Diet and habitat use of two sympatric species of *Philodryas* (Colubridae), in south Brazil

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Abstract. Feeding habits and habitat use of the colubrid snakes *Philodryas olfersii* and *P. patagoniensis* in southern Brazil are presented here. *Philodryas olfersii* and *P. patagoniensis* are sympatric in the study area and both dwell in open and forested areas. Specimens preserved in collections and observations of snakes in the field yielded the data. Both species are diet generalists, feeding on small vertebrates, mainly frogs. *Philodryas patagoniensis* has a broader diet, a less variable frequency of food items, and fed on heavier prey than *P. olfersii*. Seasonal variation in diet occurs in both species. The semi-arboreal *Philodryas olfersii* is more slender and has a longer tail than the terrestrial *P. patagoniensis*, characters that may reflect differences in microhabitat use. There are a strong relationship between habitat use and frequency of a given food type. Differences in the use of food resources between *P. olfersii* and *P. patagoniensis* seem to reflect differences in foraging microhabitats used by each species.

Introduction

Habitat and diet composition in snakes seem to be closely related and some authors suggest that microhabitat preferences are related to local finding of prey (Henderson and Binder, 1980; Reinert, 1993; Martins et al., 2002). Studies on preserved specimens in scientific collections combined with field observations result in valuable information on the ecology of snakes, including habitat use and diet composition (e.g., Henderson and Horn, 1983; Henderson et al., 1987; Shine et al., 1996; Marques and Sazima, 1997; Shine et al., 1998; Rodrígues-Robles et al., 1999).

Philodryas olfersii and *P. patagoniensis* are medium-sized colubrid snakes abundant in several localities of South America, being largely sympatric (Thomas, 1976). *Philodryas patagoniesis* is regarded as predominantly terrestrial, whereas *P. olfersii* is both arboreal and terrestrial (see Sazima and Haddad, 1992; Fowler and

Salomão, 1994a; Marques et al., 2001). Available data on feeding habits indicate that both species prey on a wide variety of small vertebrates (Amaral, 1978; Lema et al., 1983; Sazima and Haddad, 1992; Gonzaga et al., 1997; Rocha and Vrcibradic, 1998; Carvalho-Silva and Barros-Filho, 1999; Lopez, 2003). In this study we compare morphology, habitat, substrate use, and diet of sympatric *P. olfersii* and *P. patagoniensis* in south Brazil.

Material and methods

Field work was carried out at the Hillside Plateau of Santa Maria, Rio Grande do Sul State (29°43′S, 53°42′W, 100 m a.s.l.). For each individual of *Philodryas olfersii* and *P. patagoniensis* observed in the field we recorded information of habitat (forest/forest edges or open areas) and microhabitat (substrate use) (cf. Hartmann, 2001). All observed individuals were collected and deposited in the collection of the Universidade Federal de Santa Maria (ZUFSM). Additionally, we examined preserved specimens housed in the collections of Fundação Zoobotânica do Rio Grande do Sul (MCN), Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Universidade Federal de Santa Maria (ZUFSM) and Instituto Butantan (IB). The examined samples included only specimens collected in the Plateau Hillside of Rio Grande do Sul, southern Brazil. This area is covered mainly by grassland ("pampas"), deciduous forests, disturbed and cultivated areas (Lindman and Ferri, 1974; Vieira, 1984). The climate is seasonal, with higher temperatures (17.9-19.2°C) in the austral spring and lower temperatures (8.7-17°C) in the winter. Rainfall is well distributed throughout the year (1600 mm) (Vieira, 1984; Melhem-Adas, 1996).

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A total of 140 preserved specimens of *P. olfersii* and 155 *P. patagoniensis* was examined. For each specimen we recorded the snout-vent length (SVL) and tail length (TL), in mm. The snakes were weighed to the nearest 0.5 g after draining excess preservation liquid through a ventral incision (cf. Martins et al., 2001). Relative tail length (TL/SVL) and stoutness (mass/total length) were recorded for each specimen. Mean size of the larger sex relative to the smaller was used to verify the degree of sexual dimorphism in SVL and relative TL. The difference between the obtained value and 1.0 was used as a sexual dimorphism index (SSD) (see Gibbons and Lovich, 1990; Shine, 1994a).

Digestive tract of each specimen was dissected for gut contents and number of prey type. Intact prey was weighed and measured, and prey partly digested had their mass and size estimated through comparison with intact specimens. To detect possible diet differences between juveniles and adults, reproductive maturity was assessed through gonad examination (see criteria in Shine, 1977).

Results

Body size. Mature males of *P. olfersii* averaged 641 mm SVL ($s = 124$, $n = 68$, range = 535-840) and mature females averaged 843 mm SVL ($s = 117$, $n = 54$, range = 600-1120). Mature males of *P. patagoniensis* averaged 673 mm SVL ($s = 93$, $n = 58$, range = 500-840) and mature females averaged 829 mm SVL ($s = 134$, $n = 73$, range = 580-1220). Sexual body size dimorphism was evident in adults of both species, females being significantly larger than males ($t = 9.11$, df = 120, $P < 0.001$ for *P. olfersii*; $t = 7.54$, df = 129, $P < 0.001$ for *P. patagoniensis*). The degree of sexual size dimorphism was greater for *P. olfersii* (0.31) than for *P. patagoniensis* (0.23). The two species did not differ significantly in body size ($t = 1.57$, df = 124, $P = 0.11$ for males; $t = 0.16$, df = 125, $P = 0.53$ for females).

Relative tail length. Males presented longer relative tail length than females in both species ($t = 7.84$, df = 102, $P < 0.001$ for *P. olfersii*; $t = 10.06$, df = 121, $P < 0.001$ for *P. patagoniensis*). *Philodryas olfersii* exhibited larger relative tail length compared to *P. patagoniensis* ($t = 3.81$, df = 106, $P < 0.001$ for males; $t = 8.51$, df = 117, $P < 0.001$ for females) (fig. 1).
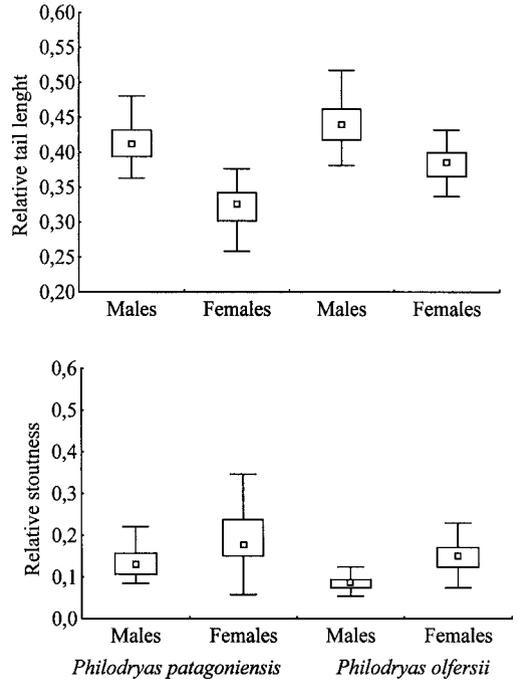

Figure 1. Mean (middle horizontal line), standard errors (boxes), and standard deviation (vertical bars) of relative tail length and stoutness in males and females of *Philodryas olfersii* and *P. patagoniensis* from southern Brazil.

Stoutness. Females of both species were heavier than males ($U = 589.5$, $Z = 5.74$, $P < 0.001$ for *P. patagoniensis*; $U = 138$, $Z = 7.11$, $P < 0.001$ for *P. olfersii*). *Philodryas patagoniensis* was more robust than *P. olfersii* ($U = 161$, $Z = 7.43$, $P < 0.001$ for males; $U = 757$, $Z = 3.79$, $P < 0.001$ for females) (fig. 1).

Habitat. *Philodryas olfersii* was found mostly in forested areas and forest edges, whereas *P. patagoniensis* was frequently observed in open habitats (fig. 2A). Although both species used the same type of habitats, the use frequency differed significantly between them ($\chi^2 = 24.32$, df = 1, $P < 0.001$). Both species were found active only at daytime.

Microhabitat. *Philodryas olfersii* was observed active both on the ground and on vegetation (fig. 2B). In the forest *P. olfersii* was observed more frequently on the vegetation ($n = 10$) than on the ground ($n = 7$). All individuals of *P. patagoniensis* were observed on the
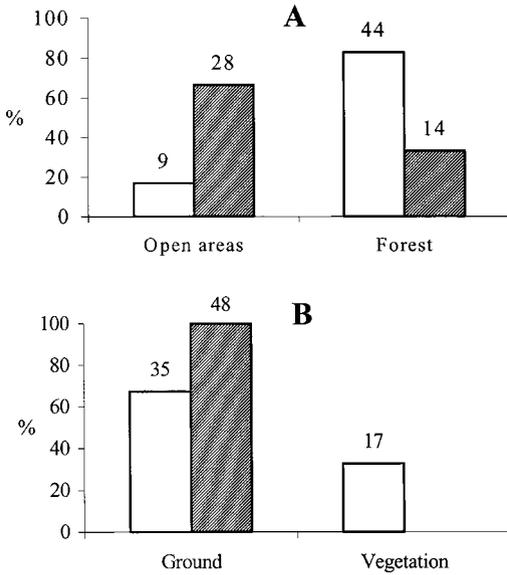
Figure 2. Percentage and number the snakes (above the columns) found: A — in open areas and forest (including forest edges), B — on the ground on the vegetation. Open columns *Philodryas olfersii*; shared columns *Philodryas patagoniensis*. Santa Maria, Rio Grande do Sul, Brazil.

ground ($n = 48$) (fig. 2B). Inactive individuals of *P. olfersii* were observed on the vegetation (in sheltered places, as leaf axils of bromeliads), under tree bark, fallen logs or in burrows. Only one specimen of *P. patagoniensis* was observed resting under a fallen tree trunk on the forest floor. Males of *P. olfersii* were more frequent on vegetation than females (11 males; 6 females), whereas females were more frequent on the ground (20 females and 15 males). Differences were not significant ($\chi^2 = 2.18$, df = 1, $P = 0.13$). *Philodryas olfersii* females with oviductal eggs ($n = 2$) were found only on the ground.

Diet. Forty-five out of 140 (32%) *P. olfersii* specimens, and 71 out of 155 (45%) *P. patagoniensis* contained identifiable prey in their guts. Two specimens of *P. olfersii* and six of *P. patagoniensis* contained two prey item in the stomach. Relative prey mass ranged 0.005-0.130 ($\bar{x} = 0.080 \pm 0.050$, $n = 8$) for *P. olfersii* and from 0.014 to 0.250 ($\bar{x} = 0.055 \pm 0.062$, $n = 19$) for *P. patagoniensis*. Mean relative prey

mass did not differ between species ($t = 0.97$, df = 23, $P = 0.33$).

All prey items were vertebrates, frogs being the most frequent prey for both species (table 1). Juveniles of *P. patagoniensis* and *P. olfersii* preyed on ectothermic prey and a diet shift occurred with body size increase. Snakes were present only in the diet of *P. patagoniensis*, and lizards were preyed on more frequently by *P. patagoniensis*. Lizards were preyed mainly in spring/summer (table 2). Birds were preyed on mainly in spring/summer by both species (table 2). *Philodryas patagoniensis* preyed more on leptodactylid than on hylid frogs. All identifiable frogs preyed on by *P. patagoniensis* were terrestrial (*Scinax fuscovarius* and *Leptodactylus* spp.) (cf. Kwet and Di-Bernardo, 1999). The only arboreal frog (*Hyla pulchella*, Hylidae) was recorded from the gut of *P. olfersii* (table 1).

Both sexes of *P. olfersii* and *P. patagoniensis* exploited all prey types. There were no significant differences in the proportion of ectothermic and endothermic prey by males and females of both species ($\chi^2 = 0.27$, df = 1, $P = 0.607$, for *P. patagoniensis*, and $\chi^2 = 0.51$, df = 1, $P = 0.476$, for *P. olfersii*). Apparently, *P. olfersii* males preyed more on birds than females did, the latter feeding more on mammals (table 3). *Philodryas patagoniensis* females seemed to prey more on lizards and birds than males did (table 3).

Discussion

Description of the preferred habitat currently is available for a very few snake species (Reinert, 1993). In the present study *P. olfersii* and *P. patagoniensis* exhibited a nonrandom use of the available landscape, which indicates habitat selection for both species. The patterns of substrate use also differed between the two species and agree with previous data: *P. olfersii* is regarded as a semi-arboreal snake whereas *P. patagoniensis* is viewed as essentially terrestrial (Sazima and Haddad, 1992;

Table 1. Prey item found in gut of juveniles and adults in *Philodryas* species. Numbers in parentheses indicate the percentage of total number of prey.

Prey taxon	*Philodryas olfersii*		*Philodrvas patagoniensis*	
	Juveniles	Adults	Juveniles	Adults
AMPHIBIA ANURA				
Leptodactylidade				
Leptodactylus sp.		1 (2.1)		2 (2.6)
L. ocellatus			1 (1.3)	3 (3.8)
L. fuscus		1 (2.1)	1 (1.3)	4 (5.2)
L. gracilis			1 (1.3)	
Hylidae				
Hyla pulchella		1 (2.1)		
Scinax fuscovarius			1 (1.3)	2 (2.6)
Unidentified	5 (10.6)	17 (36.2)		19 (24.7)
REPTILIA SAURIA				
Teiidae				
Terns oculatus		1 (2.1)		3 (3.8)
Scincidae				
Mabuya dorsivittata				5 (6.6)
Gymnophtalmidae				
Pantodactylus schreibersii				3 (3.8)
Unidentified		1 (2.1)		7 (9.1)
SERPENTES				
Colubridae				
Liophis poecilogyrus				1 (1.3)
Philodryas patagoniensis				1 (1.3)
Pseudablabes agassizii				1 (1.3)
Unidentified			1 (1.3)	
MAMMALIA				
Unidentified		11 (23.5)	1 (1.3)	12 (15.6)
AVES*				
Unidentified	2 (4.3)	7 (14.9)		8 (10.5)
Total	47 (100)		77 (100)	

* Among nine birds registered for *Philodryas olfersii*, six were nestlings and the remaining three were identified only due to presence of feathers.

Fowler and Salomão, 1994a, 1994b; Marques et al., 2001). However, the presence of birds in the diet of *P. patagoniensis* indicates that this snake occasionally forages on vegetation (as already recorded for other localities, see Sazima and Haddad, 1992; Carvalho-Silva and Barros-Filho, 1999; Cechin, 1999; Lopez, 2003).

Philodryas olfersii is a green snake whereas *P. patoniensis* is a brown snake (see color plates in Sazima and Haddad, 1992 and Marques et al., 2001). These color differences are consistent with the differences in frequency of habitat and microhabitat use, *P. olfersii* being camouflaged against the background of green foliage in the forest, whereas *P. patagoniensis* is camouflaged against the terrestrial background in grasslands.

Camouflaging colors are advantageous for a diurnally active snake, both to hunt for prey and to evade visually oriented predators.

The more slender body and longer tail length of *P. olfersii* may be explained by its markedly arboreal habits (Lillywhite and Henderson, 1993; Martins et al., 2001), as a slender body and mass reduction are advantageous for arboreal snakes (see Lillywhite and Henderson, 1993). Several analyses have indicated that arboreal snakes have long tails, particularly species of Colubridae (Lillywhite and Henderson, 1993). Longer tails may be advantageous to arboreal snakes by allowing greater equilibrium and a better distribution of body mass on branches (Lillywhite and Henderson, 1993;

Table 2. Seasonal variation in prey type eaten by *Philodryas olfersii* and *Philodryas pataaoniensis* from southern Brazil.

Prey type	*Philodryas olfersii*		*Philodryas patagoniensis*	
	Spring/ Summer	Autumn/ Winner	Spring/ Summer	Autumn/ Winner
Anurans	12	11	14	11
Lizards	1	1	11	2
Serpents	–	–	3	1
Birds	5	1	6	0
Mammals	7	3	8	3

Table 3. Number and prey type eaten by males and females in *Philodryas* species. Numbers in parentheses indicate the percentage of total number of prey.

Prey type	*Philodryas olfersii*		*Philodryas patagoniensis*	
	Male	Female	Male	Female
Anurans	10 (21,7)	14 (30,5)	18 (23,4)	16 (20,8)
Lizards	1 (2,1)	1 (2,1)	5 (6,5)	13 (16,9)
Serpents	–	–	1 (1,3)	3 (3,9)
Birds	6 (13,1)	3 (6,6)	1 (1,3)	7 (9)
Mammals	4 (8,6)	7 (15,3)	5 (6,5)	8 (10,4)
Total	46 (100)		77 (100)	

Fowler and Salomão, 1994b). Within the genus *Philodryas*, the green species (e.g., *P. aestivus*, *P. olfersii*, *P. viridissimus*) frequently inhabit forests and seem to be more arboreal than the brown species of open areas (e.g., *P. patagoniensis*, *P. nattereri*, *P. mattogrossensis*), as indicated by their morphology (see Fowler and Salomão, 1994b; Marques, 1999; pers. obs.). The data here obtained for *P. olfersii* and *P. patagoniensis* strengthen this suggestion.

Although there were no differences in SVL between the two species studied, the SSD was greater for *P. olfersii*. In most snakes, females tend to be larger than males because fecundity is size-dependent (Shine, 1993). One possible disadvantage of slender body in arboreal snakes is that it may limit the reproductive potential of females (Lillywhite and Henderson, 1993). Thus, in contrast to terrestrial snakes, females of arboreal species probably tend to increase their abdominal cavity by increasing their body length rather than their body width and consequently have greater SSD. Data for pythons are consis-

tent with this view, as arboreal species such as *Morelia viridis* have greater SSD than the terrestrial species within Pythonidae (see Shine, 1994a).

The ontogenic diet shifts recorded for the two species of *Philodryas* are a common trend among snakes, and may be largely a consequence of ontogenetic shifts in body size (Shine, 1994b). Adults of *P. olfersii* and *P. patagoniensis* may be considered as diet generalists as already recorded (e.g., Lema et al., 1983; Vanzolini, 1986; Sazima and Haddad, 1992; Rocha and Vrcibradic, 1998; Di-Bernardo, 1999; Cechin, 1999; Lopez, 2003), and seasonal dietary changes probably are related to prey availability fluctuations (see Luiselli, 1996; Capizzi et al., 1995; Capizzi and Luiselli, 1997). Both species are fast moving snakes constricting and/or envenoming their preys (Sazima and Haddad, 1992; pers. obs.), a tactic which enables them to feed on a wide array of vertebrates. Thus, the taxonomic composition of diet may be related to the habitat used during foraging. The high incidence of lizards in the gut of *P. patagoniensis* confirm that this snake forage mostly on the ground in the grassland, where most lizards are abundant (Hartmann, 2001). Other prey types such as leptodactylid frogs and snakes recorded for *P. patagoniensis* (and rare or absent for *P. olfersii*) are associated with terrestrial substrate and open habitats (Kwet and Di-Bernardo, 1999; Lema, 1994). Thus, diet differences between the two species clearly reflect differences in prey availability associated with different habitats used by each species. Additionally, data on relative mass of prey indicates that *P. patagoniensis* can subdue heavier prey than *P. olfersii*, which may be related to its greater robustness.

Comparisons between sympatric snakes show that they may use similar prey types, but from different sub-groups (Arnold, 1972). Differences in food resource use by congeneric snakes have been reported for several species including the genus *Philodryas* (Mushinsky and Hebrart, 1977; Vitt, 1980, 1983). In the present study, al-

though prey types overlapped, there were differences in frequency of prey types ingested by *P. olfersii* and *P. patagoniensis*, and thus a partial food resource partitioning was indicated. Resource partitioning is recorded between ecologically similar or phylogeneticaly closely related snakes, and according to some authors (see Greene, 1973; Shine, 1977) the partitioning may reduce interspecific competition and allow the coexistence of these species. However, field data indicate that the prey types used by the two species of *Philodryas* here studied are not limited resources (Cechin, 1999; Hartmann, 2001). In a lizard community in Australia, Pianka (1986) found that in many cases diet overlap between species does not indicate competition, but rather that the food resources consumed are abundant in a particular habitat, and we think that the same may apply for some snake species. Thus, the phylogenetic closeness between *P. olfersii* and *P. patagoniensis* (Thomas, 1976) may mostly be reflected in their diet similarities. On the other hand, differences in habitat and microhabitat use may be related to the differences in frequency of prey types fed on by each species.

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