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Feeding Habits and Habitat Use in *Bothrops pubescens* (Viperidae, Crotalinae) from Southern Brazil

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ABSTRACT.—***Bothrops pubescens* is a member of the *neuwiedi* complex that occurs in southern Brazil and Uruguay. We studied the ecology of *B. pubescens* from a field site (at Santa Maria, Rio Grande do Sul, Brasil) and based on preserved specimens from the state of Rio Grande do Sul, Brasil. In Santa Maria, individuals were collected during visual encounter surveys (VES), in pitfall traps with drift fences and during incidental encounters. Most snakes found in the field were on the ground, mainly on leaf litter, in mosaics of light and shadow or in completely shaded areas. In disturbed areas, snakes were usually associated with country houses and agricultural fields. Snakes were found much more frequently in forests and forest edges than in open habitats. The diet of *B. pubescens* comprised small mammals (56.2% of individual prey found), anurans (21.2%), lizards (7.5%), snakes (7.5%), birds (5.0%), and centipedes (2.5%). Prey predator mass ratios ranged from 0.002–0.627, and larger snakes tended to consume larger prey. *Bothrops pubescens* seems to be able to survive in disturbed areas, mainly those close to forests, and this ability may be facilitated by its generalized feeding habits.**

Snakes of the *Bothrops neuwiedi* complex are terrestrial, have a moderate body size, and usually inhabit open areas in central and southern South America (Campbell and Lamar, 2004; Martins et al., 2001, 2002). In spite of the wide distribution of subspecies in the *neuwiedi* complex, the biology of these snakes is still poorly known, except for a recently published study on the ecology of *Bothrops pauloensis* (Valdujo et al., 2002).

Bothrops pubescens occurs from extreme southern Brazil to Uruguay, in the southern limit of the distribution of the *neuwiedi* complex (Vieira and Alves, 1975; Lema, 1994; Campbell and Lamar, 2004). The few available studies on *B. pubescens* (formerly *Bothrops neuwiedi pubescens*) indicate that this form inhabits forests, is primarily terrestrial, and is a dietary generalist (Skuk et al., 1985; Martins et al., 2001, 2002). However, few detailed studies on the ecology of *B. pubescens* are available, except for a recent article on its reproductive biology (Hartmann et al., 2004). Here we present results on feeding habits and habitat use in this snake.

We obtained data on the ecology of *B. pubescens* in the field and through analysis of preserved specimens.

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TABLE 1. Prey of *Bothrops pubescens* from Rio Grande do Sul, southern Brazil.

Prey category/type	Prey identity	Number of records
Centipedes	unidentified centipedes	2
Amphibians	*Leptodactylus ocellatus*	1
	Leptodactylus fuscus	2
	Leptodactylus gracilis	1
	Physalaemus cuvieri	1
	unidentified frogs	12
Lizards	*Tupinambis merianae*	2
	Teius oculatus	1
	unidentified lizards	3
Snakes	*Oxhyrhopus rhombifer*	1
	Tomodon dorsatus	1
	unidentified snakes	4
Birds	unidentified birds	4
Mammals	Rodentia	44
	Marsupialia	1

Field studies were conducted in the region of the Central Depression in the State of Rio Grande do Sul, municipality of Santa Maria (29°43′S, 53°42′W, elevation about 100 m), from March 1996 to March 1998. Individuals were collected during visual encounter surveys (VES), in pitfall traps (200 liters, about 1 m high buckets) with drift fence (three lines of 10 traps; see additional details in Cechin and Martins, 2000), and incidental encounters. VES were generally made by two people, in all habitat types available (grasslands, forest edges, and forests). Catch per unit effort was measured as the number of individual snakes per person-hours (p-h) of search (see Valdujo et al., 2002). VES were performed mainly during daytime (for logistical reasons): grasslands 590 p-h by day and 120 p-h at night, forest edges 574 p-h by day and 162 p-h at night, and forests 407 p-h by day and 92 p-h at night. For each snake found, we recorded (1) date and time of observation and (2) habitat. Some additional field information was obtained from people who inhabit the study site and the surrounding area and who collected specimens for us. All *B. pubescens* found were collected, preserved, and deposited in the collection of the Universidade Federal de Santa Maria (ZUFSM), Setor de Zoologia.

We obtained diet and morphometric data through the examination of 289 museum specimens in the following institutions: Pontificia Universidade Católica do Rio Grande do Sul (MCP), Universidade Federal de Santa Maria (ZUFSM), and Instituto Butantan (IB). We excluded any specimens previously maintained in captivity. We also recorded tail coloration in 60 juveniles to check whether the possession of a light tail (used to lure prey) was a variable character in juvenile *B. pubescens* (see Martins et al., 2002). Only specimens from Brazil (State of Rio Grande do Sul) were examined. This region is characterized by forests and high-elevation grasslands in the northern part of Rio Grande do Sul, and low-elevation grasslands with forest patches in the south (Brazil and Uruguay; Moreira and Costa, 1982). Temperature is highly variable throughout the year: January is the warmest month, with mean temperatures around 25°C, and July is the coldest month, with mean temperatures ranging from 4–7°C (Inventário Florestal Nacional, Florestas Nativas-Rio Grande do Sul, Ministério da Agricultura, Brasília, Brazil, 1983).

We obtained data on feeding habits by examining the gut contents of each specimen, revealed through ventral incisions. For each specimen, we recorded snout–vent length (SVL), tail length (TL; both to the nearest 1 mm), body mass (to the nearest 0.5 g, after draining excess of preservative liquid), number of food items, and, whenever possible, the direction of ingestion of prey. When well preserved, prey items were weighed and their SVL or body length measured. Some food items were identified through comparison with preserved specimens from the same locality, housed in the UFSM collection. Any vestige of prey in the final portion of the gut was examined under a stereomicroscope. Fur, feathers, scales, bones, nails, and teeth were all used as evidence of prey type.

Sexual maturity was inferred through the analysis of gonads. Males were considered mature if they presented enlarged and opaque efferent ducts, whereas females were considered mature when bearing vitellogenic follicles larger than 8 mm and/or embryos in the oviduct (see Shine, 1977). Males and females with SVL above the smallest mature specimen were considered adults (Shine, 1977). Based on these data, we considered as adult those males with SVL larger than 380 mm and those females with SVL larger than 620 mm.

A total of 36 individuals of *B. pubescens* were obtained during visual searches ($N = 19$), in pitfall traps ($N = 9$), and by local collectors ($N = 8$). All individuals observed during visual searches ($N = 19$) were on the ground, mainly on leaf litter. Most of these places were mosaics of light and shadow or completely shaded areas. In disturbed areas, snakes found by us and by local collectors were usually associated with country houses and agricultural fields. Of the nine snakes captured in pitfall traps, five were adult males, and four were juveniles.

Snakes were found much more frequently in habitats associated with forests (forests and forest edges) than in open habitats during VES (capture rates of 0.023 and 0.0 snake/p-h, respectively; $\chi_1^2 = 62.97$, $P < 0.001$). Capture rate was not significantly different between forest edges (0.018 snake/p-h) and forests (0.029 snake/p-h; $\chi_1^2 = 0.14$, $P = 0.705$).

Of 249 specimens examined, 80 (32.1%) contained prey or evidence of prey, in the gut (Table 1). The frequency of prey type was as follows: small mammals (56.2% of individual prey found); anurans (21.2%); lizards (7.5%); snakes (7.5%); birds (5.0%); and centipedes (2.5%). Only seven snakes had more than one prey item in the gut. Twenty-eight (80.0%) of 35 prey for which direction of ingestion could be detected were ingested head first. Feeding frequency was not different between juveniles and adults (Fisher exact test, $P = 0.31$), between adult males and adult females (Fisher exact test, $P = 0.47$), or between mature and immature females (Fisher exact test, $P = 0.32$). However, feeding frequency was lower in immature males than in adult males (Fisher exact test, $P = 0.03$).

Prey predator mass ratios ranged from 0.002–0.627 (mean ± SD = 0.159 ± 0.165, $N = 29$). Prey mass was dependent on predator mass ($F_{1,56} = 26.3$; $r^2 = 0.38$; $P < 0.001$), that is, larger snakes tended to consume larger prey. Even so, large snakes did not appear to ignore

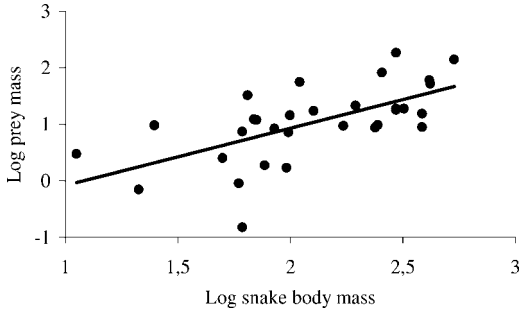

FIG. 1. Prey mass in relation to snake body mass in *Bothrops pubescens* ($N = 29$) from Rio Grande do Sul, southern Brazil.

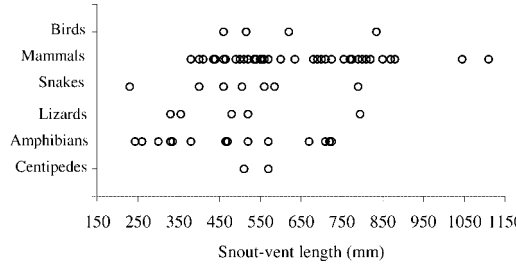

FIG. 2. The occurrence of different prey categories in relation to snout–vent length in *Bothrops pubescens* ($N = 80$) from Rio Grande do Sul, southern Brazil.

small prey (Fig. 1). There was no ontogenetic shift in relative prey mass (slope of the regression line not significantly different from one; ($t_{27} = 0.36$, $N = 29$, $P > 0.05$). Males and females consumed prey of similar mass ratios ($Z_{27} = 0.102$, $P = 0.918$).

The SVL of snakes that consumed ectothermic prey (527 ± 174 mm, $N = 31$) was slightly lower than the SVL of those that consumed endothermic prey (660 ± 179 mm, $N = 49$; $F_{1,29} = 4.0$; $P = 0.054$; Fig. 2); therefore, there is some evidence for an ontogenetic shift in prey type in *B. pubescens*.

The minimum SVL of a snake with an endothermic prey in the gut was 350 mm, whereas the maximum SVL of a snake with an ectothermic prey in the gut was 795 mm (Fig. 2). Females consumed endotherms more frequently than males (26 and 14 endotherms, 11 and 16 ectotherms in females and males, respectively; Fisher exact test, $P = 0.04$).

All immature individuals examined exhibited a white tail tip. One juvenile was observed in the field coiled with its tail tip moving slowly, suggesting caudal luring behavior (390 mm SVL, with frog remains in the gut, ZUFSM 1129).

Our results indicate that *B. pubescens* is a terrestrial pitviper that inhabits mainly forests, forest edges and adjacent areas. In the few encounters of individuals in open areas the snakes were moving, perhaps between forest patches. Forest dwelling appears to be unique in *B. pubescens* because all other members of the *neuwiedi* complex inhabit open areas (Martins et al., 2001, 2002; Valdujo et al., 2002; pers. obs.). Observations of individual *B. pubescens* around human-altered habitat indicate that this snake is able to survive in disturbed areas, mainly those close to forests; other forest-dwelling *Bothrops* colonize disturbed areas (Sazima, 1992; Oliveira and Martins, 2002). This ability may be facilitated by their generalized feeding habits (Martins et al., 2002) because habitat selection and food availability tend to be strongly correlated (Reinert, 1993). In fact, the main prey types of these snakes (mammals and frogs) are common in disturbed areas (pers. obs.). Thus, these species might not be as threatened by habitat alteration (see Marques et al., 2002) as some habitat specialists in the genus (e.g., *Bothrops itapetiningae*; M. Martins and R. J. Sawaya, unpubl. data).

As in many other *Bothrops*, *B. pubescens* has a generalized diet of small vertebrates and centipedes (Martins et al., 2002). Differences in the frequency of specific prey types between species of *Bothrops* may simply be an artifact of local prey availability in the habitats in which they occur (Martins et al., 2002). In the *B. neuwiedi* complex, *B. pubescens* feeds more frequently on anurans (21.1% of prey found) than *B. pauloensis* (14.0%), which feeds more frequently on lizards (25%, Valdujo et al., 2002; 7.4% in *B. pubescens*). The later subspecies occurs in dry Cerrado habitats where lizards are common (Valdujo et al., 2002), whereas *B. pubescens* inhabits mostly forests, where frogs are more common than in dry areas. Similar differences in diet as a result of prey availability may occur with other prey types, such as small mammals.

An ontogenetic shift in diet, mainly from ectothermic prey (frogs and lizards) to endothermic prey (mammals), is common in *Bothrops* (Martins et al., 2002) and occurs in *B. pubescens*. This shift may reflect size differences among ectothermic and endothermic prey: juveniles may not feed on mammals simply because these prey are relatively large compared to lizards and frogs (Martins et al., 2002). Alternatively, variations in chemoreceptive preferences during development (see Mushinsky and Lotz, 1980) or in prey searching behavior, could result in different encounter rates for different prey types (Macias Garcia and Drummond, 1988). Ontogenetic changes in diet may also be related to the loss of caudal luring in adults of most crotaline snakes (Heatwole and Davison, 1976; Martins et al., 2002).

A greater consumption of endotherms by female *B. pubescens* may be an energetic or functional consequence of their large size. Females can reach approximately 1300 mm SVL, whereas males attain approximately 950 mm SVL. Similar dietary results were observed for other *Bothrops* (e.g., *Bothrops moojeni*, Nogueira et al., 2003; *Bothrops atrox*, M. E. Oliveira and M. Martins, unpubl. data), perhaps for the same reason. However, this sexual difference in diet was not observed in *Bothrops pauloensis*, another form of the *neuwiedi* complex (Valdujo et al., 2002). In relation to the only other well-studied form in the *neuwiedi* complex, *B. pauloensis* (Valdujo et al., 2002), feeding biology and habitat use of *B. pubescens* shows some similarities (e.g., a generalized diet with ontogenetic shift in prey types) as well as some differences (e.g., sexual differences in prey type in the latter and its lack in the former; the use of forests by the latter and dry, open areas by the former).

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