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ECOLOGICAL OBSERVATIONS ON SYMPATRIC *PHILODRYAS* (COLUBRIDAE) IN NORTHEASTERN BRAZIL

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ABSTRACT

Philodryas olfersi *and* Philodryas nattereri *were studied in a zone of sympatry in the interior of northeast Brazil during 1977 — early 1978.* Philodryas olfersi *is usually associated with habitats containing much vegetation whereas* P. nattereri *is usually associated with rocky habitats. Both species rely primarily on small vertebrates for food, and differences in diets presumably reflect differences in habitats and the associated resource base. Reproduction is seasonal, with eggs produced toward the end of the dry season. The reproductive cycle of these species is similar to that of some tropical species of lizards and snakes but very different from that of others. It is suggested that future studies on reproductive strategies of tropical reptiles attempt to identify cause and effect relationships* **by collecting data over long periods** *of time (at least a complete cycle of seasons) and combining reproductive data with ecological data.*

INTRODUCTION

Little is known of the ecology or reproductive cycles of snakes in northeastern Brazil. Indeed, the small amount of published material is anecdotal in form (Amaral, 1977; Vanzolini et al., 1980) consisting of little more than general statements. Further, with the exception of a few locality-specific summaries (Dixon and Soini, 1976; Duellman, 1978) little is known about the ecology of South American snakes in general.

In this paper, I present data on habitats, diets, morphology, and reproduction in *Philodryas nattereri* (Steindachner, 1870) and *Philodryas olfersi* (Lichtenstein, 1823) from a zone of sympatry in the interior of northeastern Brazil. The available taxonomic and ecological literature on these two species has recently been summarized (Thomas, 1976).

Study area. The field work was carried out in the immediate vicinity of Exu, Pernambuco. Exu is located in extreme northwestern Pernambuco, an area near the geographical center of the "zona da caatinga" (Lima, 1960; Vasconcelos, 1941). Following Vanzolini (1974), I considered only the core area of the sertão as "caatinga" (see also Egler, 1951; Ab'Saber, 1967 for complete discussion of terminology).

The habitat in this region is patchy, consisting of large sections of thorn forest with a canopy varying from 3 to 5 m in height. The canopy may be continuous or discontinuous. Small temporary ponds are abundant (at least during the wet season) as are rock piles of various sizes. The rock piles provide refugia for *Philodryas nattereri* whereas the associated vegetation matrix provides habitat for *P. olfersi.*

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Rainfall is generally seasonal, with the wet season extending from December through at least the second week in June. The dry season (late June through late November) may be interrupted by short rainy periods although this varies considerably from year to year. Climatological data for the study site has been summarized by Vitt and Goldberg *(ms)* and Vitt and Lacher (*in press*). The sertão is known for extended droughts and thus can be considered a highly unpredictable habitat.

METHODS AND MATERIALS

Individuals of both species of *Philodryas* were collected by hand and by use of the local "snake market." The latter consisted of a group of local children who quite skillfully collected specimens of all locally occurring snakes and lizards. A majority of snakes were processed and preserved the same day that they were collected in order to gain accurate data on diets and body weights. Each live snake was killed with nembutal. Then, snout-vent length (SVL), tail length, head length, head width, gape, body hight and body width (mid-body) were recorded to the nearest mm. Body weights were taken to the nearest g with Pesola balances. Snakes were then injected and preserved in 10% buffered formalin. Later, stomach contents were identified and reproductive condition was noted. Counts of enlarged yolking follicles and/or oviducal eggs were recorded for females. When possible, clutches of oviducal eggs were weighed. Stomach contents were identified by comparing the contents with locally collected mammals, reptiles, birds and amphibians. The width of prey items was measured with a set of dial calipers accurate to .1 mm.When food items were partially digested, it was possible to estimate prey width accurately by comparing the remaining portions with preserved or mounted individuals of the same species.

Observations on all individuals of both species encountered in the field were recorded. When possible, cloacal temperatures and associated substrate and air temperatures were recorded. These were taken with a Schultheis rapid register thermometer. The position of the snake in the habitat was recorded, as were any behavioral observations.

RESULTS

Adaptive morphology. Both *P. nattereri* and *P. olfersi* were relatively long and streamlined in body form as compared to other sympatric terrestrial snakes (Vitt, in prep.). This is evident from ratios of tail length, head length, head width, body width and body height to snout-vent length (Table 1). *Philodryas olfersi* is relatively more streamlined than *P. nattereri.*

Even though relative head widths were different between species, the difference is slight when sex is taken into consideration. It was possible to compare these two snakes statistically in respect to relative morphologies because head length, head width, gape, body height and body width were all significantly correlated ($P<.0001$) to SVL. Sexual differences in relative tail length ocurred in both species. Only in relative body height were sexual differences apparent in any of the other morphological variables for *P. nattereri.* Male *P. olfersi* were significantly different in respect to all relative morphological measurements except body width/SVL from females (Table 1). The differences between sexes in *P. olfersi* in relative head measurements reveal actual sexually dimorphic features as do diferences in relative tail lenghts between sexes of both species. All relative measurements except gape/SVL were different between species. Differences between species in actual gape (not corrected for SVL) were significant (Mann-Whitney $U = 3507.O, P = .0467$) and will discussed in relation to prey size (see diet section).

The largest individuals of both species are females and female *P. nattereri* attain greater SVL than female *P. olfersi* (Table 2, Fig. 1). Sexual dimorphism in size (SVL) was significant in *P. olfersi* but not in *P. nattereri* (Table 2). The latter may represent sampling error, because females attain larger sizes than males. Nevertheless, sexual dimorphism (if real) is not as pronounced in *P. nattereri.* This result is supported by data on the

Table 1. Comparisions (Mann-Whitney U test) of relative morphological measurements between sexes within species and between species for the tropical snakes *Philodryas nattereri* and *Philodryas olfersi*. *P* denotes level of significance.

SPECIES	Tail/SVL	Head Length/SVL	Head Width/SVL	Gape/SVL	Body Width/SVL	Body Height/SVL
Philodryas nattereri						
males	.433 (.027,41)*	.037 (.003,45)	.019 (.001,45)	.050 (.005,45)	.022 (.002,45)	.021 (.002,45)
females	.361 (.045,39)	.037 (.005,46)	.019 (.002,46)	.050 (.007,43)	.021 (.002,47)	.020 (.002,47)
U	77.0	869.0	1025.0	906.5	844.0	664.0
P**	<.0001	.1876	.9367	.6106	.0954	.0021
Philodryas olfersi						
males	.413 (.024,31)	.038 (.007,34)	.019 (.004,33)	.056 (.011,32)	.018 (.003,34)	.020 (.003,34)
females	.366 (.030,58)	.034 (.005,63)	.018 (.003,63)	.049 (.006,64)	.018 (.002,63)	.020 (.002,62)
U	195.0	371.0	597.0	439.0	979.0	981.0
P	<.0001	<.0001	.0006	<.0001	.4867	.5760
P. nattereri X *P. olfersi* (all data pooled)						
U	2750.5	2601.0	1938.5	4053.0	938.0	3514.0
P	.0108	<.0001	<.0001	.6356	<.0001	.0156

* Standard deviation of the mean and sample size
** Unless otherwise indicated, Ps are exact.

Table 2. Sexual and species comparisons (Mann-Whitney U test) in the tropical snakes *Philodryas nattereri* and *Philodryas olfersi*. *P* denotes level of significance.

SPECIES	x̄ SVL (mm)	x̄ Tail Length (m)	x̄ Body Weight (g)
Philodryas nattereri			
males	752.2 (156.3,45)*	321.8 (69.4,41)	156.3 (84.2,45)
	(424-981)**	(172-424)	(21-358)
females	796.9 (233.5,47)	274.7 (85.2,39)	187.9 (135.7,47)
	(271-1204)	(75-403)	(10-595)
U	902.5	541.5	967.0
P***	.2260	.0130	.4796
Philodryas olfersi			
males	596.0 (142.0,34)	244.3 (62.4,31)	54.7 (23.2,34)
	(223-775)	(93-318)	(6-110)
females	775.1 (150.7,65)	280.1 (54.5,58)	127.8 (53.5,65)
	(236-997)	(91-346)	(6-224)
U	244.5	450.5	222.0
P	<.0001	<.0001	<.0001
Philodryas nattereri X *P. olfersi* (all data pooled)			
U	3792.0	2514.0	2969.5
P	.0459	.0010	<.0001

* Standard deviation of the mean and sample size

** Minimum and maximum values on which statistics are based

*** Unless otherwise indicated, these are exact Ps.

length (SVL)/weight relationships (Figs. 2-3; Table 3) which show significant differences between males and females of *P. olfersi* but not *P. nattereri*. The same sampling error problem may account for the lack of differences between sexes of *P. nattereri* as the weight data are from the same individuals that were used for the SVL comparison. By pooling all length-weight data for each species, it can be concluded that *P. olfersi* is significantly different from *P. nattereri* in respect to the weight/lenght relationship (Analysis of Covariance, F = 74.094, P<.0001).

These two species are strikingly different in coloration (see Vanzolini et al., 1980, for photographs). *Philodryas olfersi* is always green dorsally, with lighter green on the ventral surface. There is no banding or striping in juveniles or adults. *Philodryas nattereri* is generally tan to beige in background color with two dark lateral stripes extending the entire length of the body (stripes become obscure in larger and presumably older individuals). Thus *P. olfersi* is cryptic in vegetation, particularly during the wet season, whereas *P. nattereri* is cryptic on rock surfaces and in vegetation during the dry season.

Diets. Stomach contents were analyzed for 99 *P. olfersi* and 92 *P. nattereri*. Of these, 27 *P. olfersi* and 33 *P. nattereri* contained food items in the gut (Table 4). *Philodryas olfersi* consumed higher percentages of small mammals and anurans than did *P. nattereri*, whereas the latter consumed relatively greater proportions of lizards. A relatively wide variety of vertebrates has been reported from stomachs of *P. olfersi*, including *Hyla sp.* (Brongersma, 1957: 460), a parrot, reptile eggs, *Hemidactylus mabouia*, *Tropidurus torquatus* and a microteiid (Thomas, 1976). Most likely, they will feed on any small vertebrate within their microhabitat. Amaral (1933) considered *P. nattereri* an opportunistic feeder and Thomas (1976) reported an unidentifiable teiid lizard as a dietary item. Dietary overlap (Schoener, 1968) was low (0.278), albeit sample sizes were not large enough for a detailed comparison. The presence of autotomized lizard tails (of 5 species) in stomachs of *P. nattereri* further documents the reliance of this snake on lizards. This also suggests

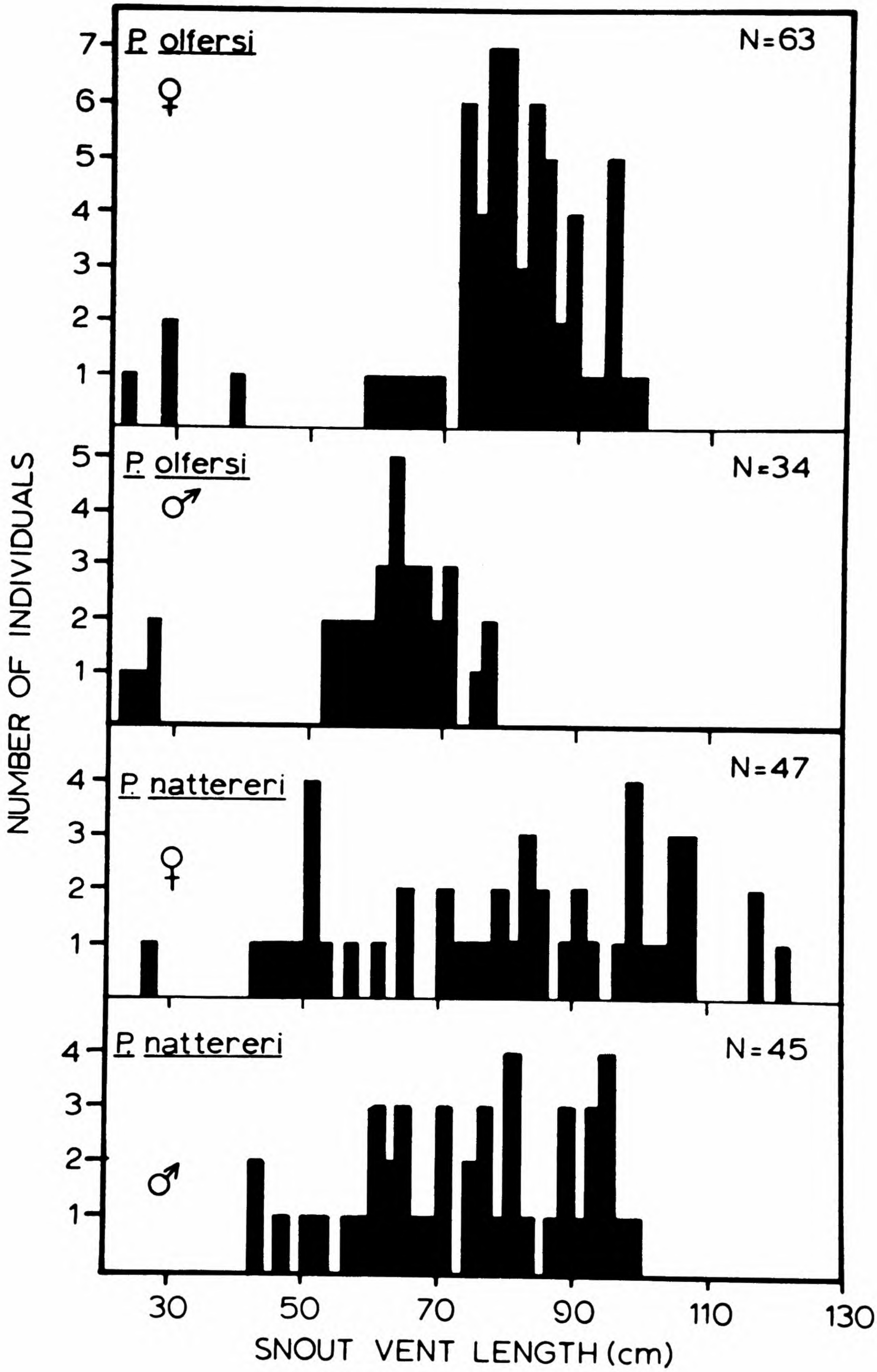

Fig. 1. Distributions of body sizes (SVL) for male and female *Philodryas olfersi* and *P. nattereri* from Exu, Pernambuco in the interior of northeastern Brazil.

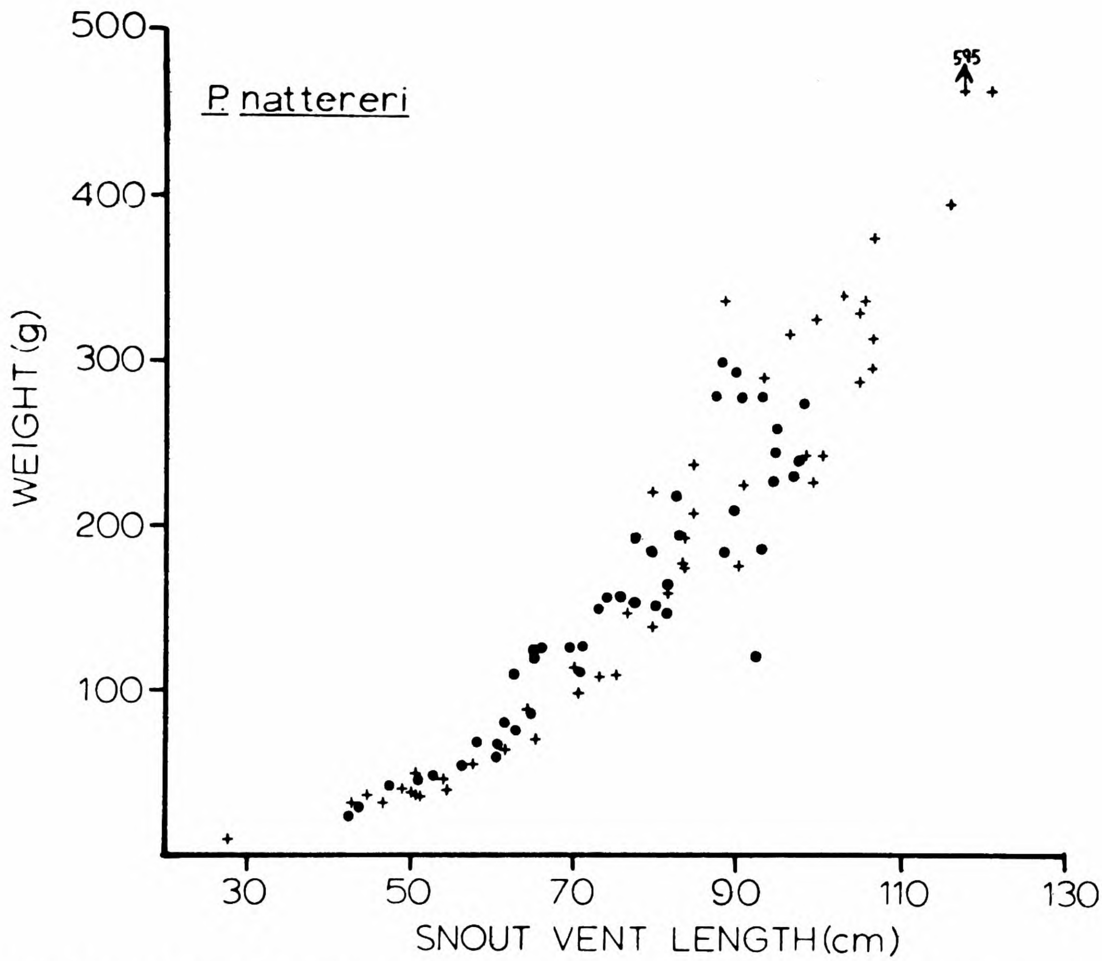

Fig. 2. Length-weight relationship for *Philodryas nattereri*. Circles represent males and crosses represent females.

the importance of tail autotomy by lizards for escape from predation by snakes (see Vitt et al., 1977). No lizard tails were found in stomachs of *P. olfersi*.

Prey size was correlated with SVL in both species of *Philodryas*. In *P. olfersi* the relation was $r_s = .73$, $P<.02$ whereas in *P. nattereri* the correlation was $r_s = .69$, $P<.01$. This suggests that as snakes grow larger, they tend to take larger prey. These results were intuitively expected because of the high correlation between snake head size and SVL and the fact that small snakes cannot take large prey. Large snakes did, however, often take small prey, and thus the prey size range available to, and used by large snakes is greater than that available to smaller snakes.

The taxonomic composition of diets lends some insight into the microhabitats used for foraging by these two snakes. The reliance on small mammals by *P. olfersi* suggests that they forage in vegetated areas, and the relatively high proportion of *Zygodontomys* suggests that much foraging takes place in habitats where there is little or no canopy (i.e., grassy fields; K.E. Streilen, pers. comm.). On the other hand, the high incidence of lizards in stomachs of *P. nattereri* suggests that these snakes forage a great deal in and around rock habitats where most lizards were abundant. Some foraging by *P. nattereri* may occur away from rock piles as suggested by the presence of several teiid lizards and the skink *Mabuya heathi* in the diet. Often these lizards are most abundant in areas that are relatively open, with low vegetation.

Differences in foraging behaviors are also suggested by the taxonomic composition of the diets of these snakes. Many of the lizards captured by *P. nattereri* were rapidly mov-

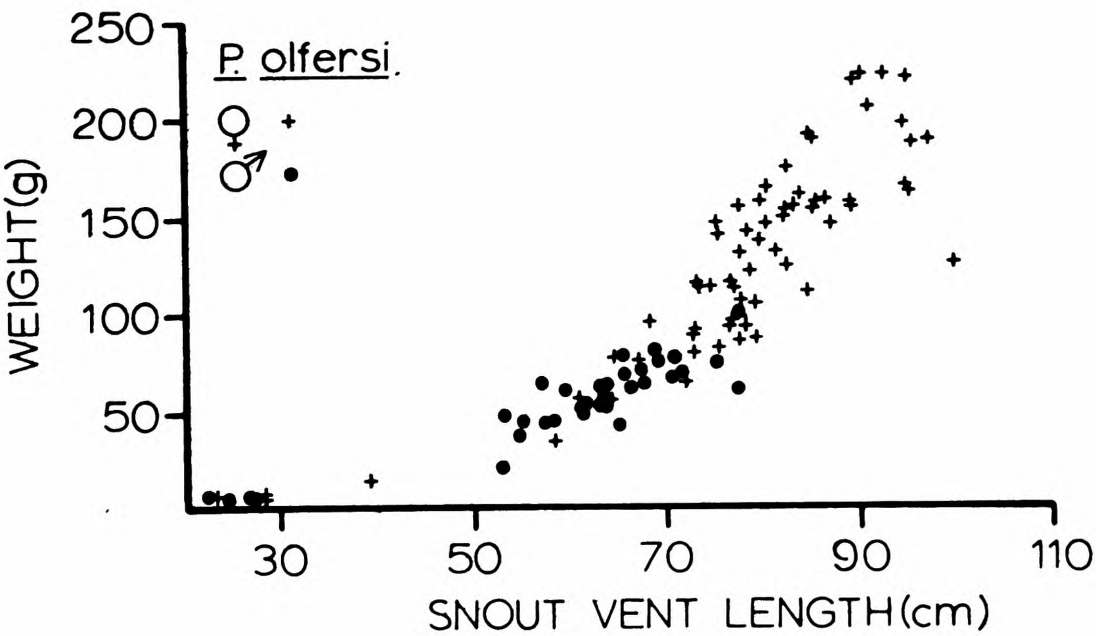

Fig. 3. Length-weight relationship for *Philodryas olfersi*. Circles represent males and crosses represent females.

Table 3. Length-weight relationship (log SVL x log body weight is best fit) for *Philodryas* from northeastern Brazil. *P* denotes level of significance.

SPECIES	N	r^2	F	P*	Analysis of Covariance (within species)	
					F	P*
Philodryas natterei						
males	*45*	.907	418.34	<.0001	3.2098	.0766
females	47	.966	1262.1	<.0001		
Philodryas olfersi						
males	34	.943	524.84	<.0001	10.9430	.0013
females	65	.928	811.84	<.0001		

* These are exact Ps unless otherwise indicated

ing species *(Cnemidophorus ocellifer, Ameiva ameiva, etc.)*. Most likely, these lizards were ambushed by *P. nattereri* which often remain motionless in areas where teiid lizards forage. Along the edge of a small stream, I observed a *P. nattereri* that had just captured a *C. ocellifer*. The ambush took place in a small open area near a rock pile. Grassy vegetation dominated the flora. The snake presumably had been lying in wait along the edge of the open area and when the lizard foraged near the snake, the snake secured the lizard in its mouth. Coils were used to hold the lizard, apparently until the venom took effect. Another *P. nattereri* was collected while in the process of robbing a bird nest situated in a small bush, also near a rock pile. I never observed a *P. olfersi* feeding in the field.

The diets of these two species of snakes suggest that prey items are taken differently and from different microhabitats. The fact that most prey items were terrestrial supports

Table 4. Diet summary for *Philodryas olfersi* and *P. nattereri* from northeastern Brazil.

PREY CATEGORY	*Philodryas olfersi*				*Philodryas nattereri*			
	No.	% Total No.	Freq.	% Freq.	No.	% Total No.	Freq.	% Freq.
Mammals								
Calomys	2	7.4	1	5.9	0	0	0	0
Cercomys	1	3.7	1	5.9	0	0	0	0
Rattus	0	0	0	0	1	3.0	1	3.0
Zygodontomys	13	48.1	4	23.5	1	3.0	1	3.0
Unid. mammals	4	14.8	4	23.5	3	9.1	3	9.1
Birds								
Unid. birds	1	3.7	1	5.9	2	6.1	2	6.1
Lizards								
Ameiva	2	7.4	2	11.8	5	15.2	5	15.2
Gymnophthalmus	0	0	0	0	1	3.0	1	3.0
Cnemidophorus	0	0	0	0	10	30.4	10	30.4
Tupinambis	0	0	0	0	1	3.0	1	3.0
Unid. lizards	0	0	0	0	1	3.0	1	3.0
Lizard Tails								
Ameiva	0	0	0	0	1	3.0	1	3.0
Cnemidophorus	0	0	0	0	1	3.0	1	3.0
Mabuya	0	0	0	0	2	6.1	2	6.1
Tropidurus	0	0	0	0	1	3.0	1	3.0
Phyllopezus	0	0	0	0	1	3.0	1	3.0
Anurans								
Hyla maxima	1	3.7	1	5.9	0	0	0	0
Hyla rubra	1	3.7	1	5.9	0	0	0	0
Unid. anurans	2	7.4	2	11.8	1	3.0	1	3.0
TOTALS	27	99.9	17	100.1	33	99.9	33	99.9

my contention that these snakes, even though streamlined in body form, are for the most part terrestrial.

Habitats and predator escape behaviors. Philodryas nattereri were most often encountered in rock piles whereas *P. olfersi* were most often encountered on the ground in habitats with heavy vegatation.

Predator escape behaviors for both species can be categorized as "flight." Generally, individual *P. nattereri* fled into deep crevices in rocks. None was observed to climb vegetation for escape. Individual *P. olfersi* fled rapidly over the surface of the ground disappearing into the undergrowth. None was observed to actually climb vegetation for escape, even though several were first encountered in vegetation.

Locally ocurring snakes preying on *Philodryas* included *Clelia occipitolutea* and *Micrurus ibiboboca*. Several birds and mammals undoubtedly prey on these snakes, and it is likely that both eggs and juveniles are occasionally eaten by large teiids such as *Tupinambis* and *Ameiva*.

Reproduction. Both *Philodryas* are oviparous. Female *P. olfersi* containing oviducal eggs were collected during September, October and November. Thomas (1976) reported presence of eggs in *P. olfersi* from September through January in a variety of localities. Individuals with enlarged yolking follicles were collected from August through December. No females collected during other months showed any indication of reproductive activity. Thus the reproductive season in *P. olfersi* is late in the dry season. Female *P. nattereri* with oviducal eggs were collected during July and September, and females with enlarged yolking occurred from May to August. Thus the reproductive season for *P. nattereri* is somewhat earlier than of that of *P. olfersi*, but eggs are laid toward the end of the dry season. Clutch size was significantly correlated with SVL for *P. olfersi* ($r^2 = .33, F_{1,38} = 18.48, P < .001$) and *P. nattereri* ($r^2 = .45, F_{1,13} = 9.99, P < .01$)(Fig. 4). The mean and variance of SVL for reproductive females were 831.4 (78.0) and 944.9 (129.8) for *P. olfersi* and *P. nattereri*, respectively, and their respective mean clutch sizes were 6.6 (1.95) and 7.6 (2.14). The slightly larger clutch size in *P. nattereri* may simply reflect the slightly larger size attained by females of that species and the concordant increase in clutch size with SVL.

Eggs of both species were relatively large and somewhat similar in size (Table 5), although sample sizes of *P. nattereri* with oviducal eggs were too small to allow statistical comparisons. Clutch weight/body weight was much greater in *P. olfersi* than *P. nattereri*, but the differences may again simply reflect a bias due to the small sample of *P. nattereri*. Indeed, the one female on which the data are based for *P. nattereri* was an unusually large one with an unusually small clutch.

Thermal ecology. Both species of *Philodryas* are heliothermic. Attainment of eccritic body temperatures is effected through basking in direct sunlight or basking on warm rocks surfaces *(P. naterreri)*. Three *P. olfersi* had mean cloacal temperatures of 34.71 C (SE = 1,75) and the mean air temperature at the time and place where body temperatures were recorded was 24.77 C (SE = 3.64). One *P. nattereri* had a body temperature of 35.8 C. These recorded thermal data are consistent with data reported for other heliothermic reptiles (Brattstrom, 1965).

DISCUSSION

Philodryas olfersi and *P. nattereri* resemble North American *Masticophis* in morphology and certain aspects of their ecology. They are fast moving snakes and feed on a wide variety of prey. Differences in the ecology of these two species are consistent with differences in coloration, *P. nattereri* being cryptically colored when in rocky habitats and *P. olfersi* being cryptic when in vegetated habitats. Differences in diets presumably reflect differences in prey availability associated with the different habitats used by each species.

Philodryas in northeastern Brazil reproduce primarily during the dry season, and reproduction is definitely seasonal. This pattern is similar to that of at least some sympa-

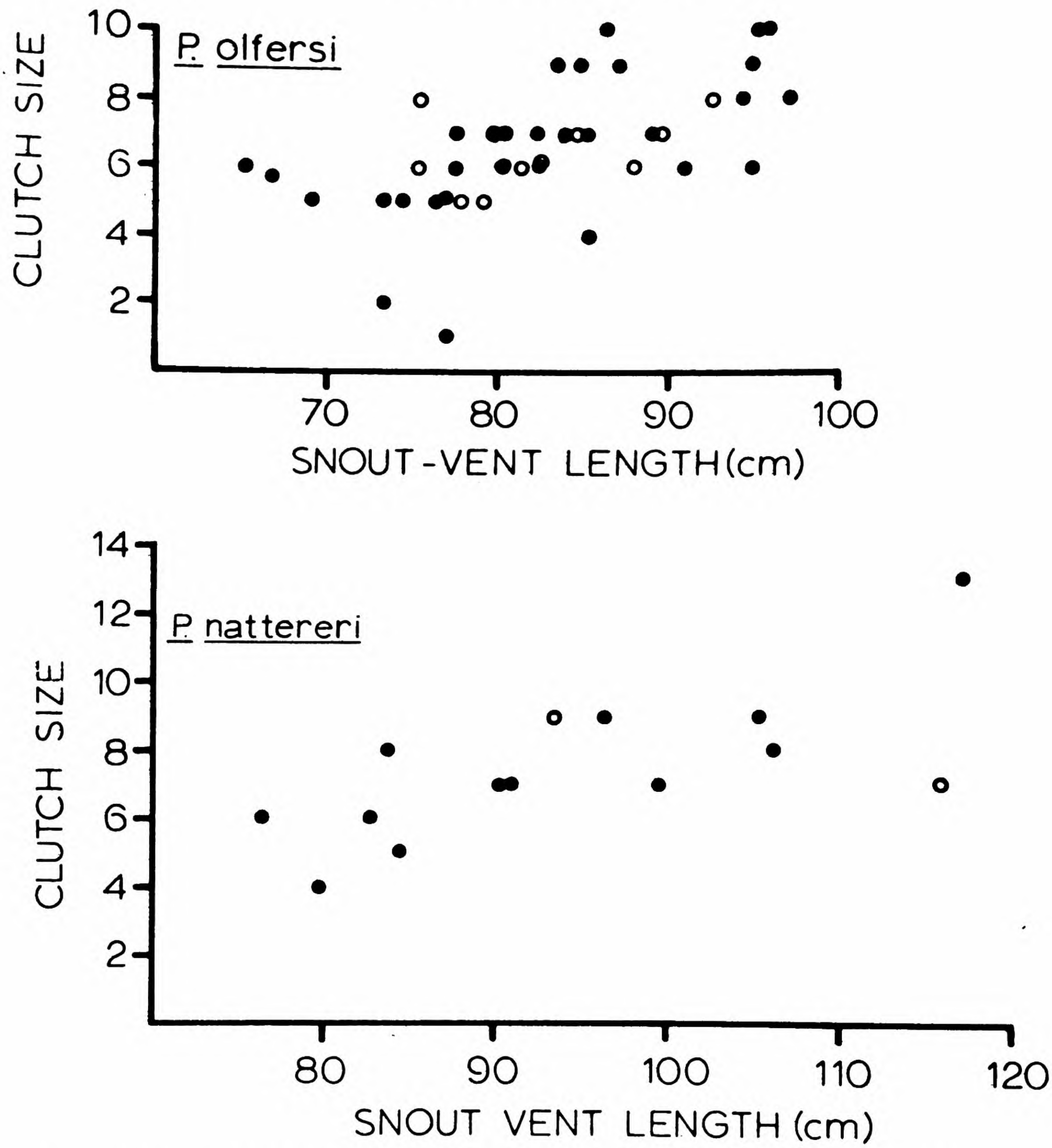

Fig. 4. Clutch size and SVL relationship for *Philodryas olfersi* and *P. nattereri*. Closed circles represent counts of enlarged yolking follicles whereas open circles are counts of oviducal eggs.

tric lizards (Vitt and Goldberg, *ms*) and different than that reported for some lizards and snakes in other tropical habitats (see for exemple Fitch, 1970, 1973; Duellman, 1978). The data presented here and elsewhere (Barbault, 1976, Vitt and Lacher, *in press*; other papers cited above) strongly suggests that there may be no such entity as a "tropical reptile reproductive strategy". Available evidence suggests that a diversity of reproductive strategies exists among "tropical" species of snakes and lizards that until large quantities of data on reptilian reproduction, coupled with ecological data are accumulated, identification of causal relationships effecting reproductive cycles in "tropical" reptiles is difficult. The diversity of reproductive strategies extant in reptiles ocurring between the Tropic of Cancer and the Tropic of Capricorn is not surprising in view of the diversity of habitats in the "tropics". It is suggested that future inverstigators working on reproductive strategies in tropical snakes collect data on seasonality of breeding, egg and clutch size, and as

Table 5. Statistics on egg size (mm), weight (g), the ratio of total clutch weight to body weight (clutch/body), and size (mm) and weight (g) of hatchling *Philodryas olfersi* and *P. nattereri* from northeast Brazil.

SPECIES	$\bar{x}$ Egg Length *(SE,N)	$\bar{x}$ Egg Width (SE,N)	$\bar{x}$ Egg Weight (SE,N)	Clutch/Body (SE,N)	$\bar{x}$ Hatchling SVL, Wt. (N)
P. olfersi	43.29 (2.10,10)	16.50 (0.72,10)	7.37 (0.78,9)	0.350 (0.04,9)	229.5, 6.50 (2)
P. nattereri	40.15 (____, 2)	14.70 (____, 2)	4.71 (____, 1)	0.084 (____, 1)	no data

• SE = standard error ($s_{\bar{x}}$) of the mean and N = sample size (number of females)

complete a set of ecological data as possible. Without the latter interpretation of reproductive data is difficult. Also, it is strongly suggested that future investigators gather data on assemblages of species occurring at one locality in the tropics so that diversity in reproductive strategies in one environment may be assessed.

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