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# ***BIOLOGIA GERAL E EXPERIMENTAL***

**PAULO EMÍLIO VANZOLINI  
(1924-2013)**

**Artigos completos publicados em BGE**

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## BIOLOGIA GERAL E EXPERIMENTAL

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# **Biologia Geral e Experimental**

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## P.E. VANZOLINI

A partida da última expedição do Dr. Vanzolini foi acompanhada por seus amigos e pela família no dia 28 de abril de 2013, e bem ao seu estilo lembramos os versos da música que ele fez “*quando eu for eu vou sem pena, pena vai ter quem ficar*”. Vanzo deixa, além das saudades, um rico acervo intelectual tanto na ciência quanto na música e, como ele mesmo dizia, se considerava o último dos viajantes. Tive o privilégio de aprender com ele a conhecer um pouco o mundo, em muitas das suas viagens das quais participei e também no Museu de Zoologia da USP onde ele começou a trabalhar na década de 1940 e foi seu diretor entre 1963 a 1993. Vanzolini foi um grande incentivador de BGE, tendo colaborado com vários trabalhos desde quando a revista começou em 2000 na Universidade Federal de Sergipe, com a ajuda dos meus estudantes de biologia da UFS. Como memória, neste volume nós reproduzimos os artigos do velho amigo Paulo Emílio Vanzolini publicados em BGE.

*Celso Morato de Carvalho*

# Biologia Geral e Experimental

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## A CONTRIBUTION TO THE ECOGEOGRAPHY OF THE BRASILIAN CERRADOS

P. E. Vanzolini<sup>1</sup>

### ABSTRACT

A survey was made aimed at evaluating the relative importance of gallery forest (on the river levees), backswamp and interfluvial cerrados to the general zoogeography of the domain, especially with regard to conservation problems. The sampling scheme comprised T-shaped arrays of pit-fall traps, the cross-member along the levee (in the gallery forest) and the stem extending across the backswamp. This scheme was used at two localities, on the left bank of the Rio Tocantins across the town of Ipueiras and on the right bank of a tributary, the Rio Manoel Alves Pequeno (or da Natividade), near its mouth. As a control, a grid of traps was set in the interfluvial cerrado between the Tocantins and the Manoel Alves. During a period of 6-8 days 136 frogs (8 species), 55 lizards (7 species) and one snake were collected. Among the lizards, *Tropidurus torquatus* showed preference for the backswamp, while *T. oreadicus* preferred the levee; *Gymnodactylus amarali* clearly preferred interfluvial cerrado. Among the frogs, *Physalaemus cuvieri*, the most abundant species, showed preference for the proximity of the river, *Chiasmocleis centralis* for the backswamp. The gallery forest was not found in this area to harbor a characteristic set of species. The animals sampled in this survey should not suffer from the interruption by flooding of gallery forest, either as residential areas or as faunal corridors. It remains to be seen whether the shores of hydroelectric lakes are ecologically analogous to river backswamps.

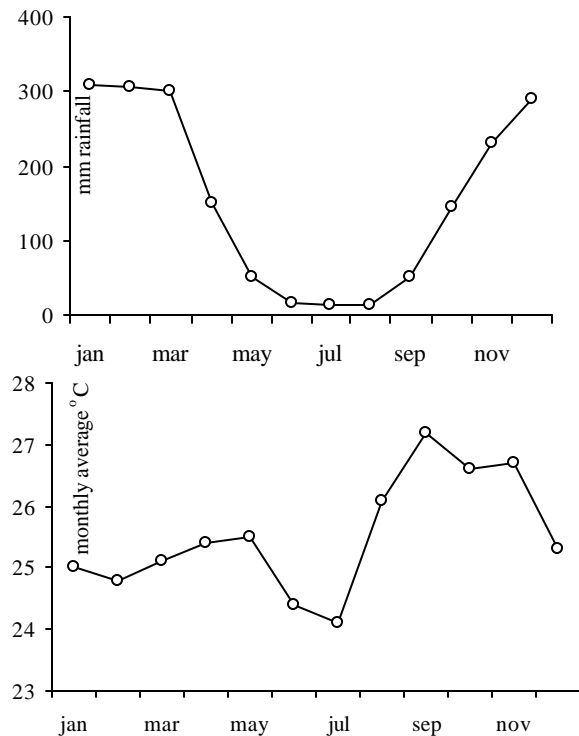
### INTRODUCTION

The core area of the morphoclimatic domain of the cerrados (Ab'Saber, 1977; Pinto, 1990) is a continuous area of some 1.8 million square kilometers, of highlands of moderate altitude (300 - 900 m), with gentle, rolling topography, with a characteristically hierarchical drainage, covered by a type of vegetation traditionally called "cerrado" in Brasil, to which has frequently been applied, erroneously, I think, the name of "savanna". There is in fact a certain physiognomical resemblance, but the differences are major. Specifically, contrary to, e.g., African

savannas, cerrados have no water-saving adaptations, morphological (wax, thorns) or physiological (deciduousness, restriction of transpiration by closure of stomata). The climate (Graphs 1 and 2) is characterized by two contrasting seasons (BRASIL, 1941). Winter temperatures are cool, but equable. The monthly averages vary between 23.2° and 26.6 ° C in summer and between 21.9° and 27.1° in winter. The contrary happens to precipitation. Of a total of 1600 - 1800 mm/year, the 7 summer months contribute from 89 to 97 %, the 5 winter months 3 to 11 %. The very deep (up to 30 meters) soils store enough water to see to the demands of the

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1. Museu de Zoologia, Universidade de São Paulo.



Graphs 1 and 2. Monthly rainfall and average temperature at Porto Nacional, Tocantins (data from BRASIL, 1941).

vegetation, which does not need, as said, water-saving adaptations.

A characteristic feature of the cerrados is the presence of gallery, or ciliary, forests. The competence of rivers, their capacity of carrying materials in suspension, is a function of their velocity (Goudie, 1988). During flood, as the river overflows the banks, the current, by friction, loses speed and thus competence, and the heavier sediments are dropped. In this way is gradually built a longitudinal ridge, a *levee*, of coarse, sandy, well-aerated sediments, backed by a wider or narrower low, seasonally flooded area, the *backswamp* (in Brasil, *varjão*) where the finer silt is deposited, originating compact, poorly aerated soils. The gallery forests start at headwaters along creeks as rows of tall columnar burití palms (*Mauritia*), who like to keep their feet wet, but as soon as a levee appears, the proper gallery forest is established (Rodrigues & Leitão-Filho, 2000). The term “gallery forest” is sometimes

loosely applied to any forest in a riparian position, but the proper sense of the term is strictly the forest on the levees of cerrado rivers.

The large Central Brazilian rivers run to the Amazon, and so the gallery forests of the fluvial system form a dendritic pattern converging towards the north. It is easy to understand that, if there is a fauna adapted and limited to ciliary forests (Alho, 1990; Hanski, 1999), the latter will function not only as areas of residence, but also, and very importantly, as faunal corridors, whose interruption may have drastic consequences to the fauna. The same reasoning can be applied to the backswamps. These two formations are unavoidable victims of dam building; it is thus essential that they be considered in any impact assessment. This is the problem I addressed in this work.

## Design

In order to test the faunal roles of gallery forest and backswamp, as well as, additionally, the importance of microhabitats and of the interactions between habitats, three areas were sampled: Area A (Fig. 1), on the left bank of the Rio Tocantins, directly across the city of Ipueiras, at approximately 11° 14' S, 48° 28' W. There was good, tall (15 m), dense gallery forest, backed by an extensive backswamp, grading rapidly into poor, battered cerrado.

Area B (Fig. 2), on the right bank of the Rio Manoel Alves Pequeno (or “da Natividade”), a tributary of the Tocantins on its right bank, close to the mouth, some 9 km SSE of Area A, at ca. 1119, 4827. The levee was high, but the ridge narrow and the forest sparse, rapidly passing into rather well-preserved cerrado.

Area C (Fig. 2), control, in a well-preserved patch of interfluvial cerrado between the rivers Tocantins and Manoel Alves. at ca. 1117, 4827, with three strata of vegetation, grass, shrubs and scattered trees.



Figure 1. Rio Tocantins, sampling area A.



Figure 2. Confluence of Rios Manoel Alves and Tocantins, sampling areas B and C.

We used pitfall traps, consisting of 20 liter buckets, diameter at the mouth 30 cm, buried flush with the ground, 4 meters apart, connected by 40 cm tall drift fences of black plastic sheet.

In Area A we placed 25 buckets inside the gallery forest, parallel to the river, and 45 buckets on a perpendicular row crossing the backswamp. They stayed in place for 8 days (April 23 - 30). In Area B we used a similar design, with 25 buckets on the levee and 43 inland. They stayed in place for 7 days (April 24 - 30). In Area C we arranged a grid of 5 x 8 buckets, which stayed in place for 6 days (April 25 - 30).

The traps were visited twice daily, in the morning and in the afternoon. The Appendix lists the materials collected, bucket by bucket and day by day.

### Statistics

I used throughout the  $\chi^2$  test, which is non-parametric and allows to locate the excesses and deficiencies of frequencies. The notations are:

- gl degrees of freedom
- ns not significant at the 5% level
- \* significant at the 5% level
- \*\* significant at the 1% level
- \*\*\* significant at the 0.1% level

### Species present

#### Anura

#### Leptodactylidae

- Adenomera martinezi* (Bokermann, 1956)
- Barycholos ternetzi* (Miranda-Ribeiro, 1937)
- Leptodactylus mystaceus* (Spix, 1824)
- Leptodactylus podicipinus* (Cope, 1862)
- Physalaemus cuvieri* Fitzinger, 1826
- Pseudopaludicola mystacalis* (Cope, 1887)

#### Microhylidae

- Chiasmocleis centralis* Bokermann, 1952
- Elachistocleis ovalis* (Schneider, 1799)

#### Sauria

#### Gekkonidae

- Gymnodactylus amarali* Barbour, 1925

#### Gymnophthalmidae

- Colobosaura modesta* (Reinhardt & Luetken, 1862)
- Micrablepharus maximiliani* (Reinhardt & Luetken, 1862)

#### Polychridae

- Anolis chrysolepis brasiliensis* Vanzolini & Williams, 1970

#### Tropiduridae

- Tropidurus oreadicus* Rodrigues, 1987
- Tropidurus torquatus* (Wied, 1820)

#### Amphisbaenia

#### Amphisbaenidae

- Bronia* sp in description by Carolina Castro-Mello, 2003

#### Serpentes

#### Colubridae

- Apostolepis cf. cearensis* Gomes, 1915

## Analysis

### Homogeneity of the areas (Table 1)

The three areas sampled, two of them riparian, differing in topography and vegetation, and one inland, differ significantly in the proportion of frogs and lizards (the only species of snake collected was not included in the analysis). As could be expected, the cerrado (Area C) is poorer in amphibians, both in number of species and of individuals ( $\chi^2=42.930$  \*\*\*, gl 2). Otherwise they do not differ significantly in the composition of the frog fauna ( $\chi^2=11.945$  ns, gl 14), but differ regarding the lizards ( $\chi^2=54.734$  \*\*\*, gl 14). The difference resides mainly in the preference of *Tropidurus torquatus* for the backswamp and of *Gymnodactylus amarali* for the cerrado.

Table 1. Herpetofauna of the study areas.

	Area			Sum
	A	B	C	
Anura				
<i>Adenomera martinezi</i>	5	-	-	5
<i>Barycholos ternetzi</i>	14	6	-	20
<i>Leptodactylus mystaceus</i>	1	-	-	1
<i>Leptodactylus podicipinus</i>	5	4	-	9
<i>Physalaemus cuvieri</i>	48	22	2	72
<i>Pseudopaludicola mystacalis</i>	14	2	-	16
<i>Chiasmocleis centralis</i>	10	-	-	10
<i>Elachistocleis ovalis</i>	2	1	-	3
Sum	99	35	2	136
Sauria				
<i>Gymnodactylus amarali</i>	1	-	4	5
<i>Anolis chrysolepis brasiliensis</i>	1	1	-	2
<i>Tropidurus oreadicus</i>	-	9	3	12
<i>Tropidurus torquatus</i>	14	1	-	15
<i>Micrablepharus maximiliani</i>	-	4	-	4
<i>Ameiva ameiva</i>	11	4	1	16
<i>Cnemidophorus</i> cf. <i>ocellifer</i>	-	-	1	1
Sum	27	19	9	55

### The gallery forest and the backswamp (Tables 2 and 3)

Areas A and B permit an investigation of the faunistic personality of the segments of the

Table 2. Distance from the levee, area A.

	Buckets			Sum
	1-25	26-50	51-70	
Anura				
<i>Adenomera martinezi</i>	-	-	5	5
<i>Barycholos ternetzi</i>	5	5	4	14
<i>Leptodactylus mystaceus</i>	-	-	1	1
<i>Leptodactylus podicipinus</i>	-	2	3	5
<i>Physalaemus cuvieri</i>	22	8	17	47
<i>Pseudopaludicola mystacalis</i>	3	2	10	15
<i>Chiasmocleis centralis</i>	-	8	2	10
<i>Elachistocleis ovalis</i>	1	1	-	2
Sum	31	26	42	99
Sauria				
<i>Gymnodactylus amarali</i>	-	-	1	1
<i>Anolis chrysolepis brasiliensis</i>	-	-	1	1
<i>Tropidurus torquatus</i>	4	2	7	13
<i>Ameiva ameiva</i>	8	-	3	11
Sum	12	2	13	27

landscape. To do so, we assembled the buckets according to their distance from the top of the levee. In Area A we established 3 groups: buckets 1-25, inside the gallery forest, buckets 26 - 50 in the next 100 meters inland; and buckets 51 - 70 in the backswamp. In Area B we contrasted the forest (buckets 1 - 25) with the adjoining cerrado (buckets 26 - 68). Frogs and lizards were analyzed separately.

The distribution of frogs in Area A is heterogeneous ( $\chi^2=37.652$  \*\*\*, gl 14): *Physalaemus cuvieri*, although occurring all over, prefers the proximity of the river; *Chiasmocleis centralis* favors the backswamp. The lizards of Area A showed no preferences ( $\chi^2=6.948$  ns, gl 4).

In Area B the data, acknowledgedly scarce, showed no heterogeneity.

### Comments

This study was undertaken at a not particularly favorable time of the year, past the reproductive season of the frogs and well into the dry season; not many specimens were collected,



Table 3. Area B, distance from the levee.

	Buckets		Sum
	1-25	26-68	
Anura			
<i>Barycholos ternetzi</i>	4	2	6
<i>Leptodactylus podicipinus</i>	2	2	4
<i>Physalaemus cuvieri</i>	6	16	22
<i>Pseudopaludicola mystacalis</i>	-	2	2
<i>Elachistocleis ovalis</i>	-	1	1
Sum	12	23	35
Sauria			
<i>Anolis chrysolepis brasiliensis</i>	-	1	1
<i>Tropidurus oreadicus</i>	6	3	9
<i>Tropidurus torquatus</i>	-	1	1
<i>Ameiva ameiva</i>	4	-	4
Sum	10	5	15

notably only one snake. The design, however, permits some conclusions.

As to the major aims of the study, the gallery forest was not found, for the fauna sampled, to harbor a characteristic ensemble. I think this conclusion, at present valid for the time of the year and for the intensity of the sampling effort, will stand with regard to the terricolous element of the fauna: this will suffer no harm from the damming of rivers. On the contrary, even these limited data ascribe to the backswamp an important faunistic role, with corresponding conservation implications. I think it is indispensable to undertake a study similar to the present one on the shores of stabilized reservoirs, to verify whether these shores are the analogues of riverine backswamps.

Besides these conservationist considerations, there are some interesting ecological facts. The diversity in microhabitat preferences among widespread cerrado animals seems very promising. I am thinking especially of the differences between

*Tropidurus torquatus* and *T. oreadicus*, two of the commonest cerrado lizards. The decided preference of *Gymnodactylus amarali* for interfluvial cerrado is also noteworthy, as are the fine-grained discrepancies among frog species.

## ACKNOWLEDGMENTS

This research was undertaken during studies of viability of large hydroelectric dams by Themag Engenharia e Gerenciamento, on behalf of REDE Empresas de Energia Elétrica. I thank them. C.W. Myers, and especially W. R. Heyer, contributed cogent and welcome criticisms. Celso Morato de Carvalho and Carolina Castro-Mello did the field work and identified the majority of specimens.

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## Appendix. Raw data.

Bucket	Day/hr *	Species	Bucket	Day/hr *	Species
A1	24 M	<i>Physalaemus cuvieri</i>	A 20	23 M	<i>Ameiva ameiva</i>
A 2	23 T	<i>Tropidurus torquatus</i>		25 T	<i>Tropidurus torquatus</i>
	24 M	<i>Physalaemus cuvieri</i>		26 T	<i>Ameiva ameiva</i>
		<i>Barycholos ternetzi</i>	A 21	23 T	<i>Ameiva ameiva</i>
A 3	24 M	<i>Barycholos ternetzii</i>		24 M	<i>Physalaemus cuvieri</i>
	24 T	<i>Physalaemus cuvieri</i>		25 M	<i>Barycholos ternetzii</i>
	25 M	<i>Apostolepis cf. cearensis</i>	A 22	23 T	<i>Ameiva ameiva</i>
A 4	25 M	<i>Physalaemus cuvieri</i>		24 T	<i>Ameiva ameiva</i>
A 5	25 M	<i>Barycholos savagei</i>		25 M	<i>Physalaemus cuvieri</i>
		<i>Physalaemus cuvieri</i>			<i>Pseudopaludicola mystacalis</i>
A 6	24 M	<i>Physalaemus cuvieri</i>		28 T	<i>Ameiva ameiva</i>
A 7	23 T	<i>Tropidurus torquatus</i>	A 23	23 M	<i>Ameiva ameiva</i> 2
	25 M	<i>Physalaemus cuvieri</i>		25 M	<i>Physalaemus cuvieri</i>
		<i>Pseudopaludicola mystacalis</i>			<i>Barycholos ternetzii</i>
A 8	24 M	<i>Physalaemus cuvieri</i> 3			<i>Pseudopaludicola mystacalis</i>
	25 M	<i>Physalaemus cuvieri</i>	A 25	24 M	<i>Physalaemus cuvieri</i>
A 9	25 M	<i>Physalaemus cuvieri</i>	A 26	24 M	<i>Barycholos ternetzi</i>
A 10	24 M	<i>Physalaemus cuvieri</i>	A 28	24 M	<i>Physalaemus cuvieri</i>
A 11	25 M	<i>Elachistocleis ovalis</i>	A 29	24 T	<i>Tropidurus torquatus</i>
A 12	24 M	<i>Physalaemus cuvieri</i>	A 30	24 M	<i>Chiasmocleis centralis</i>
	25 M	<i>Physalaemus cuvieri</i>		25 M	<i>Leptodactylus podicipinus</i>
A 15	24 M	<i>Physalaemus cuvieri</i>	A 33	23 M	<i>Barycholos ternetzii</i>
	28 T	<i>Tropidurus torquatus</i>		24 M	<i>Pseudopaludicola mystacalis</i>
A 16	24 M	<i>Physalaemus cuvieri</i>	A 35	25 M	<i>Barycholos ternetzi</i>
A 18	25 M	<i>Physalaemus cuvieri</i>	A 36	25 T	<i>Tropidurus torquatus</i>
				29 M	<i>Leptodactylus podicipinus</i>
A 38	24 M	<i>Chiasmocleis centralis</i> 2	A 56	25 M	<i>Pseudopaludicola mystacalis</i>
A 39	24 M	<i>Chiasmocleis centralis</i>	A 57	24 M	<i>Adenomera martinezi</i>
	25 M	<i>Physalaemus cuvieri</i>			<i>Pseudopaludicola mystacalis</i>
A 40	24 M	<i>Chiasmocleis centralis</i>		25 M	<i>Physalaemus cuvieri</i> 2
	25 M	<i>Barycholos ternetzi</i>	A 58	26 T	<i>Anolis chrysolepis brasiliensis</i>
		<i>Pseudopaludicola mystacalis</i>		28 M	<i>Colobosaura modesta</i>
		<i>Physalaemus cuvieri</i>	A 59	24 M	<i>Ameiva ameiva</i>

Continued

Bucket	Day/hr *	Species	Bucket	Day/hr *	Species
A 43	24 M	<i>Physalaemus cuvieri</i> 2		25 M	<i>Chiasmocleis centralis</i>
		<i>Barycholos ternetzi</i>		26 M	<i>Leptodactylus podicipinus</i>
	25 M	<i>Physalaemus cuvieri</i>	A 60	23 T	<i>Tropidurus torquatus</i>
A 44	24 M	<i>Elachistocleis ovalis</i>		24 M	<i>Physalaemus cuvieri</i>
		<i>Chiasmocleis centralis</i>		27 M	<i>Leptodactylus podicipinus</i>
A 45	24 M	<i>Chiasmocleis centralis</i>	A 61	24 M	<i>Physalaemus cuvieri</i>
A 47	24 M	<i>Chiasmocleis centralis</i>		24 T	<i>Physalaemus cuvieri</i>
A 50	24 M	<i>Physalaemus cuvieri</i>			<i>Ameiva ameiva</i>
	25 M	<i>Physalaemus cuvieri</i>		25 M	<i>Physalaemus cuvieri</i> 2
A 51	27 M	<i>Leptodactylus mystaceus</i>		27 M	<i>Pseudopaludicola mystacalis</i>
A 55	24 M	<i>Physalaemus cuvieri</i>	A 62	24 M	<i>Adenomera martinezi</i>
	25 M	<i>Physalaemus cuvieri</i> 2		25 M	<i>Adenomera martinezi</i>
		<i>Adenomera martinezi</i>			<i>Barycholos ternetzi</i>
	26 T	<i>Tropidurus torquatus</i>	A 63	24 M	<i>Physalaemus cuvieri</i>
A 56	24 M	<i>Physalaemus cuvieri</i>		24 T	<i>Tropidurus torquatus</i>
	25 M	<i>Physalaemus cuvieri</i> 2	A 64	24 T	<i>Tropidurus torquatus</i>
A 64	25 M	<i>Physalaemus cuvieri</i>	B 5	25 M	<i>Physalaemus cuvieri</i>
		<i>Barycholos ternetzi</i>		25 T	<i>Ameiva ameiva</i>
		<i>Tropidurus torquatus</i>	B 6	25 M	<i>Physalaemus cuvieri</i>
A 65	24 M	<i>Physalaemus cuvieri</i>			<i>Barycholos ternetzi</i>
	27 M	<i>Pseudopaludicola mystacalis</i> 2	B 7	25 M	<i>Physalaemus cuvieri</i>
	29 M	<i>Gymnodactylus amarali</i>			<i>Barycholos ternetzi</i>
A 66	23 T	<i>Tropidurus torquatus</i>	B 8	26 M	<i>Physalaemus cuvieri</i>
	25 M	<i>Barycholos ternetzi</i>	B 10	25 M	<i>Tropidurus oreadicus</i>
	26 M	<i>Leptodactylus podicipinus</i>	B 13	26 T	<i>Ameiva ameiva</i>
	27 M	<i>Adenomera martinezi</i>	B 14	26 T	<i>Tropidurus oreadicus</i>
		<i>Pseudopaludicola mystacalis</i> 2	B 15	26 M	<i>Barycholos ternetzi</i>
A 67	25 M	<i>Physalaemus cuvieri</i>	B 21	27 M	<i>Leptodactylus podicipinus</i>
		<i>Pseudopaludicola mystacalis</i>		30 M	<i>Tropidurus oreadicus</i>
A 68	24 T	<i>Tropidurus torquatus</i>	B 22	25 T	<i>Tropidurus oreadicus</i>
	25 M	<i>Barycholos ternetzi</i>	B 23	27 M	<i>Micrablepharus maximiliani</i> 2
	25 T	<i>Ameiva ameiva</i>	B 24	30 M	<i>Ameiva ameiva</i>

## Continued

Bucket	Day/hr *	Species	Bucket	Day/hr *	Species
A 69	24 T	<i>Physalaemus cuvieri</i>	B 25	26 M	<i>Barycholos ternetzi</i>
	26 T	<i>Tropidurus torquatus</i>		26 T	<i>Tropidurus oreadicus</i>
A 70	24 M	<i>Chiasmocleis centralis</i>	B 34	25 M	<i>Physalaemus cuvieri</i>
		<i>Pseudopaludicola mystacalis</i>	B 36	26 T	<i>Micrablepharus maximiliani</i>
			B 37	27 M	<i>Elachistocleis ovalis</i>
B 1	25 T	<i>Tropidurus oreadicus</i>		28 T	<i>Tropidurus oreadicus</i>
B 2	25 M	<i>Physalaemus cuvieri</i> 2	B 40	25 M	<i>Pseudopaludicola mystacalis</i>
B 3	27 M	<i>Leptodactylus podicipinus</i>	B 43	25 M	<i>Barycholos ternetzi</i>
B 4	25 T	<i>Ameiva ameiva</i>	B 44	25 M	<i>Physalaemus cuvieri</i>
B 48	25 M	<i>Physalemus cuvieri</i>	B 66	25 T	<i>Physalemus cuvieri</i>
	25 T	<i>Pseudopaludicola sp.</i>		26 M	<i>Physalemus cuvieri</i>
B 50	25 M	<i>Barycholos ternetzi</i>	B 67	26 M	<i>Physalemus cuvieri</i>
	27 M	<i>Leptodactylus podicipinus</i>		28 T	<i>Tropidurus oreadicus</i>
B 52	26 T	<i>Tropidurus oreadicus</i>			<i>Micranblepharus maximiliani</i>
B 54	25 M	<i>Physalemus cuvieri</i>			
B 55	25 M	<i>Physalemus cuvieri</i>	C 12	26 T	<i>Tropidurus oreadicus</i>
B 56	26 T	<i>Physalemus cuvieri</i>	C 19	26 M	<i>Physalemus cuvieri</i>
B 57	25 M	<i>Physalemus cuvieri</i>	C 20	26 M	<i>Gymnodactylus amarali</i> 2
B 58	25 M	<i>Physalemus cuvieri</i> 2	C 21	26 M	<i>Ameiva ameiva</i>
	26 M	<i>Physalemus cuvieri</i>	C 23	26 M	<i>Physalemus cuvieri</i>
B 59	26 M	<i>Physalemus cuvieri</i> 2		27 M	<i>Tropidurus oreadicus</i>
B 62	28 T	<i>Anolis chrysolepis brasiliensis</i>	C 25	29 M	<i>Tropidurus oreadicus</i>
B 63	26 M	<i>Physalemus cuvieri</i>	C 27	26 M	<i>Gymnodactylus amarali</i>
		<i>Leptodactylus podicipinus</i>	C 31	30 M	<i>Cnemidophorus cf. ocellifer</i>
B 64	30 M	<i>Tropidurus torquatus</i>	C 36	29 M	<i>Gymnodactylus amarali</i>

\* - Days of April, 2002. M, morning; T, afternoon.

# ***BIOLOGIA GERAL E EXPERIMENTAL***

## **On the eggs of Brazilian *Podocnemis* (Testudines, Podocnemididae)**

**P.E.Vanzolini**



**UNIVERSIDADE FEDERAL DE SERGIPE**

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## On the eggs of Brazilian *Podocnemis* (Testudines, Podocnemididae)

P. E. Vanzolini

## INTRODUCTION

Four species of *Podocnemis* occur in the rivers and lakes of Brazilian Amazonia: *P. erythrocephala* (Spix, 1824), *P. expansa* (Schweigger, 1812), *P. sextuberculata* Cornalia, 1849, and *P. unifilis* Troschel, 1848. There are two extra-limital species of the genus, *P. lewyana* A. Duméril, 1852, which occurs principally in the valley of Magdalena in Colombia, and *P. vogli* Müller, 1935, in the Orinoco drainage of Venezuela. Another species of the family, *Peltocephalus dumerilianus* (Schweigger, 1812) is also widespread in Amazonia.

Among the Brazilian species, *P. erythrocephala* is limited to the Rio Negro drainage, in itself a large area; the others have exceedingly broad distributions, essentially pan-Amazonian. They are all subject to heavy human predation, as the meat is a real delicacy and the eggs regionally much appreciated.

The degree of pressure is not the same on all forms. Formerly, *P. expansa*, “tartaruga” par excellence (the most prestigious animal in Amazonia), which is very visible during reproduction, as it lays in large bands on traditional beaches, and is a large animal, magnificent as food, used to be under heavy pressure. Besides the demand for the meat, the eggs were harvested as a source of fat, especially lamp oil. It is now protected in the traditional beaches, and the pressure has been relieved.

*P. unifilis*, “tracajá” is the second in size and esteem. The meat is very good and the eggs are eagerly sought, being widely credited with aphrodisiac virtues. Tracajá is not hard to catch with appropriate gear, but are protected during reproduction by laying individually on any type of ground, and thus frequently passing unnoticed. The nests are reasonably well disguised; trained dogs and horses are used to look for them.

*P. sextuberculata*, “pitiú” or “iaçá” (Vanzolini & Gomes, 1979), and *P. erythrocephala*, “irapuça” (Mittermeier & Wilson, 1974), are small species, that lay in small groups on sand beaches of any description. They do not get special attention, but, on being stumbled upon, are not spared.

*P. dumerilianus* (“cabeçudo”), is the least frequent species and a secretive breeder, which lays individually in leaf litter and rotten wood. It is not particularly persecuted. I have never been able to obtain a clutch.

The Brazilian government has been in recent years making a genuine effort to protect the fauna in general, and especially those species whose preservation results in improved living conditions for local populations, including the persistence of traditional ways of life — in the case the use of turtles as a food supply of extended cultural significance. To these efforts at conservation I feel a certain lack of basic scientific information. It has long been the practice of this Museum in field excursions to supplement materials important to systematics (our primary business) with materials and data relevant to ecology, and especially to conservation. We have assembled some amount of information on turtles, and here I present data, thus far not available, on egg shape and volume in *Podocnemis*.

## MATERIALS

I have used in this work 17 samples with a total 248 eggs, all catalogued in our collection. With the exception of a sample of *unifilis* eggs, mentioned below, all were collected by Museum field parties; the circumstances of collection were routinely recorded in the field, and are usually available, of course at different levels of detail and clarity.

In the context of the present investigation, i.e. shape and volume of eggs, two aspects are all-important: (i) have the eggs reached definitive size and shape and (ii) are they traceable to single clutches or to (commercial) pools of eggs. The latter are common in Amazonia, especially in the case of *P. unifilis*.

The samples used in the present work are:

*P. erythrocephala*. Two sets of 8 eggs each (MZUSP 2886, 2887) obtained by autopsy, at the Rio Cuieiras, which enters the Rio Negro from the left (east) some 60 km upriver from Manaus; collected on October 26-27, 1973. No further details in the field notes.

*P. expansa*. Three samples (MZUSP 2870, 2871 and 2893, respectively 5, 4 and 6 eggs). The first two



samples were collected by myself on the well-known Taboleiro Leonardo, Rio Trombetas. This seasonal beach was brought into the literature by myself (Vanzolini, 1967); it is a traditional laying site, now very efficiently protected by the government. *P. expansa* and *P. unifilis* abound there and *P. sextuberculata* is not hard to find. My specimens were collected on October 8 and 9, 1965. The third sample, from the same locality, is not accompanied by field notes. (This sample was eventually proved not to belong to *P. expansa*, as will be discussed below).

The eggs I obtained at the Taboleiro had already been laid and buried but had been dug out by other females nesting in the same sites. The eggs of each sample were close together, and I do not doubt that they belonged to single clutches. Of course, having been laid, they were mature.

*P. sextuberculata*. I have 5 samples of this little-known species: MZUSP 2872 (6 eggs) from autopsy of a female at Taboleiro Leonardo; MZUSP 2875 (18) and 2888 (30) from the Rio Solimões near the mouth of the Rio Juruá; 2878 (16) from Jacaré, a village on the left bank of the Rio Solimões; 12884 (12), from Lake Miua, also on the Solimões. These Solimões samples are not accompanied by field notes, but it is certain that they were bought from egg pools - collected from nests and thus mature.

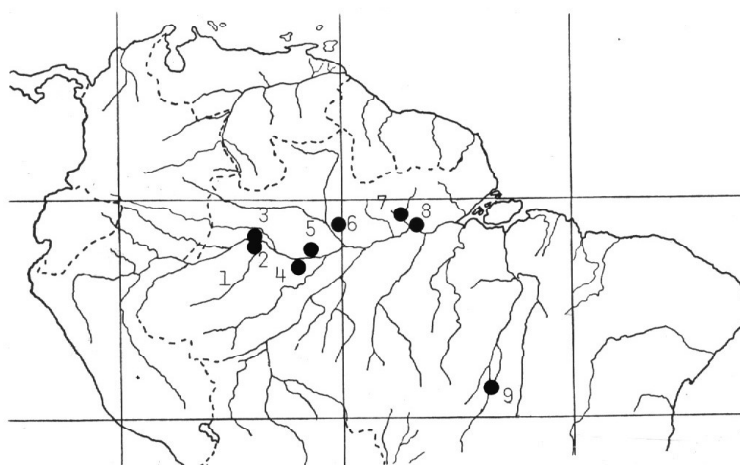
*P. unifilis*. There were 6 samples in the collection, all bought from pools offered for sale: MZUSP 2880 (18 eggs) and 2881 (6) from Coari, on the right bank of

the Rio Solimões; 2890 (36) from Fonteboa, also on the right bank of the Solimões; 2874 (10), Taboleiro Leonardo, Rio Trombetas; 2891 (13) and 2892 (19), from Oriximiná, near the mouth of the Trombetas.

Thus with the exception of the eggs of *P. erythrocephala*, I am fairly secure that all our samples are constituted by mature eggs, having reached full size and shape. It may be added that all *P. unifilis* eggs have a perfect calcareous shell.

Well after this work was started I realized that direct measurement of the volume of at least some eggs was indispensable to constrain the results of geometrical methods. The few apparatus described in the literature for the direct measurement of turtle egg volume are difficult to build and to operate. I decided to measure volumes by filling empty egg shells with water and weighing them before and after (I thank Isaías Raw for the suggestion). The only species of *Podocnemis* amenable to this treatment is *P. unifilis*, the only one with a calcareous shell. I applied to IBAMA, the Brazilian fish and wildlife agency, for fresh eggs, and was promptly supplied with 23 eggs (MZUSP 4014) from Praia do Ari, Rio Araguaia.

*Comment.* I find it important to stress that this is an opportunistic investigation, not a properly designed one. There is justification, though. Some ground has been broken, and a first frame of reference is available



Map 1. 1, Rio Juruá (mouth at 02° 37' S, 65° 50' W). 2, Fonteboa (0232, 6602). 3, Jacaré (0224, 6608). 4, Coari (0406, 6309). 5, Lago Miua (0346, 6213). 6, Rio Cuieiras (mouth at 0250, 6030). 7, Taboleiro Leonardo (0120, 5645). 8, Oriximiná (0146, 5551). 9, Praia do Ari (1255, 5031).

for further research, by necessity logistically difficult: vast areas and precise seasons are involved. Progress has been made in some methodological aspects, especially in the estimation of egg volume. Goes without saying that this type of work is very rewarding to the professional systematist, always preoccupied with his unrequitable indebtedness to the fauna, and with the hard relationships between collecting and conserving.

### METHODS

The eggs of freshwater turtles vary around the shape of an ellipsoid of revolution, characterized by one major ("length") and one minor ("width") orthogonal diameters. How much individual eggs differ from an ellipsoid with the same diameters is estimated through a dimensionless parameter first proposed by Preston (1953) as the "bicone" of bird eggs, and later applied, very didactically, by Maritz & Douglas (1994) to reptilian eggs.

In the present work the direct measurement of volume was done as follows: (i) the egg was blown empty, washed and dried; (ii) one of the holes bored to empty the egg was plugged with plasticine, and the egg weighed in a Pesola dynamometer; (iii) it was next filled with tap water and weighed again. The difference in grams between the two weights was taken as the volume of the egg in cubic centimeters.

As to the indirect (geometrical) estimates of egg volume, the procedure, following Maritz & Douglas (1994) was:

1. The eggs were photographed next to a scale (Plate 1), the photographs enlarged a little over twice and xerox copies made of the enlargements. On the xerox copies were measured: (i) the major (L) and (ii) the minor (W) diameters, and (iii) the length of a secant (D) inclined  $30^\circ$  over the major diameter and passing through the interception of the diameters.

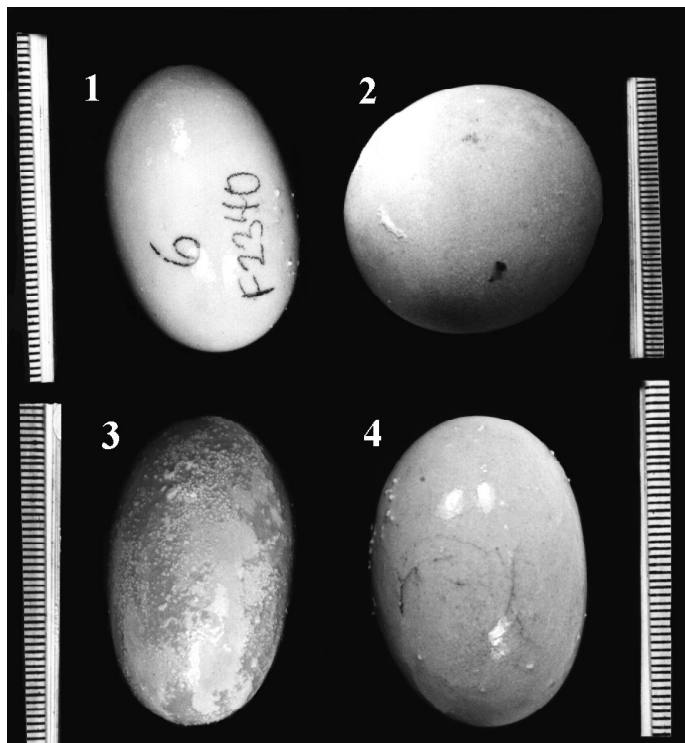


Plate 1. *Podocnemis* eggs.

1. *P. erythrocephala* 2886 (egg 6), Rio Cuieiras. L: 40 mm; W: 24; D: 33; c (bicone): -0.034; e (excentricity): 3.58; V (2): 12 cm<sup>3</sup>.
2. *P. expansa* 2870 (1), Taboleiro Leonardo. L: 44 mm; W: 43; D: 43; c: -0.086; e: 0.99; V (2): 43 cm<sup>3</sup>.
3. *P. sextuberculata* 2875 (16), Boca do Juruá. L: 42 mm; W: 24; D: 36; c: 0.217; e: 3.76; V (2): 13 cm<sup>3</sup>.
4. *P. unifilis* 2890 (31), Fonteboa. L: 38 mm; W: 27; D: 35; c: 0.117; e: 3.07; V (2): 15 cm<sup>3</sup>.

As will be discussed below, I tested the congruence of the measurements on photos by measuring the same eggs with calipers, in replicate. No differences were found, and so in what follows only the photo measurements are used, since this introduced no bias and especially since there is no direct way of measuring the secant.

2. The three measures (L, W and D) were applied to Maritz & Douglas's formulas for the bicone  $c$  and the volume  $V(1)$  of the eggs:

$$c = \frac{4L^2}{3D^2} * \left( \frac{LD}{W * SQR(4L^2 - 3D^2)} - 1 \right)$$

$$V(1) = \pi / 6000 * \left( \frac{3c^2 + 14c + 35}{35} \right) * LW^2$$

The measurements are taken in millimeters and the resulting volumes in cubic centimeters.

3. Finally, the excentricity and volume were estimated by the formula for the ellipsoid of revolution.

$$e = (SQR(a^2 - b^2)) / a$$

where  $a = L/2$  and  $b = W/2$ ,

$$V(2) = \pi / 6000 * LW^2$$

The units are the same as before.

#### Statistical methods

Only very simple statistical methods were used, following Dixon & Massey (1983), Zar (1999), Vanzolini (1993) and Siegel (1956, 1975).

In the text and tables the following conventions are followed:

N, specimens in sample

R, range of the variable

m, mean  $\pm$  its standard deviation

s, sample standard deviation

V, coefficient of variation

V (d), volume directly measured

V (1), volume estimated by the bicone

V (2), volume estimated by the ellipsoid

Levels of significance are indicated as

*	significant at the 5% level,
**	at the 1%,
***	at the 0.1%,
ns	not significant at the 5% level.

In the tables of Tukey's test, vertical lines to the left of the table encompass samples that do not differ at the 5% level.

#### Podocnemis unifilis

Of this species we have 7 samples, spanning some 1,100 km of Amazon; to it belongs the sample whose volumes were directly measured. Analysis of the tracajá data, especially in what concerns matters of method, may well serve as background to the other species.

#### MZUSP 4014

We start with the questions directly related to measurement. Sample 4014 comprises 23 eggs, of which all measurements could be reliably taken. Besides being measured on the photograph, each egg was submitted to two replicate measurements with calipers. Analysis of variance reveals ( $F = 0.103$  ns) that, in the case of the major diameter (L), the mean of the photographic measurement (45.9 mm) does not differ significantly from those of the caliper replicates (46.1 and 46.2 mm). The data for the minor diameter (W) also closely agree. I thus consider valid the measurements taken on xerox copies of photographs.

The means of the 3 estimates of the volume (Tables 1 and 2) closely agree among themselves; in the analysis of variance  $F = 1.207$  ns.

This, however, refers to averages, not to indivi-

dual measurements. These must be addressed by regression analysis, egg by egg, taking as independent variables the two geometrical estimates and as dependent variable, to be predicted, the direct measurement. In neither case was the regression significant: in the estimate by the bicone  $F = 0.050$  ns, in that by the ellipsoid  $F = 0.129$  ns.

Complementarily, it must be noted that the mean of the bicone for this sample,  $0.033 \pm 0.0371$ , does not differ significantly from zero. This confirms the applicability of the ellipsoid formula, which is simple and depends on only two measurements easily taken and current in the literature. I rather like this conclusion.

Table 1. Sample 4014, *P.unifilis*. V(d), volume determined directly. V(1), by means of the bicone. V(2), by the ellipsoid.

Egg	V(d)	V(1)	V(2)
1	22	20	19
2	22	19	22
3	22	18	20
5	22	22	22
8	19	20	19
9	21	22	21
10	20	23	23
11	21	22	23
12	21	21	21
13	20	23	21
14	22	22	22
15	22	21	20
16	22	22	21
17	21	22	22
18	22	20	21
19	23	22	22
20	23	22	21
21	23	21	21
23	23	21	20

Table 2. Sample 4014, *P. unifilis*, estimates of egg volume.

Method	N	R	m	s	V
V(d)	19	19-23	$21.7 \pm 0.25$	1.1	5.1
V(1)	19	18-23	$21.1 \pm 0.31$	1.3	6.3
V(2)	19	19-24	$21.1 \pm 0.28$	1.2	5.8

Another way of arguing for the equivalence of the two geometrical methods of estimating the volume of *P. unifilis* eggs consists in regressing the two estimates for a number of samples. In the case of the 7 *unifilis* samples at hand, the coefficient of regression  $b = 1.051 \pm 0.0362$ , not significantly different from 1, and the intercept  $a = -1.144 \pm 1.2283$ , not significantly different from zero; that is to say, to convert one estimate into the other, multiply by one and add nothing. The relationship is practically perfect: the coefficient of determination  $r^2 = 0.9941$ .

*Volume.* Table 3 shows the statistics of the distributions of frequencies of egg volume, V (2), of the 7 samples of *P. unifilis*. Analysis of variance affords  $F = 41.730$  \*\*\*, which leads to Tukey's test - its results are shown on Table 4. It becomes clear that it is not possible to adopt an average or a modal value of egg volume for the species. Even a geographical common denominator is not possible: the two Coarí samples differ significantly.

As a matter of caution I repeated the analysis for egg volume as determined by the bicone, V (1) (this was done for all species); the results were always in exact agreement, in all details.

Table 3. *P. unifilis*, statistics of the distributions of frequencies of V(2).

Sample	N	R	m	s	V
4014 Araguaia	23	19 - 24	$21.3 \pm 0.25$	1.2	5.6
2874 Leonardo	10	15 - 19	$16.1 \pm 0.44$	1.4	8.7
2891 Oriximiná	13	14 - 18	$14.9 \pm 0.30$	1.1	7.1
2892 Oriximiná	19	15 - 19	$16.4 \pm 0.27$	1.2	7.2
2880 Coarí	18	14 - 21	$15.9 \pm 0.35$	1.5	9.3
2881 Coarí	6	10 - 12	$11.7 \pm 0.32$	0.7	6.3
2890 Fonteboa	35	10 - 20	$14.9 \pm 0.38$	2.3	15.1

Table 4. *P. unifilis*, V(2), Tukey's test.

Sample	m	N
2881 Coarí	11.7	6
2891 Oriximiná	14.9	13
2890 Fonteboa	14.9	35
2880 Coarí	15.9	18
2874 Leonardo	16.1	10
2892 Oriximiná	16.4	19
4014 Araguaia	21.3	23

*Parameters of shape.* The statistics concerning the bicone are shown on Table 5. Although some values of the bicone differ significantly from zero, while others do not, analysis of variance showed homogeneity of the samples ( $F = 1.877$  ns); it was thus possible to compute the last row of Table 5, with average values of all samples. Thus, although the values of the volume of *P. unifilis* eggs vary widely between and within localities, shape, in what concerns departure from the ellipsoid, is constant over all.

The excentricity of the generating ellipsis is

analyzed in Tables 6 and 7. Analysis of variance shows heterogeneity ( $F = 19.380$  \*\*\*), and Tukey's test shows a situation less simple than that for the bicone. Three groups can be discerned: (i) Leonardo, (ii) Araguaia and (iii) the remainder. The fact that Araguaia is in a solitary position might have been expected: these are eggs laid in the core of the cerrados, while all others were laid in Amazonian forest. However, the fact that Leonardo differs significantly from Oriximiná, on the same river, precludes acceptance of a geographical factor in Amazonia.

Table 5. *P. unifilis*, statistics of the distributions of frequencies of the bicone.

Sample	N	R	m	t	s
2874 Leonardo	10	- 0.086 - 0.226	$0.0971 \pm 0.03659$	2.654*	0.1157
2880 Coarí	18	- 0.131 - 0.173	$- 0.0168 \pm 0.01984$	0.848 ns	0.0842
2881 Coarí	6	- 0.248 - 0.194	$0.0018 \pm 0.05920$	0.031 ns	0.1450
2890 Fonteboa	35	- 0.724 - 0.467	$0.0161 \pm 0.03000$	0.537 ns	0.1775
2891 Oriximiná	13	- 0.017 - 0.238	$0.0765 \pm 0.01812$	4.223**	0.0653
2892 Oriximiná	19	- 0.077 - 0.214	$0.0566 \pm 0.01814$	3.120**	0.0791
4014 Araguaia	23	- 0.450 - 0.241	$0.0075 \pm 0.03096$	0.149 ns	0.0234
General	124	- 0.724 - 0.467	$0.0280 \pm 0.01250$	2.319*	0.1342

Table 6. *P. unifilis*, statistics of the distributions of frequencies of the excentricity.

Sample	N	R	m	s	V
2874 Leonardo	10	3.60 - 4.11	$3.90 + 0.049$	0.16	4.0
2880 Coari	18	3.30 - 3.60	$3.42 + 0.025$	0.11	3.2
2881 Coari	6	2.93 - 3.37	$3.19 + 0.062$	0.15	4.7
2890 Fonteboa	35	1.93 - 3.59	$3.12 + 0.061$	0.36	11.5
2891 Oriximiná	13	3.19 - 3.68	$3.41 + 0.040$	0.15	4.3
2892 Oriximiná	19	3.19 - 3.60	$3.37 + 0.028$	0.15	3.6
4014 Araguaia	23	3.21 - 4.06	$3.61 + 0.053$	0.25	7.0

Table 7. *P. unifilis*, excentricity, Tukey's test.

Sample	m	N
2890 Fonteboa	3.12	35
2881 Coari	3.19	6
2892 Oriximiná	3.37	19
2891 Oriximiná	3.41	13
2880 Coari	3.42	18
4014 Araguaia	3.63	17
2874 Leonardo	3.90	10

*Comment.* The following conclusions seem reasonable:

1. The two methods (bicone and ellipsoid) of estimating volume are equivalent, in what concerns averages, and agree with direct measurement.

2. Individual (inter-sample), as against geographical variation seems to be the rule for volume and for excentricity; the bicone is homogeneous throughout the sample space.

Against this background we may place the other Brazilian species of the genus, for which we have the same measurements as for *unifilis*, except of course direct measurement of volume.

#### **Podocnemis sextuberculata**

This species ranks second in the number, 5, of available samples.

The congruence of the two methods of volume estimation was verified, as previously, both by comparison of means and by regression of V (1) on V (2). The comparisons of means yielded values of *t*

between 0.075 and 1.289, not significant at any number of degrees of freedom. The coefficient of regression was  $1.005 \pm 0.0223$ , not significantly different from 1; the intercept was  $-0.252 \pm 1.642$ , not significantly different from zero. Thus, in what follows, we'll deal again only with V (2), the volume estimated through the ellipsoid.

The data on volume are shown on Table 8. The analysis of variance indicates heterogeneity ( $F = 52.319$  \*\*\*). Tukey's test (Table 9) shows extreme variability; two samples from Boca do Juruá are in agreement, but the third sample from the same locality disagrees with them.

Turning to the shape of the eggs, there is no variability in the bicone (Table 10; analysis of variance,  $F = 0.925$  ns). Thus an over-all bicone was computed and can provisionally be used to characterize the species. With regard to the excentricity (Table 11), analysis of variance indicated heterogeneity ( $F = 13.922$ ), although the multiple comparison tests failed to identify units; no over-all excentricity was computed.

TABLE 8. *P. sextuberculata*, statistics of the distributions of frequencies of V(2).

Sample	N	R	m	s	V
2872 Leonardo	6	16 - 23	$19.2 \pm 0.89$	2.2	11.7
2884 Lago Miua	12	18 - 27	$21.9 \pm 0.65$	2.3	10.4
2875 Boca Juruá	17	11 - 14	$13.0 \pm 0.16$	0.7	5.1
2876 Boca Juruá	18	10 - 20	$13.4 \pm 0.51$	2.2	16.2

TABLE 9. *P. sextuberculata*, V(2), Tukey's test.

Sample	m	N
2872 Leonardo	19.2	6
2884 Lago Miua	21.9	12
2875 Boca Juruá	13.0	17
2876 Boca Juruá	13.4	18
2888 Boca Juruá	16.9	30

TABLE 10. *P. sextuberculata*, statistics of the distributions of frequencies of the bicone.

Sample	N	R	m	t	s
2872 Leonardo	6	- 0.074 - 0.096	- 0.140 $\pm$ 0.04447	0.315 ns	0.1089
2884 Lago Miua	12	- 0.115 - 0.092	0.0253 $\pm$ 0.02601	0.973 ns	0.0901
2875 Boca Juruá	17	-0.094 - 0.281	0.0625 $\pm$ 0.02549	2.452*	0.1051
2876 Boca Juruá	18	- 0.228 - 0.214	0.0229 $\pm$ 0.03503	0.654 ns	0.1486
2888 Boca Juruá	30	- 0.122 - 0.217	0.0626 $\pm$ 0.01712	3.657**	0.0937
2878 Jacaré	16	- 0.048 - 0.086	0.0388 $\pm$ 0.01073	3.616**	0.0411
General	99	- 0.228 - 0.281	0.0424 $\pm$ 0.01030	4.113***	0.1025

TABLE 11. *P. sextuberculata*, statistics of the distributions of frequencies of the excentricity.

Sample	N	R	m	s	V
2872 Leonardo	6	3.19 - 3.71	3.469 $\pm$ 0.0786	0.192	5.6
2884 Lago Miua	12	3.62 - 4.06	3.854 $\pm$ 0.0381	0.132	3.4
2875 Boca Juruá	17	3.39 - 3.93	3.755 $\pm$ 0.0301	0.124	3.3
2876 Boca Juruá	18	3.31 - 4.01	3.777 $\pm$ 0.0411	0.175	4.6
2888 Boca Juruá	30	3.32 - 4.06	3.668 $\pm$ 0.0343	0.188	5.1
2878 Jacaré	16	3.16 - 3.67	3.446 $\pm$ 0.0288	0.115	3.3

### **Podocnemis expansa**

Of this, the most neuralgic of Amazonian turtles, we had at the begining three samples (later reduced to two), from a single locality, Taboleiro Leonardo. It is actually a very important locality; it unfailingly receives every year a large number of breeding turtles (Padua & Alho, 1982) , which enjoy full protection. In fact, it is an ideal place to do research on *Podocnemis* reproduction, as three of the four Brazilian species are common there.

The relevant data are summarized on Table 12. It is immediately apparent that in all characters analyzed samples 2870 and 2871 tend to agree between themselves and to widely disagree with 2893. In fact, analysis of variance, followed by Tukey's test (see, for an example, Table 13) makes that very plain, and I consider sample 2893 as not belonging to *P. expansa*. That such a conclusion can be reached with sureness is to me one

the good points of this work.

Of the two other species that occur in the area, sample 2893 fits very closely *P. sextuberculata*, both in volume and in the shape parameters; although I am morally certain that there is where it belongs, I am not using the sample in the present study.

In *P. expansa* again the two estimate of the volume were congruent, judging from the means, whose differences showed values of *t* below 1. The regressions, however, gave conflicting results: for sample 2870  $b = 0.782 \pm 0.0574$  significantly different from 1. For sample 2871  $b = 1.183 \pm 0.0935$ , not significantly different from 1.

Another point to be mentioned is that the two means for the bicone did not differ significantly between themselves, but one differed significantly from zero, while the other did not. All in all, data on this all-important species are few and unsatisfactory.

TABLE 12. *P. expansa*, statistics of the distributions of frequencies of the volume and shape parameters.

Character	Sample	N	R	m	s	V
V(2)	2870	5	25 - 43	32.1 ± 2.88	6.4	20.0
	2871	4	27 - 31	28.7 ± 0.85	1.7	5.9
	2870 + 2871	9	25 - 43	30.6 ± 1.67	5.0	16.4
	"2893"	6	13 - 18	16.0 ± 0.78	1.9	12.0
bicone	2870	5	- 0.193 - 0.0702	- 0.0231 ± 0.04506 ns	0.1008	
	2871	4	-0.228 - 0.0660	0.1561 ± 0.04148 ns	0.0830	
	2870 + 2871	9	- 0.228 - 0.0702	- 0.0822 ± 0.03771 ns	0.0113	
	"2893"	6	- 0.0677 - 0.188	0.413 0 ± 0.04239***	0.1058	
excentricity	2870	5	0.494 - 1.905	1.343 ± 0.2729	0.610	45.4
	2871	4	1.444 - 2.348	1.784 ± 0.2164	0.433	24.3
	2870 + 2871	9	0.494 - 2.348	1.539 ± 0.1857	0.557	36.2
	"2893"	6	2.945 - 3.703	3.480 ± 0.1116	0.2730	7.9
V(1)	2870	5	25 - 39	31.7 ± 2.27	5.07	16.0
	2871	4	26 -31	28.1 ± 1.01	2.02	7.2
	2870 + 2871	9	25 -39	30.1 ± 1.41	4.24	14.1

TABLE 13. *Podocnemis*, Taboleiro Leonardo, V(2), Tukey's test.

Sample	m	N
<i>unifilis</i> 2874	16.1	10
" <i>expansa</i> " 2893	17.2	6
<i>sextuberculata</i> 2872	19.2	6
<i>expansa</i> 2871	28.7	4
<i>expansa</i> 2870	32.2	5

**Podocnemis erythrocephala**

Two samples, of 8 eggs each, are at hand. They are reportedly from two autopsied females; nothing else is on file.

The data are on Table 14. It is remarkable that the two samples differ significantly in volume and

excentricity but not in bicone; this does nor differ significantly from zero in either case.

The differences between two samples from the same locality, collected at the same time, must be due to different stages of maturation of the eggs; these data must be used with caution.



TABLE 14. *Podocnemis erythrocephala*, statistics of the distributions of frequencies of the volume and shape parameters.

Character	Sample	N	R	m	s	V	t
V(2)	2886	8	12 - 15	13.2 $\pm$ 0.28	0.8	6.1	4.772***
	2887	8	11 - 13	11.6 $\pm$ 0.19	0.5	4.6	
bicone	2886	8	- 0.164 - 0.127	- 0.0236 $\pm$ 0.03048 ns	0.0862		0.713 ns
	2887	8	- 0.056 - 0.138	0.0045 $\pm$ 0.02498 ns	0.0707		
excentricity	2886	8	3.49 - 3.76	3.607 $\pm$ 0.0326	0.0922	2.6	6.986***
	2887	8	3.27 - 3.39	3.341 $\pm$ 0.0198	0.0559	1.7	
V(1)	2886	8	12 - 15	13.1 $\pm$ 0.29	0.8	6.4	4.545***
	2887	8	11 - 13	11.5 $\pm$ 0.17	0.5	4.2	

## DISCUSSION

### Volume

The analyses of individual species showed, for three out of the four, very large variation from sample to sample, even within the same locality (*unifilis* at Coarí, Table 4; *sextuberculata* at Boca do Juruá, Table 9; *erythrocephala* at the Rio Cuiciras, Table 14).

This might be attributed to differences in the degree of maturation of the clutches, but not in the case of *P. unifilis*, the calcareous shell of whose eggs, once laid, is not likely to grow. Additionally, eggs bought have usually been plundered from nests.

There is thus no expectation of profitable comparison among the species; none of them can be numerically described in summary. One solid fact, however, is that, where three species occur together (Leonardo, Table 13), the eggs of *expansa* are significantly larger. It is the largest species of the genus, adult females reaching 60+ cm carapace length (*unifilis* reaches close to 50, the other two around 30).

A ranking of all samples available (Table 15) indicates that the three lesser species of the genus do not differ significantly in egg volume. This is indeed confirmed by Kruskal-Wallis's analysis of variance by

ranks (Siegel, 1975), which stops much short of significance ( $H= 6.456$  ns).

### Shape

Of the two geometrical parameters, I shall limit the discussion of egg shape to the excentricity of the generating ellipsis. The bicone is a much less intuitive character, and varies erratically in our materials.

A ranking of all samples (Table 16) shows that *expansa* has practically round eggs, and in this differs from the other three species (Kruskal-Wallis analysis of variance by ranks,  $H= 8.164$  \*), which do not differ among themselves (Kruskal-Wallis  $H= 4.033$  ns).

Another way of looking at the shape of eggs is through the relationship between the two diameters, i.e., the regression of egg width on egg length. Table 17 shows the respective statistics.

Of the samples studied, only 4 showed significant regressions. Some of negative cases can be attributed to shortness of range of the variables (Vanzolini, 1993: 93). One way of circumventing this difficulty, although with some loss of information, is to combine samples from a locality. This led to

significant regressions only in two cases, *P. erythrocephala* and *P. unifilis* from Coari.

Of all regression analyses, the only meaningful one is that of *P. expansa*. The two individual regressions are significant and do not differ between themselves. The joint regression is highly significant ( $r^2 = 0.9416$ ), which means that the relationship is important to the animal. The coefficient of regression ( $b$ ) does not differ significantly from 1; the intercept

does not differ significantly from zero: the eggs of *P. expansa* are virtually spherical (as already demonstrated above).

Another comparison that can be made is between Coari (sum) and the Fonteboa *P. unifilis* — both localities are on the Rio Solimões. The coefficients of regression differ significantly ( $t = 2.332$ , 56 df), which confirms the high heterogeneity of this species.

TABLE 15. *Podocnemis*,  $V(2)$  in all samples.

Sample	Locality	N	R	m
1. <i>unifilis</i> 2881	Coari	11	9 - 11	10.3 $\pm$ 0.20
2. <i>sextuberculata</i> 2878	Boca Juruá	16	11 - 12	11.6 $\pm$ 0.11
3. <i>erythrocephala</i> 2887	Rio Cuieiras	8	11 - 13	11.6 $\pm$ 0.19
4. <i>sextuberculata</i> 2875	Boca Juruá	17	11 - 14	13.0 $\pm$ 0.16
5. <i>erythrocephala</i> 2886	Rio Cuieiras	8	12 - 15	13.2 $\pm$ 0.28
6. <i>sextuberculata</i> 2870	Boca Juruá	18	10 - 20	13.4 $\pm$ 0.51
7. <i>unifilis</i> 2890	Fonteboa	35	10 - 20	14.9 $\pm$ 0.38
8. <i>unifilis</i> 2891	Oriximiná	13	14 - 18	14.9 $\pm$ 0.30
9. <i>unifilis</i> 2880	Coari	18	14 - 21	15.9 $\pm$ 0.35
10. <i>unifilis</i> 2874	Leonardo	10	15 - 19	16.1 $\pm$ 0.44
11. <i>unifilis</i> 2892	Oriximiná	19	15 - 19	16.4 $\pm$ 0.27
12. <i>sextuberculata</i> 2888	Boca Juruá	30	12 - 21	16.9 $\pm$ 0.48
13. <i>sextuberculata</i> 2872	Leonardo	6	16 - 23	19.2 $\pm$ 0.89
14. <i>unifilis</i> 4014	Araguaia	23	19 - 24	21.3 $\pm$ 0.25
15. <i>sextuberculata</i> 2884	Lago Miúá	12	18 - 27	21.9 $\pm$ 0.65
16. <i>expansa</i> 2871	Leonardo	4	27 - 31	28.7 $\pm$ 0.85
17. <i>expansa</i> 2870	Leonardo	5	25 - 43	32.1 $\pm$ 2.88

TABLE 16. *Podocnemis*, excentricity in all samples.

Sample	Locality	N	R	m
1. <i>expansa</i> 2870	Leonardo	5	0.49 - 1.91	1.34 ± 0.273
2. <i>expansa</i> 2871	Leonardo	4	1.44 - 2.35	1.78 ± 0.216
3. <i>unifilis</i> 2890	Fonteboa	35	1.93 - 3.59	3.12 ± 0.061
4. <i>unifilis</i> 2881	Coarí	6	2.93 - 3.37	3.19 ± 0.062
5. <i>erythrocephala</i> 2887	Rio Cuieiras	8	3.27 - 3.39	3.34 ± 0.020
6. <i>unifilis</i> 2892	Oriximiná	19	3.19 - 3.60	3.37 ± 0.028
7. <i>unifilis</i> 2891	Oriximiná	13	3.19 - 3.68	3.41 ± 0.040
8. <i>unifilis</i> 2880	Coarí	18	3.30 - 3.60	3.42 ± 0.025
9. <i>sextuberculata</i> 2878	Boca Juruá	16	3.16 - 3.45	3.45 ± 0.029
10. <i>sextuberculata</i> 2872	Leonardo	6	3.19 - 3.71	3.47 ± 0.079
11. <i>unifilis</i> 4014	Araguaia	23	3.21 - 4.06	3.61 ± 0.053
12. <i>erythrocephala</i> 2886	Rio Cuieiras	8	3.49 - 3.76	3.61 ± 0.033
13. <i>sextuberculata</i> 2888	Boca Juruá	30	3.31 - 4.06	3.67 ± 0.034
14. <i>sextuberculata</i> 2875	Boca Juruá	17	3.39 - 3.93	3.76 ± 0.030
15. <i>sextuberculata</i> 2876	Boca Juruá	18	3.31 - 4.01	3.78 ± 0.041
16. <i>sextuberculata</i> 2884	Lago Miúá	12	3.62 - 4.06	3.85 ± 0.038
17. <i>unifilis</i> 2874	Leonardo	10	3.60 - 4.11	3.90 ± 0.049

TABLE 17. Statistics of the regression of egg width on egg length.

	N	R(x)	R(y)	b	a	F	r <sup>2</sup>
<i>erythrocephala</i>							
2886 Rio Cuieiras	8	40 - 42	24 - 28	0		0	
2887 Rio Cuieiras	8	37 - 39	23 - 25	0.452 ± 0.3414		1.750 ns	
Sum	16	37 - 42	23 - 28	0.221 ± 0.0866	15.98 ± 0.571***	6.487*	0.3166
<i>expansa</i>							
2870 Leonardo	5	38 - 43	33 - 42	1.474 ± 0.4133	-22.63 ± 2.996***	12.712*	0.8091
2871 Leonardo	4	39 - 51	36 - 47	0.911 ± 0.0093	0.45 ± 2.534 ns	9159.268***	0.9998
Sum	9	38 - 51	33 - 47	0.970 ± 0.0913	-2.24 ± 1.800 ns	112.818***	0.9416
<i>sextuberculata</i>							
2872 Leonardo	6	40 - 45	28 - 31	0.256 ± 0.2935		0.763 ns	
2875 Boca Juruá	18	39 - 45	23 - 28	0.292 ± 0.1752		2.771 ns	
2876 Boca Juruá	18	39 - 46	22 - 29	0.278 ± 0.2594		1.147 ns	
2878 Boca Juruá	16	36 - 41	23 - 24	0.032 ± 0.0576		0.302 ns	
2888 Boca Juruá	31	39 - 49	24 - 29	0.411 ± 0.0927	9.09 ± 0.681***	19.668***	0.4041
Sum Boca Juruá	83	36 - 49	22 - 29	0.446 ± 0.0677	6.50 ± 0.465***	48.918***	0.3765
<i>unifilis</i>							
2874 Leonardo	10	42 - 47	25 - 27	-0.049 ± 0.2469		0.039 ns	
2880 Coarí	18	40 - 44	26 - 30	0.447 ± 0.2135		4.393 ns	
2881 Coarí	6	34 - 37	23 - 24	0.167 ± 0.1667		1.000 ns	
Sum Coarí	24	34 - 44	23 - 30	0.572 ± 0.0755	3.45 ± 0.591***	57.356***	0.7228
2890 Fonteboa	36	30 - 49	24 - 33	0.302 ± 0.0682	15.44 ± 0.509***	19.621***	0.3659
2891 Oriximiná	13	39 - 43	25 - 28	0.040 ± 0.1845		0.047 ns	
2892 Oriximiná	19	39 - 43	26 - 29	0.203 ± 0.1915		1.127 ns	
Sum Oriximiná	32	39 - 43	25 - 29	0.243 ± 0.1445		2.834 ns	
4014 Araguaia	21	43 - 49	29 - 33	0.244 ± 0.1135		2.263 ns	

### Identification of eggs

The eggs of *P. unifilis*, elongate and with a calcareous shell, and of *P. expansa*, spherical, are unmistakable. It is not possible at present to discriminate biometrically between *erythrocephala* and *sextuberculata* eggs.

### CONCLUSION

This avowedly opportunistic and preliminary study permits nevertheless some conclusions capable of orienting continuation and amplification of research.

It is clear that much variability exists, and that tracking its cause and circumstances is a first design. This depends essentially on a scheme of sampling. Several areas must be sampled, with replication, and with the collection of as ample a repertoire of data as possible. Each sample must be unequivocally related to one female, herself duly measured and weighed, or at least to one nest. It will be important to note clutch size. In all forms except *P. unifilis*, autopsy should be avoided, as in species with soft-shelled eggs there is no way, besides readiness to lay, of ascertaining maturity of the eggs.

The present data on *P. unifilis* and *P. sextuberculata*, although not yet sufficient, are somewhat better than those on *expansa* and *erythrocephala*, which should deserve priority. There should be no problem in getting *expansa* eggs. The traditional beaches are well known and protected, the numbers of females that frequent them are large, it is possible to follow closely oviposition, and the collection of moderate samples of eggs will not harm the demography. On the contrary, nothing is known about *erythrocephala*; all remains to be done. It is not rare where it occurs (Mittermeier & Wilson, 1974) and with the help of local people it seems there would be no problem.

In the case of *sextuberculata* and *unifilis*, it will take some field work to locate a suitable number of properly distributed nests; this may take time and travel, but not more than that.

As to methods, it seems reasonable to conclude that the estimation of volume by means of the ellipsoid is satisfactory, and that excentricity is a good index of

shape. It would be advisable, however, to execute more direct determinations of the volume of *P. unifilis* eggs.

All in all, a reasonably thorough sampling scheme should afford a deeper look into the reproductive biology of these most attractive animals.

### ACKNOWLEDGMENTS

This work would not have been possible (it was in fact stalled for quite some time) without a sample of frozen *P. unifilis* eggs, which permitted direct measurement of the volume. For this I am indebted to IBAMA (Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis) and especially to dr. Yeda Soares Lucena Bataus, of the Goiás office. This work was not funded by any granting agency. W. Ronald Heyer and C.W. Myers helpfully criticized the manuscript.

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On some aspects of the reproductive biology of Brazilian *Crotalus*  
(Serpentes, Viperidae)

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## INTRODUCTION

As part of an ongoing investigation of the geographical differentiation of Brazilian rattlesnakes, we have studied, with basis on ten broods and on 28 general samples from the same geographical area as the broods, some aspects of their reproductive biology that can be addressed with museum materials. We believe that comparison between broods and adult samples contributes to an understanding of the dynamics of some processes, such as sexual dimorphism. Otherwise, contrasts within broods are highly informative, since they are free from a number of confounding factors, especially ecology and age.

We altogether lack ecological and genetical information on South American *Crotalus*. Our effort is thus perforce limited to the presentation of data, some of them the first on a South American species of the genus, and to a preliminary statistical analysis, looking for pattern and relating to the literature.

## MATERIALS

It will be noticed that we are using no specific or subspecific names for our materials, referring only to the genus. In fact, the systematics of Brazilian *Crotalus* is probably in a worse shape than that of any snake genus on the continent. The latest review (Hoge, 1966) consists of a series of flat statements and indefinite maps about ten supposed subspecies, without discussion of hard morphological data or of actual distributions. There is no doubt that several forms are involved; even some of the color pattern morphs recognized as taxa by Hoge will probably turn out to be valid, but the system, as it stands, is inconsistent and

unapplied. In fact, the research of which the present article is a preliminary part was designed to attempt a better understanding of the structure of the genus in Brasil. In the present context we will have our samples identified solely by geographical provenance.

This study is based on ten broods of *Crotalus*, all in the collection of Instituto Butantan, and on 25 single-locality general purpose samples from the same and from other collections.

The broods were not collected for the purpose; they are part of the Institute's systematic collection, assembled along many years. However, for all broods but one the mother has been preserved. We thus know that they were born in the Institute, or at least in the wooden boxes in which the snakes were shipped (mostly by rail) from the local of collection, usually agricultural or cattle ranches, to the Institute. We have no doubt that the lots recorded as broods are really that, and the localities assigned are of course the mothers'.

What we have no means of ascertaining is whether there has been selection of the specimens to be preserved. Since in the ten broods (134 specimens) there is only one defective individual, we presume that some sort of selection (at least discard of abnormal specimens) was exercised. Malformed individuals are very frequent in rattlesnake broods (Klauber, 1956: 199; Langlada, 1975); their absence in the materials at hand can only mean that somebody has been tidy. In two cases, however (Broods 3 and 8), there is accessory evidence, from the relationship between female length and brood size (below) that, in one case, only part of a brood was preserved and, in an other, the brood is composite. We do not expect however, this practice to have introduced any bias in the analyses in which they were used.

Two series not recorded as broods, from Floraf





Map 1. Localities of the broods and general samples used in this work. 1, São Luís. 2, Afranio. 3, Petrolina. 4, Ipirá. 5, Rui Barbosa. 6, Tapurah. 7, Xingu. 8, Salvador. 9, Guanambi. 10, Urandí. 11, Vitória da Conquista. 12, Brasília. 13, Goiânia. 14, Rio Verde. 15, Vazante. 16, Goiandira; Ouvidor. 17, Transvaal. 18, Ilha Solteira. 19, Campo Grande. 20, Colina. 21, Araçatuba. 22, Cravinhos. 23, Toriba. 24, Poços de Caldas. 25, Vargem Grande. 26, Valença. 27, Frutal do Campo. 28, Paranavaí. 29, Florai; Maringá. 30, Arapongas. 31, Ivaiporã. 32, Guarapuava. 33, Curitiba. 34, Foz do Iguaçu.

5, Frutal do Campo, S. Paulo (2251, 5031), 5 MM, mother IB 1593.

7 FF, mother IB, 33971.

6, Vargem Grande, São Paulo (2245, 4649), 5 MM,

4 FF, mother IB 1504.

7, Poços de Caldas, Minas Gerais (2148, 4634),

9 MM, FF, mother IB 26062

8, Rui Barbosa, Bahia (1218, 4027), 4 MM, 3 FF,

mother IB 26062.

9, Ipirá, Bahia (1210, 3944), 12 MM, 10 FF,

mother not preserved.

10, Urandí, Bahia (1446, 4240), 9 MM, 8 FF,

The samples (Map 1) we are calling “general” are:

- Afranio, state of Pernambuco (0831, 4100), 14 MM, 21 FF

- Apucarana, Paraná (2333, 5129), 7 MM, 7 FF (MHNCI)

- Araçatuba, São Paulo (2112, 5129), 10 MM, 7 FF

- Brasília, Distrito Federal (1546, 4748), 18 MM, 19 FF

- Campo Grande, Mato Grosso do Sul (2027, 5438), 9

MM, 11 FF

sensible limits (the literature abounds in pointless measurements to the tenth of a millimeter). The computation of regression with error in both variables is seldom found in textbooks, but is relatively easy to perform (Silva-Leme, 1959). Differences between the results of this method and those of plain least squares usually reside in the third or fourth decimal places. Thus we stick to traditional least squares.

The following conventions have been adopted with respect to the tables. In tables that include statistics of distributions of frequencies,

N, individuals in sample

R, range of the variable

m, mean  $\pm$  its standard deviation

s, sample standard deviation

V, coefficient of variation

t, Student's, for the difference between the male and female means.

In tables of regression data,

N, individuals in sample

R (x), R (y), ranges respectively of the independent and of the dependent variables b, regression coefficient (slope)  $\pm$  its standard deviation

a, intercept  $\pm$  its standard deviation

F, Fisher's, for the significance of the regression

r<sup>2</sup>, coefficient of determination

db, level of significance (*t* test) of the difference between male and female values of the slope

da, ditto for the intercept.

In all cases,

ns, not significant at the 5% level

\*, significant at the 5% level

\*\*, at the 1% level

\*\*\*, at the 0.1 level.

For sex: M, male and F, female

## Comparisons

*Crotalus* is obviously a Nearctic genus that invaded South America in the Pliocene (Vanzolini & Heyer, 1985). It is strongly differentiated in North America, much less so in South America: at least the number of sympatric species is smaller in the south. It seems obvious that there is great interest in comparing natural history data from the two continents — and a pity that not much has been done in Central America.

Our starting point in comparing northern and southern *Crotalus* is Klauber's (1956) monumental work. He not only assembled a phenomenal amount of information, but presented it in a form that permits subsequent statistical treatment of a type not feasible in his day.

We have conserved Klauber's taxonomic scheme. Very few changes have been proposed since, to us not always convincingly.

For the more recent literature we have proceeded in the same manner, re-analyzing the data when necessary and possible.

Otherwise, there is great interest in comparing data on Brazilian *Crotalus* with data on other Neotropical viviparous Viperidae, i.e., the species of *Bothrops* (*sensu lato*: we do not adopt Burger's (1971) partition of the genus). These comparisons offer an opening for the evaluation of the roles of phylogeny (North American *Crotalus*) and ecology (*Bothrops*) in the causation of

Table 2. *Crotalus*, sex ratio, general samples.

Sample	MM	FF	sum	ratio	X <sup>2</sup>
Afranio	14	21	35	0.400	0.700
Apucarana	7	7	14	0.500	0.000
Araçatuba	10	11	21	0.476	0.024
Brasília	18	19	37	0.486	0.014
Campo Grande	9	11	20	0.450	0.100
Colina	8	13	21	0.381	0.595
Curitiba	6	5	11	0.545	0.045
Foz do Iguaçu	9	5	14	0.643	0.571
Goiandira	9	5	14	0.643	0.571
Goiânia	7	4	11	0.636	0.409
Guanambi	11	11	22	0.500	0.000
Ilha Solteira	25	39	64	0.391	1.531
Itaipu	6	5	11	0.545	0.045
Ivaiporã	8	6	14	0.571	0.143
Ouvidor	5	8	13	0.385	0.346
Petrolina	11	21	32	0.344	1.563
Rio Verde	9	9	18	0.500	0.000
Salvador	16	22	38	0.421	0.474
São Luís	12	7	19	0.632	0.658
Tapurah	5	5	10	0.500	0.000
Toriba	13	9	22	0.591	0.364
Transvaal	6	6	12	0.500	0.000
Valença	5	5	10	0.500	0.000
Vitória da Conquista	9	14	23	0.391	0.543
Xingu	5	7	12	0.417	0.167
	274	293	567	0.483	0.318
				SX <sup>2</sup>	10.691

Table 3. *Crotalus*, sex ratio, data from Klauber (1936).

Sample	MM	FF	sum	ratio	X <sup>2</sup>
<i>durissus</i>	59	54	115	0.522	0.111
<i>basiliscus</i>	48	44	92	0.522	0.087
<i>enyo</i>	39	22	61	0.639	2.369
<i>molossus</i>	159	120	279	0.570	2.726
<i>adamanteus</i>	26	16	42	0.619	1.190
<i>atrox</i>	399	284	683	0.584	9.682
<i>tortugensis</i>	21	7	28	0.750	3.500
<i>lucasensis</i>	198	149	347	0.571	3.460
<i>ruber</i>	154	118	272	0.566	2.382
<i>exsul</i>	17	4	21	0.810	4.024
<i>scutulatus</i>	234	143	377	0.621	10.983
<i>confluentus</i>	1105	964	2069	0.534	4.804
<i>nuntius</i>	122	63	185	0.659	9.408
<i>abyssus</i>	18	12	30	0.600	0.600
<i>lutosus</i>	229	157	386	0.593	6.715
<i>concolor</i>	13	9	22	0.591	0.364
<i>oreganus</i>	795	594	1389	0.572	14.543
<i>mittchellii</i>	57	29	86	0.663	4.558
<i>pyrrhus</i>	133	60	193	0.689	13.806
<i>stephensi</i>	42	23	65	0.646	2.777
<i>tigris</i>	26	15	41	0.634	1.476
<i>cerastes</i>	180	140	320	0.563	2.500
<i>polystictus</i>	9	8	17	0.529	0.029
<i>horridus</i>	66	106	172	0.384	4.651
<i>lepidus</i>	90	71	161	0.559	1.121
<i>triseriatus</i>	101	80	181	0.558	1.218
<i>willardi</i>	15	13	28	0.536	0.071
<i>ravus</i>	10	1	11	0.909	3.682
<i>miliarius</i>	116	104	220	0.527	0.327
<i>catenatus</i>	57	55	112	0.509	0.018
	4538	3465	8003	0.567	71.931
				SX <sup>2</sup>	113.182

made leads to a suspicion that a misprint has occurred. However, two other authors have data on *C. horridus*, Brown (1992), northeastern New York state (487 males, 523 females), and Berish (1998), Florida (74 males, 41 females). The three sets of data are incompatible (chi square 18.650 \*\*\*). Comparing Brown's to Berish's data (Klauber's is a mixed sample, but theirs are geographically homogeneous), chi square is again significant (10.745 \*\*). Martin (1992) found on the Appalachian Mountains an excess of females: 258:527, ratio 0.309, chi square 60.925 \*\*\*. It is thus obvious that there is geographic differentiation in the sex ratio

of *C. horridus* and that the species should not be treated as a unit.

Eliminated *C. horridus* from Klauber's list, the 29 remaining forms can thus be analyzed: (i) in all samples males prevail (ratios 0.51 to 0.91); (ii) however, ratios deviating significantly (at the 1% level) from evenness are only 4, *atrox*, *s. scutulatus*, *viridis oreganus* and *mittchelli pyrrhus*, all represented by large samples.

Fitch & Glading (1947) observed, in *C. viridis oreganus* from central California, a strongly male-biased sex ratio: 294:195, chi square 10.021. Their data agree with Klauber's (chi square 1.233). Julian (1951) has

agreement with Julian's (1951) ratio of 0.588 for the period 1939-1949 (Table 4).

Diller & Wallace (1984), working with *Crotalus viridis oreganus* in northern Idaho, observed a sex ratio of 0.380, but conceded that the sample was biased (nature of the bias not disclosed). The ratio in a sample stated to be unbiased was 0.461, not significantly different from evenness. In four small clutches (19 specimens) the ratio was 0.579, also not significantly different from 0.500. This is in disagreement with Klauber.

Seigel (1986) found in *Sistrurus catenatus* from Missouri a sex ratio of 0.529 (45 males, 40 females), not significantly different from 0.5.

Macartney *et al.* (1990) have data on *C. viridis oreganus* in British Columbia. Sex ratios of broods and of snakes one and two years old varied from 0.342 to 0.588, neither the individual groups nor the aggregate differing significantly from 0.500.

Brown's (1992) data for *C. horridus* have been discussed above. He found a sex ratio of 0.642, not significantly different from evenness. He also states to have observed seasonal variation. We recalculated his data and came up with a chi square of 5.950, ca. 0.40 for 6 degrees of freedom; there seems to be no seasonal variation.

Brown & Lillywhite (1992) found in two broods of *C. cerastes* from the Mojave Desert respectively 3: 3 and 4: 5 males: females; the ratios obviously do not differ from 0.5, but the samples are very small.

Fitch & Pisani (1993) have data on *Crotalus atrox* collected during five rattlesnake roundups in different parts of Oklahoma. They present only aggregate data, which result in a ratio of 0.594 (371 males, 254 females), significantly different from 0.5. We find no geographical

difference between northern and southern Oklahoma, and the sex ratio fully agrees with Klauber's for the same species: chi square is 0.119 for one degree of freedom.

From Fig. 1 in Aldridge & Brown (1995) it is possible to read the frequencies of males and females of *Crotalus horridus* from New York State: 53:23, a ratio of 0.697, significantly different from evenness at the 5% level (chi square = 5.921 \*).

Beaupre *et al* (1998) found, for the same *C. atrox* in central Arizona, 116 males and 65 females, a ratio of 0.641, significantly different from 0.500.

Beaupre (1995) has incidental data on the sex ratio of *C. lepidus* in the Big Bend of the Rio Grande: 35 males and 21 females, from two localities (homogeneous among themselves) afford a ratio of 0.625, not significantly different from 0.5 (chi square = 1.750).

A recent paper (Berish, 1998, cited above) throws additional light on the problem. She gathered data, from the skin trade, on Floridian *Crotalus adamanteus* and *C. horridus*, respectively 598 and 115 specimens, spanning one year and one week: really remarkable data. She lists individually 8 simultaneous samples of each species, spaced in time (data reworked as our Table 6). Sex ratio showed significant temporal variation within the duration of the study. In *adamanteus*, males predominated in the aggregate: there were 361 males and 237 females, for a chi square of 12.856 (our computation), significant at the 0.1% level. Two samples only, October 7 of the first, and October 14 of the next year, are responsible for the deviation. Removing these samples lowers the ratio to evenness. In *horridus*, males also predominated (ratio 0.640), but there was no significant variation in time. On Graph 1 we plot the sex ratios against their respective dates. It is unmistakable

Table 6. Sex ratio, Florida rattlesnakes (Berish, 1998).

Sample	MM	FF	sum	ratio	X <sup>2</sup>
<i>adamanteus</i>					
7.x	43	11	54	0.796	9.481 **
31.x	39	33	72	0.542	0.250 ns
11.xii	33	29	62	0.532	0.129 ns
20.iv	38	31	69	0.551	0.355 ns
9.vi	49	46	95	0.516	0.047 ns
7.vii	15	17	32	0.469	0.063 ns
10.viii	33	18	51	0.647	2.206 ns
14.x	109	54	163	0.669	9.279 **
<i>horridus</i>					
7.x	5	4	9	0.556	0.056 ns
31.x	16	7	23	0.696	1.761 ns
11.xii	11	6	17	0.647	0.735 ns
20.iv	3	2	5	0.600	0.100 ns
9.vi	5	5	10	0.500	0.000 ns
7.vii	4	4	8	0.500	0.000 ns
10.viii	11	6	17	0.647	0.735 ns
14.x	19	7	26	0.731	2.769 ns

Table 7. *Bothrops*, sex ratios, data from the literature.

Species	Area	M:F	ratio	X <sup>2</sup>	Source
<i>atrox</i>	Costa Rica	8:3	0.727	1.136 ns	Hirth, 1964
	Iquitos, Perú	22:10	0.688	2.250 ns	Hoge & Federsoni, 1978
<i>nummifer</i> young	Costa Rica	31:39	0.443	0.417 ns	Solórzano, 1988
adult	Costa Rica	41:48	0.461	0.275 ns	Solórzano, 1988
<i>asper</i>	E Costa Rica	98:80	0.551	0.910 ns	Solórzano & Cerdas, 1989
	W Costa Rica	60:67	0.472	0.192 ns	Solórzano & Cerdas, 1989
<i>godmani</i>	Costa Rica	320:337	0.487	0.220 ns	Campbell & Solórzano, 1992
<i>yucatanicus</i>	S México	40:79	0.336	6.391 *	McCoy & Censky, 1992
<i>moojeni</i>	Goiás, Brasil	26:50	0.342	3.789 ns	Leloup, 1975
<i>jararaca</i> young	S. Paulo, Brasil	11:20	0.355	1.306 ns	Sazima, 1992
adult	S. Paulo, Brasil	25:28	0.472	0.085 ns	Sazima, 1992

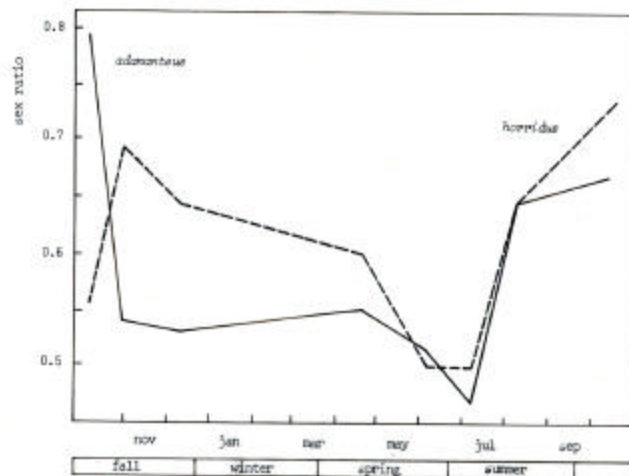
Graph 1. *Crotalus* from Florida, sex ratio against time (data from Berish, 1998).

Table 8. *Crotalus*, broods, statistics of the distributions of frequencies of body length.

	N	R	m	s	V	t
Brood 1 M	4	287 - 312	303.0 ± 5.52	11.0	3.7	0.728 ns
F	4	300 - 316	308.0 ± 4.08	8.2	2.7	
3 M	11	320 - 335	329.7 ± 1.65	5.5	1.7	1.854 ns
F	13	300 - 357	339.5 ± 4.80	16.6	4.9	
4 M	4	292 - 324	313.3 ± 7.43	14.9	4.7	1.071 ns
F	7	303 - 317	306.9 ± 1.91	5.0	1.6	
5 M	5	303 - 314	307.4 ± 2.11	4.7	1.5	1.573 ns
F	7	302 - 321	312.6 ± 2.32	6.1	2.0	
6 M	5	272 - 300	290.8 ± 5.05	11.3	3.9	1.520 ns
F	4	288 - 310	301.8 ± 4.97	9.9	3.3	
7 M	9	292 - 303	297.3 ± 1.24	3.7	1.3	0.548 ns
F	5	296 - 303	298.4 ± 1.36	3.0	1.0	
8 M	4	310 - 345	329.3 ± 8.96	17.9	5.4	0.524 ns
F	3	321 - 325	323.7 ± 1.33	2.3	0.7	
9 M	12	323 - 374	343.9 ± 4.03	14.0	4.1	1.048 ns
F	10	333 - 387	350.2 ± 4.44	14.0	4.0	
10 M	9	284 - 298	290.7 ± 1.76	5.3	1.8	2.137 *
F	8	290 - 313	297.8 ± 2.91	8.2	2.8	
Floraí M	21	339 - 395	360.8 ± 2.93	13.4	3.7	0.671 ns
F	11	301 - 390	365.0 ± 6.77	22.4	0.2	
Guarupava M	7	301 - 325	314.4 ± 3.60	9.5	3.0	1.661 ns
F	10	309 - 350	324.7 ± 4.40	14.2	4.4	

Table 9. *Crotalus*, general samples, sexual differences in body length, Mann-Whitney test.

Sample		N	R	U	z
Afranio	M	14	337 - 1530	20 ns	0.067 ns
	F	21	905 - 1296		
Apucarana	M	7	564 - 1004	20 ns	1.220 ns
	F	7	481 - 1199		
Araçatuba	M	10	250 - 1193	20 ns	1.215 ns
	F	12	322 - 1216		
Brasília	M	19	320 - 1115	20 ns	1.215 ns
	F	18	345 - 1188		

Table 9. Continued

Sample		N	R	U	z
Toriba	M	13	402 - 1030		0.115 ns
	F	15	504 - 1043		
Transvaal	M	7	319 - 1274	10 ns	
	F	6	531 - 1019		
Valença	M	5	470 - 725	3 ns	
	F	5	516 - 1066		
Vazante	M	27	256 - 1443		0.990 ns
	F	14	247 - 1187		
Vitória da Conquista	M	8	205 - 1175		2.252 ns
	F	14	368 - 1103		
Xingu	M	5	311 - 1071	11 ns	
	F	6	330 - 1035		

Table 10. *Crotalus*, broods, statistics of the distributions of frequencies of total length.

		N	R	m	S	V	t
Brood 1	M	4	313 - 340	329.0 ± 5.87	11.7	3.6	2.119 ns
	F	4	322 - 340	330.8 ± 5.06	10.1	3.1	
Brood 3	M	10	353 - 370	362.5 ± 1.91	6.0	1.7	10.735 ***
	F	13	344 - 387	369.1 ± 3.47	12.5	3.4	
Brood 4	M	4	317 - 354	342.3 ± 8.84	17.7	5.2	1.801 ns
	F	7	324 - 341	329.4 ± 2.3	6.1	1.9	
Brood 5	M	5	330 - 336	332.2 ± 1.2	2.7	0.8	2.091 ns
	F	7	324 - 343	334.3 ± 2.32	6.1	1.8	
Brood 6	M	5	301 - 359	236.0 ± 9.4	21.0	6.5	1.446 ns
	F	4	310 - 334	324.5 ± 5.25	10.5	3.2	
Brood 7	M	9	320 - 331	326.1 ± 1.28	3.9	1.2	10.345 ***
	F	5	316 - 325	319.8 ± 1.74	3.9	1.2	
Brood 8	M	4	338 - 382	364.0 ± 10.89	21.8	6.0	0.792 ns
	F	3	349 - 356	353.7 ± 2.33	4.0	1.1	
Brood 9	M	12	353 - 408	376.2 ± 4.28	14.8	3.9	3.268 **
	F	10	355 - 413	374.7 ± 4.76	15.0	4.0	
Brood 10	M	9	312 - 327	319.0 ± 1.89	5.7	1.8	0.223 ns
	F	8	312 - 336	318.9 ± 3.22	9.1	2.9	

Table 11. *Crotalus*, general samples, sexual differences in total length, Mann-Whitney test.

Sample		N	R	U	z
Afranio	M	14	370 - 1676		0.1684 ns
	F	21	982 - 1442		
Apucarana	M	7	618 - 1110	9 ns	
	F	7	513 - 1281		
Araçatuba	M	10	272 - 1315		0.5934 ns
	F	12	351 - 1296		
Brasília	M	18	354 - 1249		1.0757 ns
	F	18	368 - 1281		
Campo Grande	M	9	352 - 1415		0.1899 ns
	F	11	346 - 1381		
Colina	M	8	656 - 993		0.5794 ns
	F	13	584 - 887		
Curitiba	M	5	883 - 1157	7 ns	
	F	5	325 - 1377		
Foz de Iguaçu	M	9	334 - 1004		1.6667 ns
	F	5	345 - 1234		
Goiandira	M	8	700 - 1191	20 ns	
	F	5	861 - 1133		
Goiânia	M	7	364 - 1433	12 ns	
	F	4	550 - 1106		
Guanambi	M	11	590 - 1431		1.6745 ns
	F	11	481 - 1254		
Ilha Solteira	M	24	462 - 1165		0.6648 ns
	F	38	460 - 1046		
Itaipu	M	6	746 - 1274	14 ns	
	F	5	817 - 1122		
Ivaiporã	M	7	336 - 1041	18 ns	
	F	6	493 - 1290		
Ouvidor	M	5	738 - 1031	15 ns	
	F	8	451 - 1113		
Petrópolis	M	11	372 - 1496		0.2064 ns
	F	20	316 - 1554		



(1989) have data (total length) on broods of *B. asper*. They sorted their materials in eastern and western samples, since they say there is a strong evidence for geographical differentiation of Costa Rican snakes on the sides of the mountain backbone. The results are conflictive: on the East the females are much longer, in the West the opposite occurs.

Campbell & Solórzano (1992) have, for *B. godmani*, from Central America, graphs from which it is possible to recover the distributions of frequencies of body length. The Mann-Whitney test revealed significantly longer females ( $z = 3.676 ***$ ).

Also from a graph in McCoy & Censky's 1992 paper it is possible to recover distributions of frequencies of body length; no significant sexual differences ( $z = 1.361$ ) were revealed by the Mann-Whitney test.

#### Tail length

Analyses of the regression of tail length on body length were performed on all samples. Eighteen brood samples were large enough to be processed (Table 13). Among these only 5, not comprising both sexes of any one sample, were found to afford regressions significant at a mild 5% level. No sexual comparisons were thus possible. The impression remains that the bond between tail length and body length in neonates is rather tenuous.

It should not be forgotten at this point that the meaning of regression is not exactly the same in broods and in general samples. In a brood, homogeneous in time, the relationship between any two measurements is purely mechanical: they must be in harmony for the fulfillment of whatever function. Absence of significant regression indicates absence of a joint function; when

regression is significant, the quality of the fit reflects selective pressures. The mechanical functions usually assigned to the tail are housing the hemipenes and associated muscles (independent from body size) and participating in locomotion. It stands to reason that tail length must be relevant to the acoustical properties of the rattling. The only paper we found on the subject (Cook, Rowe & van Devender, 1994), takes into consideration rattle length, which is relevant, but not tail length.

In the contrasting case, however, of samples encompassing all or most of the size range of the form, thus including specimens of diverse ages, there is the intervention of time: two measurements physically uncorrelated (say tail length and head width), growing concurrently will obviously appear correlated. The features of the regression will depend not on mechanical properties, but on growth rates. Even so, these regressions are in practice extremely valuable, in the description and comparison of units, especially in cases such as the present one, where there is every reason to suppose that male and female general samples, by being random, have similar age structures.

As usual in snakes, samples with broad ranges of both variables show highly significant regressions of tail length on body length (Vanzolini, 1991: 392). Among the 38 samples studied only 4 did not show significant regression (Table 14): Goiandira females, Ouidor males and Tapurah males and females, probably due to lack of large adults and of juveniles, especially the latter. But a majority of samples, being very favorable to the analysis of regression, afforded interesting results.

Analysis of sexual differences in regression proceeds through two stages (Vanzolini, 1993). First are compared the two coefficients of regression (slopes). If

Table 14. Continued

Sample		N	R (x)	R (y)	b	a	F	r <sup>2</sup>	db	da
Goiânia	M	7	334 - 1287	30 - 146	0.116 ± 0.0047	-9.05 ± 17.0344 ns	606.624 ***	0.9918	**	
	F	4	513 - 1039	37 - 72	0.065 ± 0.0082	3.08 ± 9.299 ns	63.517 *	0.9695		
Guanambi	M	11	510 - 1310	50 - 151	0.113 ± 0.0117	-5.19 ± 10.281 ns	93.487 ***	0.9122	ns	*
	F	11	452 - 1170	29 - 84	0.072 ± 0.0057	-0.82 ± 5.741 ns	158.182 ***	0.9462		
Ilha Solteira	M	24	416 - 1045	46 - 120	0.122 ± 0.0104	-11.31 ± 4.152 ns	138.240 ***	0.8622	**	
	F	38	430 - 1046	30 - 80	0.070 ± 0.0053	2.99 ± 1.968 ns	159.834 ***	0.8162		
Itaipu	M	6	682 - 1166	64 - 108	0.098 ± 0.0173	0.38 ± 6.793 ns	31.906 **	0.8886	ns	*
	F	4	760 - 986	57 - 73	0.070 ± 0.0068	29.95 ± 3.431 ns	106.772 ***	0.9816		
Ivaiporã	M	7	303 - 935	33 - 109	0.124 ± 0.0198	-8.82 ± 10.357 ns	106.204 ***	0.9550	*	
	F	6	460 - 1198	33 - 92	0.082 ± 0.0078	-6.52 ± 8.478 ns	110.234 ***	0.9650		
Ouvidor	M	5	674 - 945	64 - 91	0.092 ± 0.0309		8.942 ns			
	F	8	421 - 1041	30 - 72	0.056 ± 0.0153	11.76 ± 4.599 ns	24.559 ***	0.8037		
Petrópolis	M	11	340 - 1335	32 - 161	0.125 ± 0.0059	10.68 ± 15.602 ns	451.797 ***	0.9805	**	
	F	20	292 - 1461	24 - 108	0.075 ± 0.0037	0.54 ± 6.793 ns	411.688 ***	0.9581		
Rio Verde	M	9	341 - 1322	32 - 116	0.079 ± 0.0083	5.43 ± 8.624 ns	90.843 ***	0.9285	ns	*
	F	9	372 - 1252	26 - 84	0.068 ± 0.0056	-1.16 ± 6.139 ns	150.204 ***	0.9555		
Salvador	M	16	304 - 1333	30 - 139	0.109 ± 0.0052	-3.85 ± 9.019 ns	448.452 ***	0.9697	**	
	F	22	373 - 1121	27 - 81	0.065 ± 0.0071	8.52 ± 3.454 ns	84.844 ***	0.8092		
São Luís	M	12	344 - 1560	32 - 145	0.094 ± 0.0038	1.90 ± 9.460 ns	617.131 ***	0.9841	ns	*
	F	5	406 - 860	24 - 64	0.085 ± 0.0082	-7.06 ± 7.382 ns	107.890 ***	0.9729		
Tapurah	M	5	698 - 942	76 - 107	0.117 ± 0.0384		9.229 ns			
	F	5	836 - 964	70 - 76	0.023 ± 0.0295		0.613 ns			
Toribá	M	13	402 - 1030	40 - 109	0.117 ± 0.0070	9.69 ± 6.668 ns	277.126 ***	0.9618	*	
	F	9	504 - 1043	36 - 69	0.061 ± 0.0095	7.73 ± 3.695 ns	40.907 ***	0.8539		
Transvaal	M	6	319 - 1164	28 - 126	0.113 ± 0.142	-6.65 ± 14.303 ns	63.228 ***	0.9405	ns	*
	F	6	531 - 1019	33 - 73	0.070 ± 0.0085	5.20 ± 6.371 ns	67.626 ***	0.9442		
Valença	M	5	470 - 725	45 - 75	0.117 ± 0.0273	-11.36 ± 5.439 ns	18.419 *	0.8599	ns	*
	F	5	680 - 1000	42 - 66	0.056 ± 0.0133	8.68 ± 4.359 ns	17.640 *	0.8547		
Vazante	M	27	256 - 1443	23 - 162	0.119 ± 0.0058	-10.82 ± 6.970 ns	415.410 ***	0.9432	**	
	F	14	247 - 1187	22 - 83	0.070 ± 0.0052	1.65 ± 5.189 ns	186.043 ***	0.9394		
Vitória da Conquista	M	8	650 - 1175	56 - 126	0.135 ± 0.029	-32.44 ± 10.459 *	21.531 **	0.7821	**	
	F	14	373 - 1022	27 - 81	0.072 ± 0.0093	4.23 ± 4.631 ns	60.239 ***	0.8339		
Xingu	M	4	311 - 1071	32 - 117	0.118 ± 0.0058	-6.84 ± 17.983 ns	416.592 ***	0.9929	*	
	F	6	220 - 1035	18 - 80	0.080 ± 0.0072	-3.00 ± 10.162 ***	123.500 ***	0.9685		

### Quantification of sexual dimorphism

Quantification of sexual dimorphism, a long-standing problem, must be met at two levels, that of a single sample and that of a taxonomic group. In the first case there is at present no way of escaping ratios, with their well-known statistical deficiencies (Vanzolini, 1991). In spite of these difficulties, however, ratios have a strong intuitive appeal and are defensible in particular cases (below).

In the case of several (four or more) samples, there is recourse to regression of the means of one sex on those of the other. This has been advocated by King (1989) and by Ranta, Laurila & Elmberg (1994). Both papers recommend, in a manner not quite clear to us, analysis of residuals. We think, instead, that orthodox analysis is advisable. The null hypothesis, no sexual dimorphism, implies that the regression is linear ( $y' = a + bx$ ) and passes through the origin ( $a = 0$ ) with unit slope ( $b = 1$ ). Deviations from this pattern will characterize the type of dimorphism, and the goodness of fit parameters ( $F$  and  $r^2$ ) will estimate the tightness of the relationship. In the case of  $a = 0$ , the linear equation is reduced to  $y' = bx$ , and so ratios are valid ( $b = y/x$ ).

One major difficulty in applying regression analysis to sexual dimorphism resides in the definition of the quantities to represent the sexes. In the case of broods, as already discussed, the means of measurements are adequate. In the case of general samples, however, there are problems. The most widely used variables are the means of measurements of adult specimens (e.g., Fitch, 1981). The concept of "adult" usually means "reproducing", but this is not free from trouble. It assumes cessation of growth at the attainment of sexual maturity. This is a very debatable

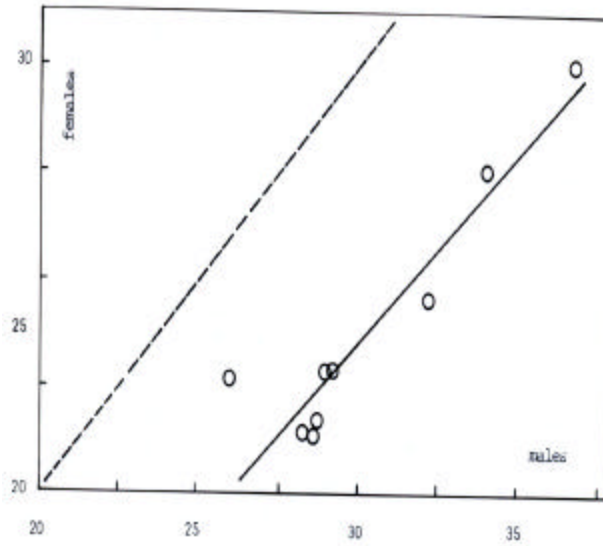
point, that can only be solved, if indeed it can be solved, case by case. In rattlesnakes in general, growth continues after sexual maturity, females even growing through pregnancy (Klauber, 1956: 141). Thus, general samples are samples of an undefinable universe; parametric methods are out. Accordingly, we regressed female against male means of broods, weighting the regressions by the number of females involved. We found no way of treating the general samples.

The results for the broods are summarized on Table 15. The table shows that all fits are excellent, as could be expected (Lande, 1980), and that the statistics of the regressions may to some extent permit to quantify the dimorphism.

In the case of body length (Graph 2),  $b$  and  $a$  do not differ significantly respectively from 1 and from zero, so it is seen that sexual dimorphism can be characterized as null.

In the case of total length (Graph 3),  $b$  does not differ significantly from 1, but  $a$  differs from zero. Notwithstanding, the line of regression falls exactly on the line of evenness. Previous conclusions about this character are confirmed, but an easy and intuitive measure of dimorphism does not result.

Finally, in the case of tail length (Graph 4), an interesting situation arises. Brood 1 stands out from the ensemble, its females having anomalously long tails. Such outliers should always be noted and expunged from the calculations. Graph 4 shows the respective scatter diagram, as well as the computed regression and the line of evenness. It is easy to see that females as a group have consistently shorter tails. An apt measure of the dimorphism, since  $b$  does not differ significantly from 1, is the intercept,  $a$ . It is negative and significantly different from zero; intercepts can be easily and accurately



Graph 4. *Crotalus*, broods, tail length, regression of female on male means.

compared (Zar, 1999).

#### Fecundity

It has been said in the section on “materials” above that we are fairly secure that our broods are legitimately that, all but one being provided with mothers of record. We also believe that these samples are not biased with regard to the aspects so far studied. We are less certain, however, of their actually representing the full complement, and no more, of the respective clutches. It will be seen below that one brood shows indications of being composite, another incomplete. It is with this caveat in mind that we introduce the matter of fecundity, as the number of young per brood.

Table 16 lists, besides our own data, the statistics of the distributions of frequencies of brood size contained in Klauber's (1956) Table 10:3, calculated by ourselves. A first feature to note is the very high variability, patent in the ranges and coefficients of

variation.

Our data fit in Klauber's table between the second and third highest ranking samples. Analysis of variance and consecutive application of Kramer's test show that our average is significantly less than that of *C. adamanteus*, undistinguishable from that of *C. v. viridis*. Variability is of the same order of magnitude.

Araujo & Perazzolo (1974) report on two broods of *Crotalus* from the southern state of Rio Grande do Sul, Brasil: 9 and 13 young. They measured but did not sex the specimens.

There is in the literature a reference to a brood of Honduran *C. durissus*: March (1928) counted 20 young from a mother “slightly less than 5 feet”. It is a high count, compatible with ours.

After Klauber (1956) very little meaningful was published about fecundity in *Crotalus*, in terms of actual broods (some autopsy data are available).

The data we have been able to assemble are shown on Table 17. It is possible to make the following

comparisons: (i) South American, vs Central American *Crotalus durissus*,  $t = 5.541^{***}$ , the Costa Rican values much higher; (ii) *Crotalus viridis oreganus*, California vs British Columbia,  $t = 6.5721$ , lower values in Canada.

The available data on *Bothrops* are shown on Table 18.

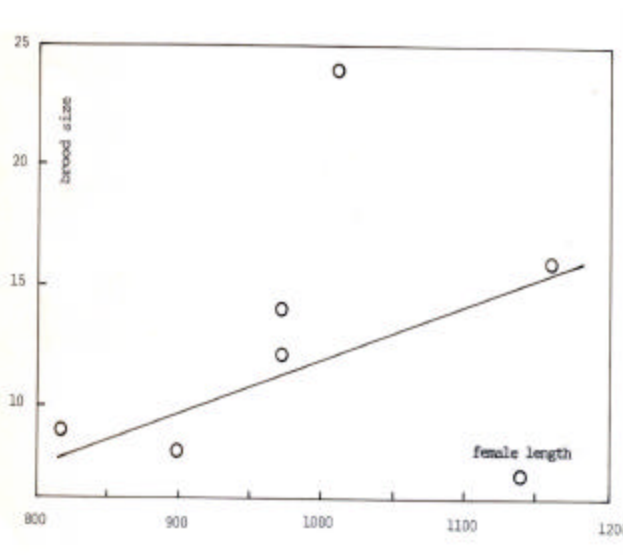
A last angle to be pursued is the relationship between mother size and number of young, an aspect

not explored by Klauber. Our data permit a first approach.

On Graph 5 it is seen that among our broods two samples are strongly aberrant from the general trend. Regressions (on body length and total length of the mother) including these specimens are not significant (Table 19). Their removal brings the regressions within significance. It is reasonable to suppose that the brood aberrantly high is composite, the low ones incomplete.

Table 18. *Bothrops*, data from the literature, brood size.

species	area	brood	source
<i>B. alternatus</i>	Brasil, Rio Grande do Sul	11, 12	Araújo & Perazzolo, 1974
	Argentina, captive	25	Serié, 1919
	zoo	3, 8, 9	Murphy & Mitchell, 1984
<i>B. atrox</i>	Honduras	64, 65, 71	Ditmars, 1943
	Costa Rica	11	Hirth, 1964
	Guyana	8, 9, 11, 16	Beebe, 1946
	Iquitos, Peru	32	Hoge & Federsoni, 1978
<i>B. moojeni</i>	Santa Cecilia, Ecuador	18, 24	Duellman, 1978
	Goiás, Brasil, captive	29	Leloup, 1975



Graph 5. *Crotalus*, regression of brood size on female body length.

and on *Sistrurus catenatus*. Males were larger in all but the last-named.

That our materials show no dimorphism in size is interesting because there is in the literature consensus about a correlation (e.g., Shine, 1994) between larger males and the presence of male combat. Our non-dimorphic snakes present male combat (Langlada, 1975a; Santos, Ferreira & Puerto, 1990; Almeida-Santos et. al., 1999), and go against the theory.

### Fecundity

Our data fit well the North America ones, near the upper end but in good agreement (Tables 16 and 17). The data from Costa Rica, however, incontrovertible as they are (15 broods) far exceed all other figures, and especially ours ( $t = 5.519$  \*\*\*).

As to *Bothrops*, it is difficult to imagine a worse disorder. It is hard to believe that *B. atrox* broods within the restricted compass of Central America vary from 11 to 71, and in tropical South America from 8 to 32. It is clear that this is one area of research in dire need of standardization.

### Theoretical context

We started this work with some hope of contributing to the theory of snake reproductive biology, particularly as regards geographical differentiation. Our samples were singularly apt: broods preserved with mothers from broad areas well represented by collections of adults. In fact, we have possibly contributed, but not exactly in the way meant, adding to and checking current theory, but rather by identifying areas of weakness — expressly on what

concerns crotaline viperids, but no doubt extensible to the whole field.

The usual conduct in searching for generalizations on life history has been the statistical manipulation at taxon level of parameters thought to be relevant, designedly obtained or retrieved from the literature. In trying to apply this approach to our data we ran into conceptual and practical difficulties.

It is clear, for instance, that “mean adult length” or any analogous parameter has no precise statistical meaning. In the manner in which it is usually estimated (taking approximately into account sexual maturity) it may eventually turn out to be robust, but this is a point to be proved.

Problems of another type are found concerning sex ratios. The cases of *Crotalus horridus* and of *C. viridis lutosus*, examined above, show that, whenever the analysis encompasses enough space and time, intra-specific variability is found. It would be imprudent to taken a given sample ratio as representative of a species.

Finally, fecundity parameters are based on the idea that there is a linear relationship between female length and brood size (e.g., Iverson, 1987). This is frequently the case, but not always; even when the relationship exists, it is not in itself sufficient to warrant the use of ratios (such as brood size/female length) as fecundity parameters. It always remains to prove that not only the regression is linear, but also that the intercept does not differ significantly from zero. In our case it does differ (Table 19).

Seigel & Ford (1987: 210) comment that “there are a number of crucial questions concerning snake reproduction that have yet to be adequately addressed (e.g., multiple clutches, tropical cycles, the relationship between hormones and behavior).” To this list might be

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