

ECOLOGY OF THE COLUBRID SNAKE *PSEUDABLABES AGASSIZII* IN SOUTH-EASTERN SOUTH AMERICA

OTAVIO A. V. MARQUES¹, RICARDO J. SAWAYA¹, FERNANDA STENDER-OLIVEIRA¹ AND
FREDERICO G. R. FRANCA²

¹Laboratório de Herpetologia, Instituto Butantan, 05535-900 São Paulo, SP, Brazil

²Departamento de Ecologia, Instituto de Biologia, Universidade de Brasília, 70910-900, Brasília, DF, Brazil

The colubrid *Pseudablabes agassizii* is a small philodryadine snake distributed in open areas in south-eastern South America. We provide information on morphology, habitat use, diel activity, diet, feeding behaviour, reproduction, and seasonal activity of this species, based on dissection of 146 specimens combined with field and captive observations. *Pseudablabes agassizii* is smaller than any other species in the Philodryadini. Females attain larger body size than males. Sexual dimorphism was also recorded for stoutness and tail length, but not for head length. Apparently, *P. agassizii* forages during the day, mainly for resting spiders in subterranean and other day-time retreats. Lycosid and other araneomorph spiders were the staple food item, but mygalomorph spiders, scorpions, and orthopteran insects were also eaten. Large spiders were subdued by venom injection, whereas smaller ones were usually swallowed alive. Ingestion of lizards is infrequent and probably represents a vestigial trait. Absence of sexual dimorphism in relative head length may be related to ingestion of small prey. The reproductive cycle of females seems to be highly seasonal with vitellogenesis occurring from the onset to the middle of the rainy season, when females are more active. Recruitment of newborns takes place at the end of the rainy season. Males show increase in testes volume in the second half of the rainy season, and mating probably occurs at the end of rainy season, when adult males are more active. At least in south-eastern Brazil, *P. agassizii* is a habitat specialist, sensitive to habitat alteration, and thus is an indicator species of environmental quality. Due to the rapid destruction of its main habitat, the Cerrado, the conservation status of this snake should be regarded as threatened.

Key words: activity, feeding, morphology, Philodryadini, reproduction

INTRODUCTION

The New World colubrids exhibit great variation in habitat, diet, and reproduction, but ecological attributes are often conserved in a particular lineage (Greene, 1997). The subfamily Xenodontinae represents the most diverse radiation of colubrids in South America (Cadle & Greene, 1993). Four genera (*Ditaxodon*, *Philodryas*, *Pseudablabes* and *Tropidodryas*) of rear-fanged snakes are grouped in the tribe Philodryadini (Ferrarezzi, 1994; Vidal *et al.*, 2000). These snakes grow to more than 600 mm snout-vent length (SVL), and all species supposedly feed on a wide range of vertebrates (cf. Vitt, 1980; Thomas, 1976; Sazima & Puerto, 1993; Marques *et al.*, 2004). However, *Pseudablabes agassizii* differs from other Philodryadini due to its small body size and specialised diet (Viñas *et al.*, 1989). This snake is relatively rare in herpetological collections, although it is widely distributed from central and south-eastern Brazil to north-eastern Argentina and Uruguay (Peters & Orejas-Miranda, 1970; Viñas *et al.*, 1989; Kiefer, 1998; Giraudo, 1999; Nogueira, 2001a). Detailed ecological data are available for some species of Philodryadini (see Vitt, 1980; Sazima & Puerto, 1993; Fowler & Salomão,

1994a,b; Hartmann, 2001; Marques & Sazima, 2004), but little is known about the natural history of *P. agassizii*.

Here we provide information on morphology, habitat use, diel activity, diet, feeding behaviour, reproduction, and seasonal activity of *P. agassizii* from central, south-eastern, and southern Brazil. Except for the southern populations, specimens of *P. agassizii* in Brazilian collections were collected exclusively within the Cerrado domain. Studies on the Cerrado fauna are important and urgent given the fast rate of destruction of these natural landscapes during recent decades (Ratter *et al.*, 1997; Oliveira & Marquis, 2002).

MATERIALS AND METHODS

Our study is based on the dissection of preserved specimens from herpetological collections, and observations in the field and in captivity. We obtained data on diet, reproduction and morphology by analyses of specimens from several localities in the Brazilian Cerrado and the grasslands of southern Brazil (see Appendix 1). The Cerrado domain from central to south-eastern Brazil has a relatively homogeneous climate characterized by two distinctive seasons: a dry one from April to September, with less rainfall and lower temperatures; and a rainy one from October to March, with higher rainfall incidence and temperature (see Nimer, 1989; Sawaya, 2004). The grasslands in southern Brazil have a highly

Correspondence: O. A. V. Marques, Laboratório de Herpetologia, Instituto Butantan Av. Vital Brazil, 1500. 05535-900 São Paulo, SP, Brazil
E-mail: otaviomarques@butantan.gov.br

seasonal climate with higher temperatures from September to March, and lower temperatures from April to August (IAPAR, 1978). Rainfall is abundant throughout the year, and there is no dry season (Nimer, 1989).

We examined 122 specimens from the collections of the Instituto Butantan (IB) and Universidade de Brasília (CHUNB), as well as 24 individuals collected at the Estação Ecológica de Itirapina (São Paulo state, Brazil), totalling 146 specimens. The following data were recorded from each specimen: (1) snout-vent length (SVL; mm); (2) tail length (mm); (3) head length (0.01 mm); (4) sex; (5) reproductive maturity (males were considered mature if they had enlarged testes or opaque deferent ducts; females were considered mature if they had either oviductal eggs or ovarian vitellogenic follicles >5 mm; see Shine, 1977a,b); (6) diameter of largest ovarian follicles or oviductal eggs (0.01 mm); (7) length, largest and smallest diameters of testes (0.01 mm; testicular volume was estimated as the volume of ellipsoid, see James & Shine, 1985); (8) right deferent duct diameter close to cloaca (0.01 mm; see Almeida-Santos *et al.*, in press); and (9) stomach and/or intestine contents.

Sexual dimorphism in SVL was tested by Student's *t*-test, and sexual dimorphism in relative mass (stoutness; using the cube-root of the mass, after draining the excess of preservative liquid through ventral incisions, see Martins *et al.*, 2001), relative tail length, and relative head length were examined with one-way analyses of covariance (ANCOVA; all variables natural log-transformed), with total length, SVL, and trunk length (SVL - head length) as covariates, respectively (Zar, 1996).

Data on habitat use and seasonal activity were obtained at the Estação Ecológica de Itirapina (EEI, ca. 2,400 ha; 22°00' to 22°15' S; 47°45' to 48°00' W; elevation c. 800 m; Cerrado domain) in south-eastern Brazil. Field work at EEI was part of a study on natural history and ecology of the local snake assemblage (see Sawaya, 2004), from September 1998 to March 2002. Pitfall traps with drift fences (Greenberg *et al.*, 1994; Cechin & Martins, 2000) were installed on three protected and conserved Cerrado habitats inside the reserve: shrubby grasslands or "campo sujo" (total area: 1009.7 ha), the border of a gallery forest (1040.7 ha), and shrubby grasslands with trees or "campo cerrado" (292.7 ha). Three sample units were installed in each habitat. Each sample unit consisted of a pair of 45 m arrays, 100 m from each other, and each array had four 100-litre plastic buckets placed every 15 m, connected by a 0.5 m high fence of plastic mesh. Each day of pitfall sampling corresponded to 72 bucket-days, along 810 m of fences. We sampled a total of 293 non-consecutive days (21,096 bucket-days). Additionally, we found snakes by incidental sightings (Martins & Oliveira, 1999), with a sampling effort of 446 days of fieldwork, and sampled altered areas outside the reserve with the aid of local collectors (see Cunha & Nascimento, 1978), with 167 collector-months of sampling effort. We used the pitfall trap and incidental sightings data to test for habitat se-

lection by *P. agassizii*. We compared the observed with expected number of snakes ($n=23$) caught in each habitat, with a chi-square test (Zar, 1996), considering the differential availability (total area) of each one inside the reserve. The expected numbers of snakes in the three habitats were 9.89 in the "campo sujo", 10.12 in the border of the gallery forest, and 2.99 in the "campo cerrado".

Additional data on seasonal activity were obtained from records of individuals received in herpetological collections. We compared the observed with expected number of snakes, registered during dry and wet seasons, with a chi-square test (Zar, 1996).

Observations on behaviour and diel activity were made on a captive female of *P. agassizii* caught at the EEI (325 mm SVL), for which we recorded twenty prey encounters. The snake was housed in a 50 × 25 × 30 cm terrarium with deep soil substrate. We offered lizards (*Hemidactylus mabouia*), scorpions (*Tityus serrulatus* and *Bothriurus araguaye*), spiders (*Lycosa* sp. and *Eunoploctenus* sp.) and insects (Orthoptera, Blataria) as prey. All feeding sequences were recorded with VHS and/or photographed. The captive specimen was monitored with a closed-circuit television system during 10 days for records of its diel activity.

As testes size and deferent duct diameter are also related to body size, we first use residuals of linear regressions between these variables and SVL (all natural log-transformed; see Pizzatto & Marques, 2002) to explore reproductive cycles of mature males throughout the year (see Fig. 2). These residuals are treated herein as relative testis volume and relative deferent duct diameter. We tested for differences in testis volume and duct deferent diameter, between February to March (peak of the male reproductive cycles, see below) and April to January, with one-way analyses of covariance (ANCOVA), with SVL as covariate to eliminate the body size effects on these variables (all variables natural log-transformed; Zar, 1996). Reproductive cycle of mature females was examined in terms of length of the largest ovarian follicle or oviductal egg throughout the year. Additional information on reproduction were obtained from two captive gravid females. We assessed fecundity as the number of oviductal eggs and large vitellogenic ovarian follicles (>10 mm). The relationship between maternal SVL and fecundity was analysed by linear regression (Zar, 1996). All statistical analyses were done using Statistica (StatSoft, 2003), and differences were considered significant when $P<0.05$.

RESULTS

MORPHOLOGY AND SEXUAL DIMORPHISM

Mature males averaged 261.6 mm SVL (SD=35.8, $n=35$, range=200.0-329.0), and mature females averaged 325.3 mm SVL (SD=47.2, $n=80$, range=226.0-453.0). This difference was highly significant ($t=7.14$, $P<<0.001$). The degree of sexual dimorphism (SSD) was 0.24 (*cf.* Shine, 1994). Adult females have

stouter body (ANCOVA, $F_{1,51}=5.32$, $P=0.03$), and shorter relative tail length than males (ANCOVA, $F_{1,107}=117.44$, $P<<0.001$). However, males and females have no significant differences in relative head length (ANCOVA, $F_{1,100}=1.22$, $P=0.27$).

HABITAT USE

From the 23 individuals for which we have habitat use data (21 caught in pitfall traps and two by incidental sightings), most snakes ($n=21$, approximately 90%) were collected in shrubby grasslands or “campo sujo”, one was found on the border of gallery forest and shrubby grasslands, and the other in shrubby grasslands with trees or “campo cerrado”. The habitat distribution of observed snakes was significantly different than expected by chance, considering the total area occupied by those three habitats ($\chi^2=22.02$, $P<0.001$, $df=2$). No snake was found in disturbed areas outside of the reserve, sampled only by local collectors and incidental sightings. In another study, between October 2003 and May 2004 (F. Spina, pers. comm.), no specimens of *P. agassizii* were found in a disturbed area (*Eucalyptus* groves) in the neighbourhood of the reserve. In that study, six sample units of pitfall traps (48 buckets along 540 m of fences) were installed, as in the present study, with 160 non consecutive days of sampling (7680 bucket-days).

DIEL ACTIVITY

Two individuals found by incidental sightings in the field were active during the day (the diel activity of snakes captured by pitfall traps could not be recorded). The captive specimen monitored was active only during

the day, moving in the terrarium mainly between 1000-1400 hr.

FOOD HABITS

Except for a lizard, all the other prey items found in the gut of *P. agassizii* were arthropods ($n=24$; Table 1). Arachnids were the most common prey, comprising 72% of the 25 items recorded. Diurnal and/or nocturnal lycosid spiders were the most common prey ($n=11$; 44%). Other prey consumed were active nocturnal spiders (Ctenidae, Titanoecidae, and Actinopodidae), one scorpion, one orthopteran, and four unidentified insects (Table 1).

FEEDING BEHAVIOUR

The captive *P. agassizii* refused lizards ($n=2$), scorpions ($n=2$), and insects ($n=2$) as prey, but accepted readily lycosid spiders ($n=14$). Spiders were usually captured by their legs, but small spiders were occasionally caught by other parts of the body. Small spiders (prey/snake mass ratio ≤ 0.014) were readily swallowed alive, being ingested cephalothorax first ($n=2$) or abdomen first ($n=6$). For large spiders (prey/snake mass ratio ≥ 0.023), the snake used alternating jaw movements to manoeuvre the prey within its mouth. These spiders were held and envenomed until they were immobile (Fig. 1A). Large spiders were swallowed cephalothorax first ($n=1$) or abdomen first ($n=5$; Fig. 1B). Snakes thus swallowed spiders more frequently abdomen first ($n=11$, $\chi^2=4.57$, $P<0.03$, $df=1$) than cephalothorax first ($n=3$). In eight predatory encounters the spider bit the

TABLE 1. List and number of prey found in the guts of *Pseudablabes agassizii* ($n=24$ snakes). Percentage from the total number of items ($n=25$) in brackets.

Prey type	N	(%)
INVERTEBRATES		
Araneae		
Mygalomorphae		
Actinopodidae: <i>Actinopus</i> sp.	1	(4)
Araneomorphae		
Ctenidae: <i>Ctenus taeniatus</i>	2	(8)
Titanoecidae: <i>Goeldia</i> sp.	1	(4)
Lycosidae: unidentified genus	11	(44)
Unidentified	3	(12)
Scorpiones		
Bothriuridae: <i>Bothriurus araguayae</i>	1	(4)
Insecta		
Orthoptera: unidentified genus	1	(4)
Unidentified	4	(16)
VERTEBRATES		
Lacertilia		
Gymnophthalmidae: <i>Micrablepharus</i> sp.	1	(4)

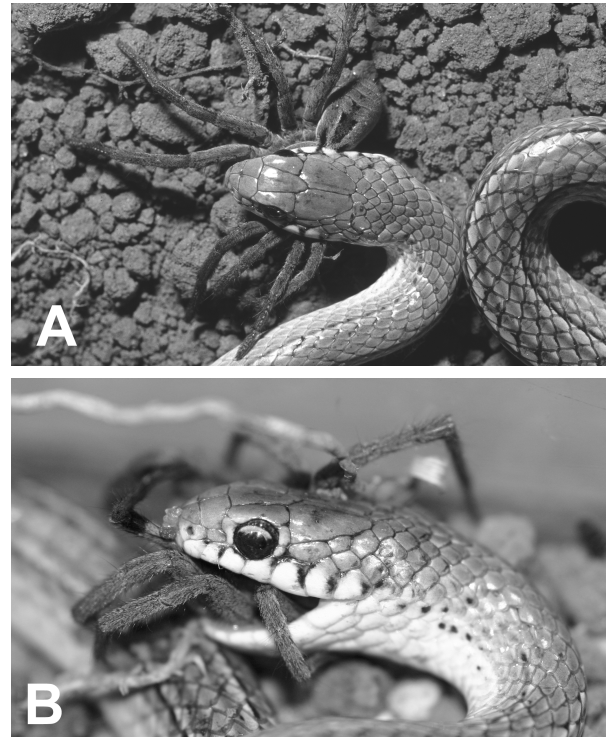


FIG. 1. *Pseudablabes agassizii* captive female: (A) holding and presumably envenoming, and (B) swallowing a spider (*Lycosa erythrognata*). Photos by O. A. V. Marques and R. Bertani, respectively.

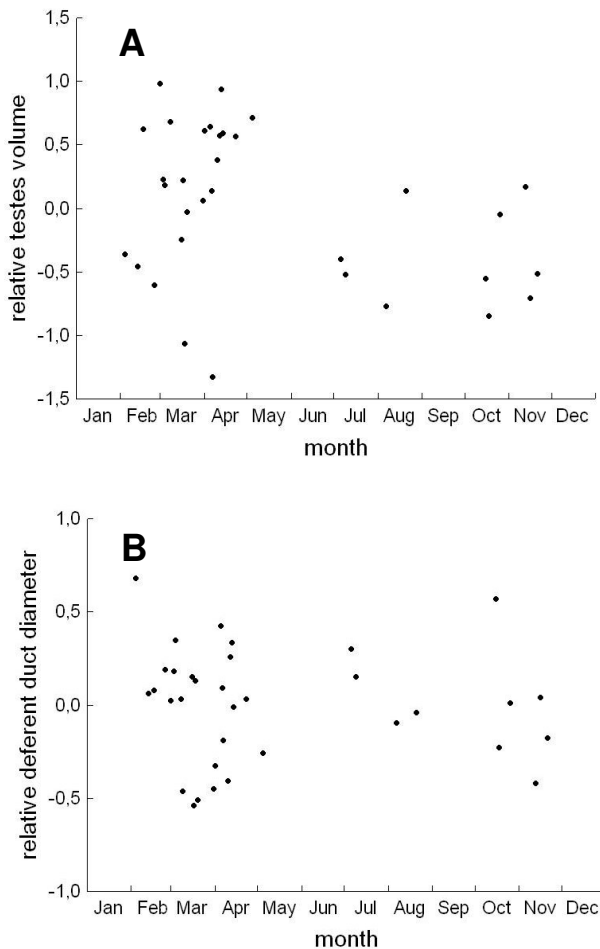


FIG. 2. Seasonal variation in relative testes volume (A), and relative deferent duct diameter (B) of mature males of *Pseudablabes agassizii* from western, south-eastern, and southern Brazil. Testes volume were significantly larger from February to April (see text).

snake's head, without any apparent damage. The time between catching the prey and the beginning of the ingestion varied from 3 to 10 min (average = 3 min 46 sec, $SD=2$ min 30 sec, $n=6$).

REPRODUCTION

Testes volume attained maximum values at the end of the rainy season and the beginning of the dry season, February to April (Fig. 2A), indicating a seasonal reproductive cycle in males. Relative testis volume was significantly larger at the peak of the reproductive cycle of the males (February to April) compared with other months (ANCOVA, $F_{1,33}=4.37$, $P=0.045$), but relative deferent duct diameter was not (ANCOVA, $F_{1,34}=0.01$, $P=0.92$; Fig. 2B). Females also showed a seasonal reproductive cycle (Fig. 3). Ovaries of adult females were inactive (diameter <5 mm) for much of the year, with vitellogenesis from the middle of the dry season to the middle of the rainy season (July - January), and ovulation from the end of the dry season throughout most of the rainy season (September - February; Fig. 3). One female (SVL = 460 mm) collected on 29 September 2001 laid eight eggs in captivity (7 October 2001), and another female (SVL = 333 mm) collected on 20

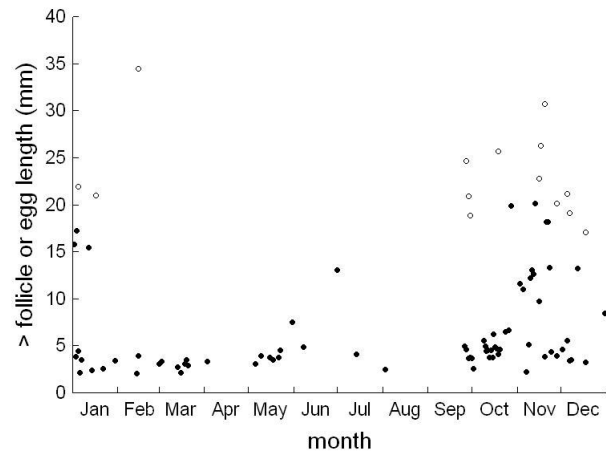


FIG. 3. Seasonal variation in diameter of the largest ovarian follicle or oviductal eggs in mature females of *Pseudablabes agassizii* from central, south-eastern, and southern Brazil. Solid circles = ovarian follicle; open circles = oviductal eggs.

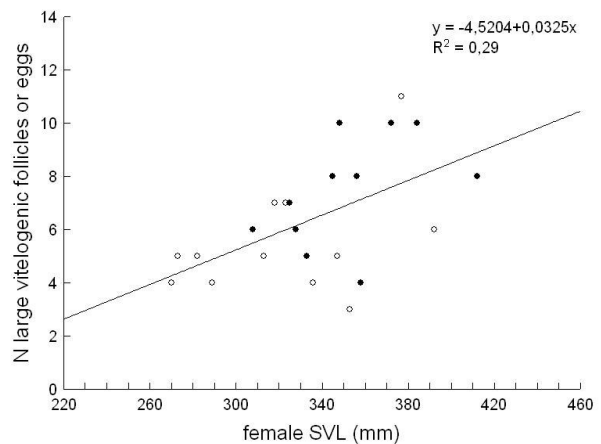


FIG. 4. Relationship between female snout-vent length and clutch size in *Pseudablabes agassizii* from central, south-eastern, and southern Brazil. ($R^2=0.29$, $P=0.003$, $n=39$). Solid circles = eggs; open circles = vitellogenic follicles >10 mm.

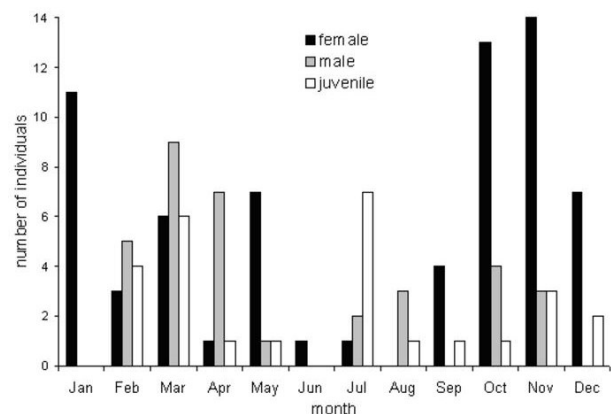


FIG. 5. Seasonal abundance of juveniles, mature males and mature females of *Pseudablabes agassizii*, from collection data of museum specimens. Shaded bars, mature males ($n=34$); solid bars, mature females ($n=68$); open bars, juveniles ($n=27$).

November 2001 laid five eggs (24 November 2001). All eggs of the first female deteriorated. The eggs of the second female averaged 27.10 mm in length (range=24.80-30.75 mm; SD=2.98), 10.02 mm in diameter (range=9.65-10.60 mm; SD=0.35), and weighed a total of 10.3 g. The relative clutch mass was 0.70 (ratio of total clutch weight and mother body weight after egg-laying). Three eggs hatched on 11 February 2002, and the neonates measured 104, 104, and 113 mm SVL. Clutch size ranged from 3 to 11, and was positively and significantly related with maternal SVL ($R^2=0.29$, $P=0.008$; Fig. 4).

SEASONAL ACTIVITY

Adult males and females were registered during all months of the year (Fig. 5), but were significantly more common in the rainy than in the dry season ($\chi^2=23.53$, $P<0.001$, $df=1$). Adult males were more active at the end of the rainy and beginning of the dry season (February - April), whereas adult females show a peak of abundance at the onset of the rainy season (October - January; Fig. 5).

DISCUSSION

BODY SIZE AND SEXUAL DIMORPHISM

P. agassizii is a small snake, adults averaging c. 300 mm SVL. This size is much smaller than that recorded for other species of Philodryadini, which may attain twice this size (see Thomas, 1976; Thomas & Fernandes, 1996; Hartmann, 2001). The small body size of *P. agassizii* is likely related to its food habits, as it feeds exclusively on relatively small prey (see below), whereas other Philodryadini usually prey on relative large vertebrates (cf. Sazima & Puerto, 1993; Hartmann, 2001).

The larger body size in female *P. agassizii* and the value of SSD indicates the absence of male-male combat (cf. Shine, 1994), which remains unrecorded for the neotropical Xenodontinae. Sexual dimorphism was verified in most morphometric parameters analysed, but not in head length. Sexual differences in body size, stoutness, and tail length are a common condition in snakes, and are usually related to reproduction (see King, 1989; Shine, 1994). Head size dimorphism in snakes may be related to intersexual dietary divergence (see Shine & Crews, 1988; Shetty & Shine, 2002). However, *P. agassizii* feeds on small prey and thus sexual differences would be unexpected.

HABITAT USE

P. agassizii is a habitat specialist, at least in south-eastern Brazil, since it was found almost exclusively in only one Cerrado habitat, the shrubby grassland or "campo sujo". The Cerrado domain is composed of distinct vegetational physiognomies (treated herein as habitats), and recent field studies indicate that some snakes select specific habitats (Nogueira, 2001b; Nogueira *et al.*, 2003; Sawaya, 2004). Other Philodryadini, such as *Philodryas olfersii* and *P.*

patagoniensis also show habitat selection (see Hartmann, 2001).

FEEDING AND DIET ACTIVITY

The specialisation of *P. agassizii* on arachnids (over 70% of prey) has been noted previously by Viñas (1985) and Cei (1993). Our data also indicate that insects are a minor dietary item. Lizards are only occasionally eaten and were refused by the captive snake. Thus, vertebrate prey may be regarded as a vestigial trait of *P. agassizii*, present in its ancestral stock. Although phylogenetic analyses are unavailable for Philodryadini, one distinct clade (*P. agassizii* + *Philodryas patagoniensis* + *Philodryas livida*) is supported by three synapomorphies (H. Ferrarezzi, pers. comm.). Most species within the Philodryadini (those in the genera *Philodryas* and *Tropidodryas*) feed on vertebrates (Sazima & Puerto, 1993; Hartmann, 2001). Food habits of *P. livida* are unknown, whereas *P. patagoniensis* prey upon vertebrates (Hartmann, 2001; Marques *et al.*, 2004). However, at least some populations of *P. patagoniensis* from Uruguay usually prey on spiders (Vidal, 2002). Additionally, one specimen of *P. patagoniensis* from southern Brazil consumed one grasshopper and a freshwater shrimp (M. Di-Bernardo, pers. comm.). Thus, the main prey of *Pseudablabes* (arachnids and other arthropods) occurs in the diet of at least one of its close relatives, and was probably occasionally present in the diet of their ancestor. The specialization of *P. agassizii* on arachnids is thus an autapomorphic trait since such habits are absent in other Philodryadini and xenodontine snakes in general. A comprehensive study on the phylogeny and habits of the Philodryadini would provide useful tools for evaluating our suggestions. Spiders may be regarded as a dangerous prey and few snakes eat them: *P. agassizii* and some sonorine snakes are the only New World snakes that prey primarily upon arachnids (see Greene, 1997). The captive specimen of *P. agassizii* swallowed spiders more frequently abdomen first, perhaps minimizing a spider's defensive response.

Data obtained herein on the captive snake, and observations in the field (Viñas, 1985; present study), indicate that *P. agassizii* is a diurnal snake, which seems characteristic for other Philodryadini as well (Vitt, 1980; Marques *et al.*, 2004). Most prey of *P. agassizii* are active at night and some others (*Bothriurus* scorpions, *Actinopus* and other spiders) are secretive and fossorial during the day (R. Bertani, pers. comm.). Hence, these nocturnal prey are probably taken in their day-time retreats. *Pseudablabes agassizii* probably forages mainly underground, although some diurnal lycosid spiders may be caught on the surface. As this snake catches and holds large prey until its struggles cease, it seems that *P. agassizii* has venom that is toxic to spiders. During the capture and/or manipulation of spiders, the prey can bite the snake, and thus predation on large spiders is rendered possible by the injection of

venom into the prey, and possibly by its own immunity to the prey's venom.

REPRODUCTION AND SEASONAL ABUNDANCE

Five clutches (from seven to 10 eggs) deposited inside ant nests were recorded by Vaz-Ferreira *et al.* (1970) and Vinãs (1985). The data presented here increase this range and indicate that *P. agassizii* produces small clutches when compared to the related *Philodryas patagoniensis* from south-eastern Brazil, which can produce up to 29 eggs (Fowler *et al.*, 1998; FSO pers. obs.). This low fecundity seems to be a function of the small adult size of *P. agassizii*, as the larger species *Philodryas patagoniensis* has larger clutches (FSO, pers. obs.). Moreover, hatchlings of *P. agassizii* are much smaller and lighter than those of *Philodryas patagoniensis* (Fowler *et al.*, 1998). Smaller species producing smaller offspring is a trend found in other neotropical colubrid snakes (e.g. Marques, 1998; Marques & Puerto, 1998; Hartmann *et al.*, 2002; Sawaya 2004). On the other hand, clutch sizes of *P. agassizii* are similar to those of two species of *Philodryas* in north-eastern Brazil studied by Vitt (1980), although the range of SVL of females analysed in that study was larger. Eggs of *P. agassizii* are however much smaller than those of the north-eastern *Philodryas*.

As would be expected for seasonal climates (Cerrado and grasslands in southern Brazil; see Nimer, 1989), seasonality is evident in the activity pattern and reproductive cycle of *P. agassizii*. Moreover, seasonal patterns in its activity and reproduction are similar to those described for other Philodryadini, such as *Philodryas* spp. and *Tropidodryas* spp. (Vitt, 1980; Fowler & Salomão, 1994a; Fowler *et al.*, 1998; Marques *et al.*, 2004; Marques & Sazima, 2004). Variation in rainfall and temperature (especially minimum temperature; Sawaya, 2004) may influence directly the activity of these snakes, but events in reproductive cycles may also influence their activity pattern (see below; Marques *et al.*, 2001).

The female reproductive cycle of *P. agassizii* indicates that egg-laying occurs during the warmest months, allowing clutches to maintain higher temperatures for embryonic development. The peak of female activity in the middle of the rainy season corresponds to the time when they contain vitellogenic follicles or oviductal eggs, when ovulation should also occur. Females probably increase their activity in warmer periods when they may be searching for appropriate thermoregulation or oviposition sites (Marques *et al.*, 2001). The preponderance of adult males from February to April indicates that this is likely to be the mating season. In support of this hypothesis, testes of males attain a larger volume at that time (*cf.* Shine, 1977a). Males might store sperm in deferent ducts and mate later (S. M. Almeida-Santos, pers. comm.), although the absence of a peak in the deferent duct diameter cycle of *P. agassizii* indicates that the produced sperm is used immediately during mating in

February–April. Field records of mating and aggregation in another species of Philodryadini, *Philodryas olfersii*, correspond to the same period (see Fowler *et al.*, 1998, Cechin & Hartmann, 2001). If mating occurs before the dry season and males do not store sperm, then females need to store sperm until the next rainy season when fertilisation would occur.

OVERVIEW

Pseudablades agassizii is broadly distinct from other Philodryadini in its morphology and ecology. Apparently, its small body size, short tail and reduced dorsal scales (*cf.* Peters & Orejas-Miranda, 1970) reflect adaptations for locomotion in subterranean hollows and crevices, where this species forages. Additionally, ant nests may be suitable for incubation of its eggs. Thus, underground microhabitat in shrubby grassland (“campo sujo” in the Cerrado) seems to be essential for the foraging and egg-laying activity of this snake. The absence of *P. agassizii* in disturbed areas indicates that it is highly susceptible to destruction of natural shrubby grasslands, and thus it is sensitive to habitat alteration and could be an indicator species of environmental quality.

Shrubby grasslands are the dominant landscape at EEI, one of the few remnants of protected Cerrado in south-eastern Brazil (see Sawaya, 2004), and thus warrant special attention in conservation planning. The Cerrado was historically the second largest ecosystem in Brazil, about 2 million km² throughout the country, and has been greatly disturbed in recent decades mainly due to extensive agriculture and cattle ranching (Ratter *et al.*, 1997). But only 20% of this biome remains undisturbed, and only 1.2% is in preserved areas (Mittermeier *et al.*, 1999). Although the Cerrado was recently ranked among the 25 most important terrestrial diversity hotspots (Myers *et al.*, 2000), and is possibly the most threatened tropical savannah in the world (Silva & Bates, 2002), even basic information on its herpetofaunal composition and natural history are mostly unknown (Colli *et al.*, 2002). Our study suggests that *Pseudablades agassizii* is an important component of the Cerrado snake fauna by virtue its ecological specialisation, and it should be regarded as a threatened species due to rapid destruction of its main habitat.

ACKNOWLEDGEMENTS

We thank H. W. Greene, L. Luiselli, J. P. Miranda, I. Sazima, and one anonymous referee for very helpful comments that improved the manuscript; R. Bertani for identification of all arthropod prey, sharing his knowledge with us, and a photo (Figure 1B); S. M. Almeida-Santos and H. Ferrarezzi for useful comments throughout the study; F. L. Franco for providing data and pertinent literature; G. Colli for permission to access the UNB collection; D. Zanchetta and the staff of Instituto Florestal for allowing and facilitating our fieldwork at Estação Ecológica de Itirapina; C. A. Brasileiro, M. C. Kiefer, M. Martins, F. Spina, V. R. Ariedi-Jr., M. E. Oliveira, C. Monteiro, A. M. Tozetti, V. Bonato, G.

Machado, E. G. Martins, L. A. Anjos N. L. Hülle, and J. E. Natali for help during the fieldwork at EEI, and M. Martins for coordinating the Itirapina project; and F. Barbo, M. Rodrigues, A. Costa and V. Germano for assistance in laboratory. We also thank IBAMA (permit no. 02027.011485/99-25) for allowing us to collect specimens for this study, and the CNPq and FAPESP for financial support. This is publication number 20 of the project “Ecology of the Cerrados of Itirapina”.

REFERENCES

- Almeida-Santos, S. M., Pizzatto, L. & Marques, O. A. V. Reproductive synchrony in the coral snake *Micrurus corallinus* (Elapidae) from southeast Brazil. *Herpetological Natural History* (in press.)
- Cadle, J. E. & Greene, H. W. (1993). Phylogenetic patterns, biogeography, and the ecological structure of Neotropical snake assemblages. In *Species diversity in ecological communities: historical and geographical perspectives*, 281-293. Ricklefs, R. E. and Schluter, D. (Eds). Chicago: University of Chicago Press.
- Cechin, S. Z. & Hartmann P. A. (2001). *Philodryas olfersii*. Courtship. *Herpetological Review* **32**, 187.
- Cechin, S. Z. & Martins, M. (2000). Eficiência de armadilhas de queda (*pitfall traps*) em amostragens de anfíbios e répteis no Brasil. *Revista Brasileira de Zoologia* **17**, 729–740.
- Cei, J. M. (1993). Reptiles del noroeste, nordeste y este de la Argentina. *Monografie XIV. Museo Regionale di Scienze Naturali, Torino*, 1–949.
- Colli, G. R., Bastos, R. P. & Araújo, A. F. B. (2002). The character and dynamics of the cerrado herpetofauna. In *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna*, 223–241. Oliveira, P. S. and Marquis, R. J. (Eds). New York: Columbia University Press.
- Cunha, O. R. & Nascimento, F. P. (1978). Ofídios da Amazônia. X. As cobras da região Leste do Pará. *Publicações Avulsas do Museu Paraense Emílio Goeldi* **31**, 1–218.
- Ferrarezzi, H. (1994). Uma sinopse dos gêneros e classificação das serpentes (Squamata): II. Família Colubridae. In *Herpetologia do Brasil* 1, 81–91. Nascimento, L. B.; Bernardes, A. T. and Cotta, G. A. (Eds). Belo Horizonte: PUC-MG, Fundação Biodiversitas, Fundação Ezequiel Dias.
- Fowler, I. R. & Salomão M. G. (1994a). Activity patterns in the colubrid snake genus *Philodryas* and their relationship to reproduction and snakebite. *Bulletin of the Chicago Herpetological Society* **29**, 229–232.
- Fowler, I. R. & Salomão M. G. (1994b). A study of sexual dimorphism in six species from the colubrid genus *Philodryas*. *The Snake* **26**, 117–122.
- Fowler, I. R., Salomão, M. G. & Jordão, R. S. (1998). A description of the female reproductive cycle in four species from the neotropical colubrid snake *Philodryas* (Colubridae, Xenodontinae). *The Snake* **28**, 71–78.
- Giraud, A. R. (1999). New records of snakes from Argentina. *Herpetological Review* **30**, 179–181.
- Greene, H. W. (1997). *Snakes: the evolution of mystery in nature*. California: University of California Press.
- Greenberg, C. H., Neary, D. G. & Harris L. D. (1994). A comparison of herpetofaunal sampling effectiveness of pitfall, single-ended, and double-ended funnel traps used with drift fences. *Journal of Herpetology* **28**, 319–324.
- Hartmann, M. T., Del Grande, M. L., Gondim, M. J. C., Mendes, M. C. & Marques, O. A. V. (2002). Reproduction and activity of the snail-eating snake, *Dipsas albifrons* (Colubridae), in the southern Atlantic Forest in Brazil. *Studies on Neotropical Fauna and Environment* **37**, 111–114.
- Hartmann, P. (2001). *Hábito alimentar e utilização do ambiente em duas espécies simpátricas de Philodryas (Serpentes, Colubridae), no sul do Brasil*. MSc Dissertation. Universidade Estadual Paulista “Julio de Mesquita Filho”, Rio Claro, São Paulo, Brazil.
- IAPAR- Instituto Agrônomo do Paraná. (1978). *Cartas climáticas básicas do Estado do Paraná*. Londrina, PR: Instituto Agrônomo do Paraná.
- James, C. & Shine, R. (1985). The seasonal timing of reproduction: a tropical-temperate comparison in Australian lizards. *Oecologia* **67**, 464–474.
- Kiefer, M. C. (1998). Geographic distribution. *Pseudablabes agassizii*. *Herpetological Review* **29**, 54.
- King, R. B. (1989). Sexual dimorphism in snake tail length: sexual selection, natural selection, or morphological constraint? *Biological Journal of the Linnean Society* **38**, 133–154.
- Marques, O. A. V. 1998. Composição faunística, história natural e ecologia de serpentes da Mata Atlântica, na região da Estação Ecológica Juréia-Itatins, São Paulo. PhD Thesis. Universidade de São Paulo, São Paulo, Brazil.
- Marques, O. A. V., Eterovic, A. & Endo, W. (2001). Seasonal activity of snakes in the Atlantic forest in southeastern Brazil. *Amphibia-Reptilia* **22**, 103–111.
- Marques, O. A. V., Eterovic, A. & Sazima, I. (2004). Snakes of the Brazilian Atlantic Forest: An Illustrated Field Guide for the Serra do Mar range. Ribeirão Preto, SP: Editora Holos.
- Marques, O. A. V. & Puorto, G. (1998). Feeding, reproduction and growth in the crowned snake *Tantilla melanocephala* (Colubridae), from southeastern Brazil. *Amphibia-Reptilia* **19**, 311–318.
- Marques, O. A. V. & Sazima I. (2004). História natural dos répteis da Estação Ecológica Juréia-Itatins. In *Estação Ecológica Juréia-Itatins. Ambiente Físico, Flora e Fauna*, 257–277. Marques O. A. V. and Duleba W. (Eds). Ribeirão Preto, SP: Holos.
- Martins, M. & Oliveira, M. E. (1999). Natural history of snakes in forests of the Manaus region, Central Amazonia, Brazil. *Herpetological Natural History* **6**, 78–150.
- Martins, M., Araújo, M. S.; Sawaya R. J. & Nunes R. (2001). Diversity and evolution of macrohabitat use, body size and morphology in a monophyletic group of

- Neotropical pitvipers (*Bothrops*). *Journal of Zoology* **254**, 529–538.
- Mittermeier, R. A., Myers, N., Gil, P. R. & Mittermeier, C. G. (1999). *Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions*. Mexico: CEMEX, Conservation International and Agrupacion Sierra Madre.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858.
- Nimer, E. (1989). *Climatologia do Brasil* (2nd ed.). Rio de Janeiro, RJ: Fundação Instituto Brasileiro de Geografia e Estatística-IBGE.
- Nogueira, C. C. (2001a). New records of squamate reptiles in central Brazilian Cerrado II: Brazilian Region. *Herpetological Review* **32**, 285–287.
- Nogueira, C. C. (2001b). *Ecologia histórica de Bothrops spp. (Serpentes: Viperidae: Crotalinae) no Cerrado*. MsC Dissertation, Universidade de São Paulo, São Paulo, Brazil.
- Nogueira, C. C., Sawaya, R. J. & Martins, M. (2003). Ecology of the pitviper, *Bothrops moojeni*, in the Brazilian Cerrado. *Journal of Herpetology* **37**, 653–659.
- Oliveira, P. S. & Marquis, R. J. (2002). *The cerrados of Brazil: ecology and natural history of a Neotropical savanna*. New York: Columbia University Press.
- Peters, J. A. & Orejas-Miranda, B. (1970). Catalogue of the Neotropical Squamata. Part I, Snakes. *United States National Museum Bulletin* **297**, 252.
- Pizzatto, L. & Marques, O. A. V. (2002). Reproductive biology of the false coral snake *Oxyrhopus guibei* (Colubridae) from southeastern Brazil. *Amphibia-Reptilia* **23**, 495–504.
- Ratter, J. A., Ribeiro, J. F. & Bridgewater, S. (1997). The Brazilian Cerrado vegetation and threats to its biodiversity. *Annals of Botany* **80**, 223–230.
- Sawaya, R. J. (2004). *História natural e ecologia das serpentes de Cerrado da região de Itirapina, SP*. PhD Thesis. Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.
- Sazima, I. & Puerto, G. (1993). Feeding technique of juvenile (*Tropidodryas striaticeps*): Probable caudal luring in a colubrid snake. *Copeia* **1993**, 222–226.
- Shetty, S. & Shine, R. (2002). Sexual divergence in diets and morphology in Fijian sea snakes, *Laticauda colubrina* (Laticaudidae). *Austral Ecology* **27**, 77–84.
- Shine, R. (1977a). Reproduction in Australian elapid snakes I. Male reproductive cycles. *Australian Journal of Zoology* **25**, 647–653.
- Shine, R. (1977b). Reproduction in Australian elapid snakes II. Female reproductive cycles. *Australian Journal of Zoology* **25**, 655–666.
- Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia* **1994**, 326–346.
- Shine, R. & Crews, D. (1988). Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. *Evolution* **42**, 1105–1110.
- Silva, J. M. C. & Bates, J. M. (2002). Biogeographic patterns and conservation in the South American Cerrado: a tropical savanna hotspot. *Bioscience* **52**, 225–233.
- Statsoft (2003). *Statistica for Windows*, Release 6.1. Tulsa: Statsoft, Inc.
- Thomas, R. A. (1976). *A revision of the South American colubrid snake genus Philodryas Wagler, 1830*. PhD Thesis, Texas A&M University.
- Thomas, R. A. & Fernandes R. (1996). The systematic status of *Platynion lividum* Amaral, 1923 (Serpentes: Colubridae: Xenodontinae). *Herpetologica* **52**, 271–275.
- Vaz Ferreira, R., Covello de Zolessi, L. & Achaval, F. (1970). Ovoposición y desarrollo de ofidios y lacertilios en hormigueros de *Acromyrmex*. *Physis* **29**, 431–459.
- Vidal, S. C. (2002). Alimentación de los ofidios de Uruguay. Asociación Herpetológica Española – *Monografía de Herpetología* **6**, 1–129.
- Vidal, N., Kindl, S. G., Wong, A. & Hedges, S. B. (2000). Phylogenetic relationships of xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. *Molecular Phylogenetics and Evolution* **14**, 389–402.
- Viñas, M. (1985). Notas sobre la biología de (*Pseudablabes agassizii*). *Boletín de la Asociación Herpetológica Argentina* **2**, 16.
- Viñas, M., Daneri, G. & Gnida, G. (1989). Presencia de (*Pseudablabes agassizii*) em Sierra de La Ventana (Provincia de Buenos Aires) y confirmación para La Provincia de La Pampa. *Boletín de la Asociación Herpetológica Argentina* **5** (1-2), 13–14.
- Vitt, L. J. (1980). Ecological observations on sympatric *Philodryas* (Colubridae) in northeastern Brazil. *Papéis Avulsos de Zoologia* **34**, 87–98.
- Zar, J. H. (1996). *Biostatistical analysis*. New Jersey: Prentice-Hall Inc.

APPENDIX 1

SPECIMENS EXAMINED

Pseudablabes agassizii

Central Brazil: IB 4610, 5300, 10502, Campinorte, Goiás (GO); IB 52160, Corumbá de Goiás, GO; CHUNB 3671, 3681, Luziânia, GO; CHUNB 20358, São João da Aliança, GO; CHUNB 3673, 3677, 3679, Brazilândia, Distrito Federal (DF); IB 20544, 20545, 37550, Brasília, DF; CHUNB 3672, 3678, 3680, 3682, 3690, 3720, 3728, 3731, 3782, 14340, 20360, 20363, 23711, 24476, Brasília, DF; IB 68700, Cáceres, Mato Grosso (MT); IB 33797, Ponta Porã, Mato Grosso do Sul (MS); IB 15747, Rio Brilhante, MS; IB 8829, Terenos, MS.

South-eastern Brazil: IB 23378, Aguaí, São Paulo (SP); IB 18666, 31633, Agudos, SP; IB 18757, 18796, 18797, 32873, Altinópolis, SP; IB 135, 4768, 16658, 16659, 43756, Batatais, SP; IB 10319, 32658, Botucatu, SP; IB 5894, Capão da Cruz, SP; IB 10137, Franca, SP; IB 10314, Georgia, SP; IB 52761, 52762, Igarapava, SP; IB 43665, 71328-71337, “Estação Ecológica de Itirapina”, Brotas, SP; ZUEC 2496, 2872-2884, “Estação Ecológica de Itirapina”, Brotas, SP; IB 136, Lençóis Paulista, SP; IB 55727, Morro Agudo, SP; IB 5064, Pedregulho, SP; IB 27762, Pontal, SP; IB 9037, 9707, Restinga, SP; IB 53270, Ribeirão Preto, SP; IB 7196, 7757, 7786, 9099, Rubião Júnior, SP; IB 32060, Araguari, Minas Gerais (MG); IB 46427, 46429, Carbonita, MG; IB 30252, 30256, Cruzília, MG; IB 43661, Diamantina, MG; IB 26784, 29254, 40732, Ibiá, MG; IB 46969, Ituiutaba, MG; IB 12586, 12971, 13555, 13570, 15273, 15511, 15618, Miguel Bournier, MG; IB 12560, Ouro Branco, MG; IB 43071, Parque Nacional Serra da Canastra, MG; IB 37263, Uberaba, MG; IB 28285, 54114, Uberlândia, MG; CHUNB 20364, Unaí, MG.

Southern Brazil: IB 20896, Nova Restinga, Paraná, (PR); IB 10247, 10479, 10480, 15947, 15995, Palmeira, PR; IB 10467, Itapitocaí, Rio Grande do Sul, (RS); IB 7853, 7947, 8061, 8062, 8181-8184, 8213, 8323-8325, 8457-8460, Passo Fundo, RS; IB 1652-1659, Pelotas, RS; IB 16026, Restinga Seca, RS; IB 9650, 9876, Rosário do Sul, RS; IB 9867, Santa Maria, RS.

