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

P. E. Vanzolini[1]
Myriam E. V. Calleffo[2]

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[1] Museu de Zoologia, Universidade de São Paulo.

[2] Instituto Butantan, Laboratório de Herpetologia.

INTRODUCTION

As part of an ongoing investigation of the geographical differentiation of Brasilian 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 Brasilian *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 unappliable. 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 Floraí

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, Guanambí. 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, Floraí; Maringá. 30, Arapongas. 31, Ivaiporã. 32, Guarapuava. 33, Curitiba. 34, Foz do Iguaçu.

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

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 ± 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) ± its standard deviation
a, intercept ± its standard deviation
F, Fisher's, for the significance of the regression
r^2, 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 Brasilian *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^2
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^2	10.691

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

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

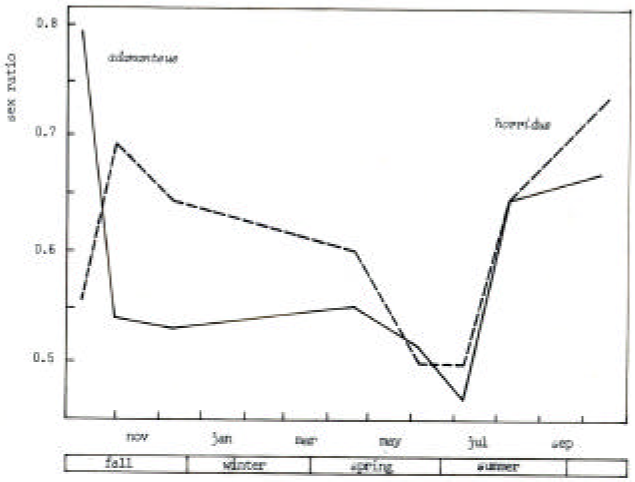
A recent paper (Berish, 1998, cited above) throws additional light on the problem. She gathered data, from the skin trade, on Floridian *Crotalus adamanteus* and *C. horridus*, respectively 598 and 115 specimens, spanning one year and one week: really remarkable data. She lists individually 8 simultaneous 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^2
		adamanteus			
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 **
		horridus			
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^2	Source
atrox	Costa Rica	8:3	0.727	1.136 ns	Hirth, 1964
	Iquitos, Perú	22:10	0.688	2.250 ns	Hoge & Federsoni, 1978
nummifer young	Costa Rica	31:39	0.443	0.417 ns	Solórzano, 1988
adult	Costa Rica	41:48	0.461	0.275 ns	Solórzano, 1988
asper	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
godmani	Costa Rica	320:337	0.487	0.220 ns	Campbell & Solórzano, 1992
yucatanicus	S México	40:79	0.336	6.391 *	McCoy & Censky, 1992
moojeni	Goiás, Brasil	26:50	0.342	3.789 ns	Leloup, 1975
jararaca 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		0.067 ns
	F	21	905 - 1296		
Apucarana	M	7	564 - 1004	20 ns	
	F	7	481 - 1199		
Araçatuba	M	10	250 - 1193		1.220 ns
	F	12	322 - 1216		
Brasília	M	19	320 - 1115		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		
Petrolina	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, Ouvidor 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^2	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		
Petrolina	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			
Toriba	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 defficiencies (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).

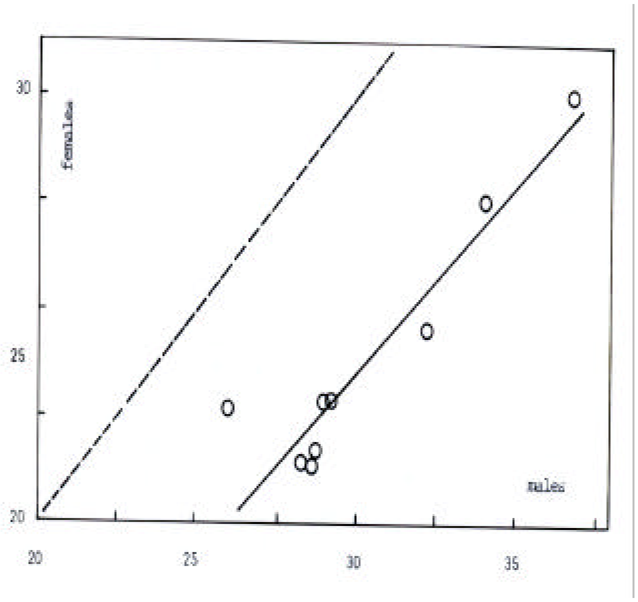
One major difficult in applying regression analysis to sexual dimorphism resides in the definition of the quantities to represent the sexes. In the case of broods, as already discussed, the means of measurements are adequate. In the case of general samples, however, there are problems. The most widely used variables are the 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 an 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 shwn 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.

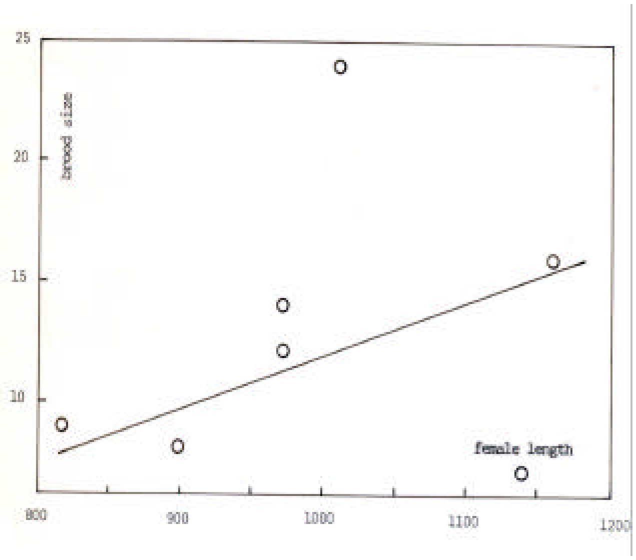
The available data on *Bothrops* are shown on Table 18.

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
B. alternatus	Brasil, Rio Grande do Sul	11, 12	Araújo & Perazzolo, 1974
	Argentina, captive	25	Serié, 1919
	zoo	3, 8, 9	Murphy & Mitchell, 1984
B. atrox	Honduras	64, 65, 71	Ditmars, 1943
	Costa Rica	11	Hirth, 1964
	Guyana	8, 9, 11, 16	Beebe, 1946
	Iquitos, Peru	32	Hoge & Federsoni, 1978
B. moojeni	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 & Puorto, 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 legth 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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