironius flavolineatus* and *C. quadricarinatus*, Pinto et al., 2010; *Mastigodryas bifossatus*, Marques and Muriel, 2007; and *Simophis rhinostoma*, Jordão and Bizerra, 1996). In general, colubrid and dipsadid snakes from southeastern Brazil that have an extended cycle of egg laying throughout the year concentrate their oviposition at the onset of the rainy season (Pizzatto and Marques, 2002; Marques and Sazima, 2004; Pizzatto et al., 2008a,b). Temperature is likely a correlated factor for this pattern in subtropical snakes because warmer temperatures facilitate normal embryonic development (Vinegar, 1977).

The seasonal nature of mating behavior is unknown for most South American colubrids except for *C. bicarinatus*, in which mating occurs at the onset of the dry season (April; Marques et al., 2009a). Thus, the mating periods of *S. pullatus* and *C. bicarinatus* do not coincide because copulation in *S. pullatus* has been recorded from the end of the dry season to the onset of the rainy season (August–October). Further observations of mating behaviors in other South American colubrids are necessary to quantify any patterns in the timing of mating among these species.

Clutch size in *S. pullatus* is low relative to female body size, but this pattern is consistent with another South American colubrid snake, *M. bifossatus*. The hatchlings of the latter species are smaller (SVL ≈ 300 mm) than those of *S. pullatus* (SVL ≈ 350 mm) (Marques and Muriel, 2007; Leite et al., 2009). The relatively small clutches of certain South American colubrids, such as *S. pullatus* and *M. bifossatus*, might be a consequence of the large size of their newly hatched offspring.

Arboreal snakes are vulnerable to habitat disturbance (Lillywhite and Henderson, 1993). The occurrence of *S. pullatus* in disturbed areas in Amazonia, as well as in urbanized areas in southeastern Brazil, illustrates the capacity of this snake to inhabit degraded forests (Martins and Oliveira, 1998; Marques et al., 2009b; Barbo et al., 2011). In contrast to the generalist nature of *S. pullatus*, snakes in the genus *Chironius* specialize on anurans (primarily eating treefrogs; Dixon et al., 1993; Marques and Sazima, 2004), a resource typically associated with preserved forests (Haddad and Prado, 2005). Thus, a decline in *Chironius* spp. in disturbed forest might be expected whereas the more-generalist *Spilotes* is able to utilize a greater variety of habitats, including disturbed areas. Having a relatively shorter tail and heavier body, *S. pullatus* is also morphologically less arboreal than members of *Chironius* (Marques, 1998).

Our study provides an ecological overview about *S. pullatus*. Although certain aspects of its biology (e.g., a strongly seasonal reproductive cycle) might well be unique to the species, several other ecological traits appear to be common to many South American colubrid snakes (e.g., activity period and certain feeding and reproductive strategies). Nevertheless, we emphasize that a robust phylogenetic hypothesis identifying the South American colubrids as a monophyletic group is not yet available. Mapping the multiple ecological attributes examined here onto a current phylogeny of South American colubrids might lend support to the monophyly of this group.

Acknowledgments.—We thank Adriano T. Fellone, Cristiene R. Martins, Kelly Kishi, and Valdir J. Germano for assistance in the laboratory; L. Castanho. A.M. Delgado, O. Parthey, and J.S. Silva for providing field data; the two anonymous reviewers as well as the Editor for their suggestions; and the curators of the following collections for loans or permission to study specimens: FUNED, IBSP, MCP, MHNCI, MNRJ, MZUFV, PUC-MG, UNIFESO, and ZUEC. This study is part of the project "História natural de serpentes sul-americanas: uma abordagem evolutiva" supported by FAPESP (2012/07334). This project is being carried out under permit SISBIO 36450-1 issued by the ICMBio - Ministério do Meio Ambiente and animal ethics protocols 983/12 approved by the Animal Ethics Committee of Instituto Butantan. The CNPq provided providential fellowships to OAVM and SMA-S.

Literature Cited

Almeida-Santos, S.M., and O.A.V. Marques. 2002. Male–male combat in the colubrid snake *Chironius bicarinatus* from the Atlantic Forest, southeastern Brazil. Amphibia-Reptilia 23:528–533.

Amaral, A. 1978. Serpentes do Brasil. Editora Universidade de São Paulo e Melhoramentos, Brasil.

Barbo, F.E., R.J. Sawaya, and O.A.V. Marques. 2011. Diversity, natural history, and distribution of snakes in the municipality of São Paulo. South American Journal of Herpetology 6:135–160.

Beebe, W. 1946. Field notes on the snakes of Kartabo, British Guiana and Caripito, Venezuela. Zoologica 31:11–52.

Bergallo, H.G. 1994. Ecology of a small mammal community in an Atlantic forest area in southeastern Brazil. Studies on Neotropical Fauna and Environment 29:197–217.

Bizerra, A.F., R.S. Jordão, and I. Sazima. 1994. Natural history notes: *Simophis rhinostoma* (diet). Herpetological Review 25:72–73.

Bogert, C.M., and V.D. Roth. 1966. Ritualistic combat of male gopher snakes, *Pituophis melanoleucus affinis* (Reptilia, Colubridae). American Museum Novitates 2245:1–27.

Brischoux, F., L. Pizzatto, and R. Shine. 2010. Insights into the adaptive significance of vertical pupil shape in snakes. Journal of Evolutionary Biology 23:1878–1885.

Capulla, M., and L. Luiselli. 1997. A tentative review of sexual behavior and alternative reproductive strategies of the Italian colubrid snakes. Herpetozoa 10:107–119.

Cunha, O.R., and F.P. Nascimento. 1978. Ofídios da Amazônia. X. As cobras da região leste do Pará. Publicações Avulsas do Museu Paraense Emílio Goeldi 32:1–218.

Dixon, J.R., J.A. Wiest, and J.M. Cei. 1993. Revision of the tropical snake *Chironius* Fitzinger (Serpentes, Colubridae). Museo Regionale di Scienze Naturali Monografie XIII:1–279.

Greene, H.W. 1997. Snakes: The Evolution of Mystery in Nature. University of California Press, USA.

Haddad, C.F.B., and C. Prado. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic Forest of Brazil. BioScience 55:207–217.

Hartmann, P.A., M.T. Hartmann, and M. Martins. 2009. Ecology of a snake assemblage in the Atlantic Forest of southeastern Brazil. Papéis Avulsos de Zoologia 49:343–360.

Hauzman, E., A.C.O.R. Costa, and R.R. Scartozzoni. 2005. Natural history notes: *Spilotes pullatus* (reproduction). Herpetological Review 36:328.

Hollis, J.L. 2006. Phylogenetics of the genus *Chironius* Fitzinger, 1826 (Serpentes, Colubridae) based on morphology. Herpetologica 62:435–453.

Jordão, R.S., and A.F. Bizerra. 1996. Reprodução, dimorfismo sexual e atividade de *Simophis rhinostoma* (Serpentes, Colubridae). Brazilian Journal of Biology 56:507–512.

Leite, P.L., S.F. Nunes, I.L. Kaefer, and S.Z. Cechin. 2009. Reproductive biology of the swamp racer *Mastigodryas bifossatus* (Serpentes: Colubridae) in subtropical Brazil. Zoologia 26:12–18.

Lillywhite, H.B., and H.W. Henderson. 1993. Behavioral and functional ecology of arboreal snakes. Pp. 1–45 in R.A. Seigel and J.T. Collins (Eds.), Snakes: Ecology and Behavior, McGraw-Hill, USA.

Loiselle, B.A., and W.G. Hoppes. 1983. Nest predation in insular and mainland lowland rainforest in Panama. Condor 85:93–95.

Marques, O.A.V. 1998. Composição Faunística, História Natural e Ecologia de Serpentes da Mata Atlântica, na Região da Estação Ecológica de Juréia-Itatins, São Paulo. Ph.D. dissertation, Universidade de São Paulo, Brazil.

Marques, O.A.V., and A.P. Muriel. 2007. Reproductive biology and food habits of the swamp racer *Mastigodryas bifossatus* (Colubridae) from southeastern South America. Herpetological Journal 17:104–109.

Marques, O.A.V., and I. Sazima. 2004. História natural dos répteis da estação ecológica Juréia-Itatins. Pp. 257–277 in O.A.V. Marques, and W. Duleba (Eds.), Estação Ecológica Juréia-Itatins: Ambiente Físico, Flora e Fauna. Holos Editora, Brazil.

Marques, O.A.V., S.M. Almeida-Santos, M.G. Rodrigues, and R. Camargo. 2009a. Mating and reproductive cycle in the Neotropical colubrid snake *Chironius bicarinatus*. South American Journal of Herpetology 4:76–80.

Marques, O.A.V., D.N. Pereira, F.E. Barbo, V.J. Germano, and R.J. Sawaya, 2009b. Os répteis do Município de

São Paulo: diversidade e ecologia da fauna pretérita e atual. Biota Neotropica 9:1–12.

Martins, M., and M.E. Oliveira. 1998. Natural history of snakes in forests of the Manaus Region, Central Amazonia, Brazil. Herpetological Natural History 6:78–150.

Mathies, T. 2011. Reproductive cycles of tropical snakes. Pp. 511–550 in R.D. Aldridge and D.M. Sever (Eds.), Reproductive Biology and Phylogeny of Snakes. Science Publishers, USA.

Muniz-Da-Silva, D.F., and S.M. Almeida-Santos. 2013. Male–male ritual combat in *Spilotes pullatus* (Serpentes: Colubrinae). Herpetological Bulletin 126:25–29.

Murphy, J.C. 1997. Amphibians and Reptiles of Trinidad and Tobago. Krieger Publishing Company, USA.

Nickerson, M.A., R.A. Sajdak, R.W. Henderson, and S. Ketcham. 1978. Notes on the movements of some Neotropical snakes (Reptilia, Serpentes). Journal of Herpetology 12:419–422.

Nimer, E. 1989. Climatologia do Brasil. 2° Edição. IBGE. Departamento de Recursos Naturais e Estudos Ambientais, Brazil.

Peters, J.A., and B. Orejas-Miranda. 1970. Catalogue of Neotropical Squamata. Part I. Snakes. United States National Museum Bulletin 297:1–347.

Pinto, R.R., R. Fernandes, and O.A.V. Marques. 2008. Morphology and diet of two sympatric colubrid snakes, *Chironius flavolineatus* and *Chironius quadricarinatus* (Serpentes: Colubridae). Amphibia-Reptilia 29:149–160.

Pinto, R.R., O.A.V. Marques, and R. Fernandes. 2010. Reproductive biology of two sympatric colubrid snakes, *Chironius flavolineatus* and *Chironius quadricarinatus*, from the Brazilian Cerrado domain. Amphibia-Reptilia 31:463–473.

Pizzatto, L., and O.A.V. Marques. 2002. Reproductive biology of the false coral snake *Oxyrhopus guibei* (Colubridae) from southeastern Brazil. Amphibia-Reptilia 23:495–504.

Pizzatto, L., M. Cantor, J.L. Oliveira, O.A.V. Marques, V. Capovilla, and M. Martins. 2008a. Reproductive ecology of dipsadine snakes, with emphasis on South American species. Herpetologica 62:168–179.

Pizzatto, L., R.S. Jordão, and O.A.V. Marques. 2008b. Overview of reproductive strategies in Xenodontini (Serpentes: Colubridae: Xenodontinae) with new data for *Xenodon neuwiedii* and *Waglerophis merremii*. Journal of Herpetology 42:153–162.

Robinson, W.D., and T.R. Robinson. 2001. Observations of predation events at bird nests in Central Panama. Journal of Field Ornithology 72:43–48.

Rossman, D.A., and K.L. Williams. 1966. Defensive behavior of the South American colubrid snakes *Pseustes sulphureus* (Wagner) *and Spilotes pullatus* (Linnaeus). Proceedings of the Louisiana Academy of Sciences 29:152–156.

Sazima, I., and C.F.B. Haddad. 1992. Répteis da Serra do Japi: notas sobre história natural. Pp. 212–236 in L.P.C. Morellato (Ed.), História Natural da Serra do Japi: Ecologia e Preservação de uma Área Florestal no sudeste do Brasil. Editora Unicamp, Brasil.

Seib, R.L. 1984. Prey use in three syntopic Neotropical racers. Journal of Herpetology 4:412–420.

Seigel, R.A., and N.B. Ford. 1987. Reproductive ecology. Pp. 210–252 in R.A. Seigel, J.T. Collins, and S.S. Novak (Eds.), Snakes: Ecology and Evolutionary Biology. Macmillan Publishers, USA.

Shine, R. 1980. Comparative ecology of three Australian snake species of the genus *Cacophis* (Serpentes: Elapidae). Copeia 1980:1831–1838.

Shine, R. 1982. Ecology of the Australian elapid snake *Echiopis curta*. Journal of Herpetology 16:388–393.

Shine, R. 1994. Sexual size dimorphism in snakes revisited. Copeia 1994:326–346.

StatSoft. 2003. Statistica for Windows, Release 6.1. StatSoft, Inc., USA.

Vinegar, A. 1977. Evolutionary implications of temperature induced anomalies of development on snake embryos. Herpetologica 30:72–74.

Vitt, L.J. 1987. Communities. Pp. 335–365 in R.A. Seigel, J.T. Collins, and S.S. Novak (Eds.), Snakes: Ecology and Evolutionary Biology. Macmillan Publishers, USA.

Zar, J.H. 1996. Biostatistical Analysis. Prentice-Hall Inc., USA.

Accepted: 6 August 2014
Associate Editor: Bryan Stuart