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

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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 and from Guarapuava, both in the state of Paraná, are composed entirely of small specimens, with body lengths between 300 and 429 mm, within the range of the genuine broods. When appropriate, we treat these samples as additional broods, but with caution, made especially necessary by the high number of specimens, 32 in the case of Floraí. We are considering Floraí and Guarapuava, for the ends of this study, to be mixed samples composed entirely of juveniles, to be used only for certain specific purposes.

What we are calling the "general" samples (as representing local populations) are the largest series available from single localities. Some include young, some not, but all, except Floraí and Guarapuava, as noted, contain large obviously adult specimens.

As to the ecology of the localities, it must initially be remembered that practically all snakes received by Instituto Butantan are sent by farmers and ranchers, in exchange for serum, and thus collected in agricultural land or pasture. It must also be remembered that the locality of record is not necessarily that of collection, but may rather be a shipping locality. This is relatively frequent in the case of Butantan snakes, many recorded from the railroad station where they were shipped, sometimes one hundred miles or more from the ranch of origin. For instance, looking at Duellman's (1958) map of the distribution of *Leptodeira annulata pulchriceps*, one will be impressed by its linearity; it is actually the route of the railroad, Noroeste do Brasil, which in time served all cattle ranches of Mato Grosso. Finally, the collection records occasionally refer only to the name of a municipality (equivalent to an American county); some of these are very large, and many were more so in the past.

Thus we prefer to examine the present localities under the broad and fruitful viewpoint of Ab'Saber's (1977) morphoclimatic domains. The localities in Pernambuco and Bahia are in the semi-arid domain of the caatingas, one of them, Urandí, geographically close to the domain of the savanna-like cerrados. The localities in Goiás and those in Minas Gerais, with the exception of Poços de Caldas, are in the domain of the cerrados, in their core area proper. The S.Paulo and Paraná localities are in what is called "seasonal semi-decidual forest", which is not well characterized in the literature, in spite of covering a large proportion of the low-relief highlands of central and southwestern Brasil (but see Torres, Martins & Kinoshita, 1997). It is in many places in geographical and presumably ecological continuity with the pluvial Atlantic Forest. Poços de Caldas is a montane locality (ca 1180 m) in semidecidual forest with patches of *Araucaria*. Thus, three of the four main domains of Brasil are represented in the Butantan collection. It must not be forgotten, on the other hand, that all the areas involved have been for many years under heavy exploitation, no virgin landscape remaining in any of them. The intensity and duration of the exploitation vary locally and are not known to us.

The ten broods are (Map 1)

Brood 1, Paranavaí, state of Paraná (23° 04' S, 52° 28' W), 4 MM, 4 FF, mother Instituto Butantan 26027.

2, Maringá, Paraná (2325, 5155), 9 MM, 1 F, mother IB 12930.

3, Arapongas, Paraná (2323, 5127), 11 MM, 13 FF, mother IB 12351.

4, Cravinhos, S. Paulo (2119, 4745), 4 MM, 7 FF, mother IB 26919.

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

- Colina, São Paulo (2043, 4833), 8 MM, 13 FF
- Curitiba, Paraná (2525, 4916), 6 MM, 5 FF
- Floraí, Paraná (2317, 5219), 21 MM, 11 FF (juveniles) in MHNCI (in Museu de História Natural "Capão da Imbuia", Curitiba, Paraná, MHNCI)
- Foz do Iguaçu, Paraná (2533, 5435), 9 MM, 5 FF
- Goiandira, Goiás (1808, 4806), 9 MM, 5 FF
- Goiânia, Goiás (1641, 4916), 7 MM, 4 FF
- Guanambí, Bahia (1413, 4247), 11 MM, 11FF
- Guarapuava, Paraná (2547, 5127), 10 MM, 7 FF (juveniles) (in MHNCI)
- Ilha Solteira, São Paulo (2023, 5121), 25 MM, 39 FF
- Itaipu, Paraná (2526, 5435), 6 MM, 5 FF
- Ivaiporã, Paraná (2415, 5145), 8 MM, 6 FF (in MHNCI)
- Ouvidor, Goiás (1814, 4750), 5 MM, 8 FF
- Petrolina, Pernambuco (0924, 4030), 11 MM, 21 FF
- Rio Verde, Goiás (1748, 5056), 9 MM, 9 FF
- Salvador, Bahia (1300, 3830), 16 MM, 22 FF
- São Luís, Maranhão (0232, 4418), 12 MM, 7 FF
- Tapurah, Mato Grosso (1250, 5629), 5 MM, 5 FF
- Toriba, São Paulo (2139, 4821), 13 MM, 9FF
- Fazenda Transvaal (hereafter simply Transvaal), Goiás (1853, 5052) 6 MM, 6 FF
- Valença, Rio de Janeiro (2215, 4343), 5 MM, 5 FF
- Vazante, Minas Gerais (1800, 4654), 27 MM, 14 FF
- Vitória da Conquista, Bahia (1451, 4050), 9 MM, 14 FF
- Xingu, Mato Grosso (1215, 5320), 5 MM, 7 FF

Data from the literature

Current restrictions of space in scientific journals have ade practically impossible the publication of raw data. It is thus becoming more and more difficult to verify and to extend published calculations. In some cases we have had recourse to "recovery" of data from graphs. Raising these to a convenient size through successive enlargement of xerox copies, we measured the desired quantities. Checks showed errors of around 1 %, which we think reasonable.

METHODS

This is essentially a statistical study. We believe that zoological research asks for simple statistical methods, close to the physical nature of the characters. The methods used here can be found in any good elementary text, such as Dixon & Massey (1983), Zar (1999) or Siegel (1956, 1975). The scheme of application follows Vanzolini (1993).

A first note is necessary regarding levels of significance. In all cases we report the actual levels found, so that the reader can make his own decision. In any event, dubious cases are infrequent, and should be resolved with common sense. Given, however, the high number of tests applied to the same materials, when we mention simply "significant" or "not significant", we refer to the 1% level.

A second note is due on the matter of regression. A reviewer of the present work commented on the often mentioned, but seldom faced (e.g. Peters, 1993) matter of the model we adopt. A simple least square model is almost universally applied in zoological research, although it is quite obvious that the independent variable, a measurement, is subject to experimental error; this is not contemplated in the model. In the particular case of tail length of squamate reptiles, however, the issue is in practice immaterial. Measurements are highly repeatable — of course in careful hands and within 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 reproductive strategies. Data are not abundant, but enough to suggest the usefulness of this line of inquiry.

Our data permit the investigation of sex ratios, of sexual dimorphism in size and of some aspects of fecundity.

Sex ratio

Table 1. *Crotalus,* sex ratio in broods.

Brood	MM	FF	sum	ratio	X^2
1, Paranavaí	4	4	8	0.500	0.000
2, Maringá	9	1	10	0.900	3.200
3, Arapongas	11	13	24	0.458	0.083
4, Cravinhos	4	7	11	0.364	0.409
5, Frutal do Campo	5	7	12	0.417	0.167
6, Vargem Grande	5	4	9	0.556	0.056
7, Poços de Caldas	9	5	14	0.643	0.571
8, Rui Barbosa	4	3	7	0.571	0.071
9, Ipirá	12	10	22	0.545	0.091
10, Urandí	9	8	17	0.529	0.029
	72	62	134	0.537	0.373
				SX^2	4.678

Nine among our 10 broods (Table 1) have sex ratios (males/males+females) between 0.36 and 0.64, average 0.54. Only one brood (Brood 2, from Maringá) has a widely different value, 0.90. Taken isolately, chi square for this extreme sample (3.200) approaches, without quite reaching, the level of 5%; for 1 degree of freedom the critical value is 3.841, and the 10% one 2.706. Compared to the neighboring locality of Arapongas, the difference is significant (Fisher's exact test, *p* ca. 0.02). In the ensemble of all samples, however, it does not affect the results. Chi square for all the 10 broods is 0.373; excluded Maringá it drops to 0.016. Even so, that deviation is so large that we call attention to it, yet with no explanation to offer.

No geographical variation is perceptible. A chi square test applied to check the homogeneity of the samples afforded a value of 8.441, for 10 degrees of freedom, with probability around 50%.

Thus, in our materials, sex ratio at birth may be considered even.

Seemingly in disagreement with our data, Lira-da-Silva *et al*. (1994) found, in broods from females collected in the general area of Feira de Santana, in Bahia (12° 15' S, 38° 57' W), a sex ratio of 0.620 (85 males, 52 females). This ratio differs significantly from 0.5 at the 5% level (chi square = 3.974 *). However, comparing our broods from the state of Bahia, all geographically and ecologically compatible with Feira de Santana, we did not obtain a significanty value of chi square. For 3 degrees of freedom we got 2.044. This is obviously a matter for further collecting.

Turning to the general samples (Table 2), ratios vary from 0.34 to 0.66, average 0.49. No individual value of chi square even approaches significance, neither does of course that of the aggregate ratio. The picture is exactly parallel to that of the broods; and so there is no differential mortality associated with sex.

There are data on one Neotropical rattler, *C. durissus* in Costa Rica (Solórzano & Cerdas, 1988). The samples comprised 214 adult males and 268 females, 62: 61 young (ratios 0,443 and 0,504). Neither sex ratio differs significantly from 0.5, nor do they differ among themselves.

There are also data, of great interest, on other, Nearctic, rattlesnake populations.

Klauber (1936) presents data on aggregate sex ratios of 30 forms of North American *Crotalus*. We have reworked his data as our Table 3.

There is a problem with Klauber's data. His sex ratio for *C. horridus*, 0.384 (66 males, 106 females) is aberrant for the group, so much so that one would expect a special comment from Klauber. That none is

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 extensive data on sex ratios of *Crotalus viridis lutosus* from a den in Utah followed for ten years by Angus M. Woodbury. His data show a strong bias in favor of males in two years (1945-46, 1948-49) and in the aggregate (general ratio 0.588) (Table 4). In general, there is a trend, in the period sampled, towards an increase in the proportion of males (b = 0.025 ± 0.0058 **)

Fitch (1949) has data on the relationship between sex ratio and age group in *C. viridis oreganus* from central California. We have reworked his data as Table 5 that shows even ratios in the young (to the fourth year), and decided male prevalence in the adult and subadult groups, leading to believe in differential survival of the sexes.

Hirth & King (1968) followed the Tooele County dens for 3 years (1966-1968), and found (Table 4) ratios not differing significantly from evenness — in two cases there was even a slight predominance of females. This is a dramatic change from data of less than 20 years before.

An interesting feature of Hirth & King's paper (primarily concerned with biomass) is that they attribute the drastic decrease in the number of rattlesnakes to human predation. This may be also the explanation for the shift in sex ratio: preferencial predation of males.

Parker & Brown (1973) returned to the same area, and published on the numbers of three species, *Masticophis t. taeniatus*, *Pituophis melanoleucus* and *Crotalus viridis lutosus*. They noted and discussed a marked change in the species composition, *Crotalus* especially showing a strong decline. They did not comment, though, on the spectacular change in sex ratio of the rattlesnake (Table 4), from an large excess of males into evenness.

Table 4. *Crotalus viridis lutosus*, Toole Co, sex ratio.

Sample	MM	FF	sum	ratio	X^2
Julian (1951)					
1939-1940	143	116	259	0.552	1.407 ns
1940-1941	85	95	180	0.472	0.278 ns
1941-1942	155	143	298	0.520	0.242 ns
1942-1943	121	94	215	0.563	1.695 ns
1943-1944	26	12	38	0.684	2.579 ns
1944-1945	81	52	133	0.609	3.162 ns
1945-1946	116	65	181	0.641	7.185 *
1946-1947	44	23	67	0.657	3.291 ns
1947-1948	56	32	88	0.636	3.273 ns
1948-1949	168	64	232	0.724	23.310 ***
Heyrend & Call, 1951					
	161	116	277	0.581	3.655 ns
Hirth & King, 1968					
1964 juv	8	2	10	0.800	1.800 ns
ad	14	23	37	0.378	1.095 ns
1965 juv	5	5	10	0.500	0.000 ns
ad	15	15	30	0.500	0.000 ns
1966 juv	8	6	14	0.571	0.143 ns
ad	17	21	38	0.447	0.211 ns
Parker & Brown, 1973					
1949-1950	168	64	232	0.724	23.310 ns
1964	22	25	47	0.468	0.096 ns
1965	20	20	40	0.500	0.000 ns
1965	25	27	52	0.481	0.038 ns
1970-1971	10	5	15	0.667	0.833 ns
1971-1972	8	4	12	0.667	0.667 ns

Table 5. *Crotalus viridis oreganus*, sex ratio (Fitch, 1949).

Age group	MM	FF	sum	ratio	X^2
young	89	69	158	0.563	1.266 ns
2nd yr	39	27	66	0.591	1.091 ns
3rd-4th yr	54	40	94	0.574	1.043 ns
ad + subad	224	160	384	0.578	5.333 *

Additionally, Heyrend & Call (1951), in a paper on rattlesnake growth based on the same Woodbury materials, cite a sample of *Crotalus viridis lutosus* with 161 males and 116 females, a sex ratio of 0.581, in full 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 that there is a large drop in the ratio in late spring and early summer. The most viable explanation invokes sexual differences in behavior, making one of the sexes at given times more susceptible to human predation (Diller & Wallace, 1984: 188). See also comments above on Hirth & King (1968).

Graph 1 suggests parallelism between the two species, but the coefficients of correlation, both Pearsonian (0.291) and Spearman's (0.560) are not significant for the 8 pairs of observations available.

Data on *Bothrops* are summarized on Table 7. In no case is there a significant departure of the sex ratio from evenness; chi-square for *moojeni* approaches but does not reach the 5% level. In the cases where two samples were available from the same general area (young and adult *B. jararaca* from S.Paulo, *asper* from both geographical halves of Costa Rica), there is also homogeneity.

Comments. Data on sex ratio are seemingly straightforward and easy to interpret; that is not quite so.

Our materials favor an even ratio. Data from other Brasilian authors (Lira-da-Silva et al., 1994) do not agree, but the situation is not entirely clear, and more data are necessary. Data from Costa Rica (Solórzano & Cerdas, 1988) agree with ours.

On the Nearctic side the situation is far from clear. There is strong evidence for variation in time, both within and between years. A most impressive instance is that of *Crotalus horridus.* Klauber's (1956) data on it are open to suspicion, but there is conflict in other observations. Berish (1998) shows, in Florida, that males in general prevail, but there is clear seasonal variation. Brown (1992, New York State) also alleged to have found seasonal variation, but statistical analysis fails to confirm. His ratio, as well as that of Aldridge & Brown (1995) for the same species and area, is statistically even. It seems, as said, that there is geographical variation in the sex ratio of *C. horridus*, and that no comprehensive statement can be made about the form.

Another highly interesting case is that of *C. viridis lutosus* from the dens in Tooele County, Utah, followed for twenty years. There has been a drastic diminution of the proportion of males (Julian, 1951; Heyrend & Call, 1951; Hirth & King, 1968). While short term shifts, such as seen by Berish (1998) are probably due to behavioral causes, and reversible, changes on the scale of years are probably due to ecological causes, and cumulative. General opinion favors vulnerability to human predation as the proximate cause of long term shifts.

The few *Bothrops* on which data are available have even ratios (Table 7). The only exception so far is *B. yucatanicus* (McCoy & Censky, 1992).

It can thus be said that the tropical forms tend to even sex ratios, i.e., the general ophidian norm (Parker & Plummer, 1987), while deviations, of varying nature and magnitude, and, in fact not well understood, are found in the Nearctic forms.

Sexual dimorphism in size and proportions

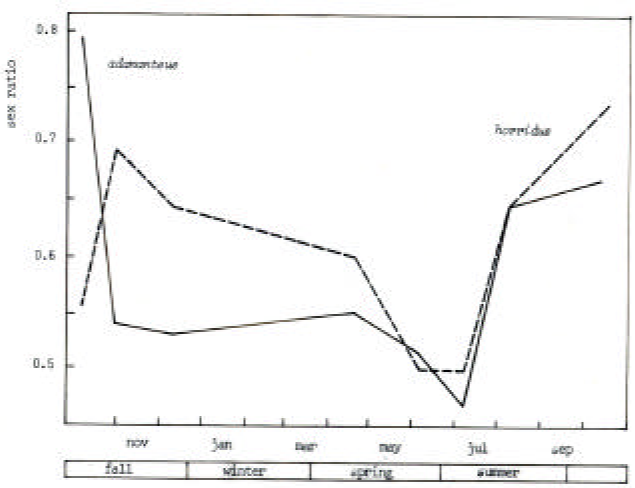
One important shortcoming of our materials is that, not having been collected for biological work, but rather for eventual systematics, they do not include data on weight. All we can do is to analyze measurements taken from museum specimens. However, a study by Vanzolini (1991) of weight-length relationships of a Brasilian crotaline, *Bothrops moojeni* showed

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).

excellent fit for three anamorphoses tried, coefficients of determination varying between 0.90 and 0.98. Thus length is a good proxy variable in growth studies of crotalines.

Sexual differences in size comprise in snakes two major aspects, size itself and tail proportions. In the case of limbless animals with cylindrical or fusiform bodies and with a smooth transition between body and tail, length must be expressed in two ways: body (or trunk, or snout-to-vent, SVL) length, basic to all analyses of proportions, and total length, relevant to locomotion.

There are some statistical preliminaries to be taken into consideration. As all individuals in a brood have exactly the same age and have been subjected to the same environmental circumstances, it is legitimate to employ parametric methods in the study of their measurements.

This can be done in two ways. The simpler one is to apply *t* tests to the differences between the male and the female means of each sample. The alternative treatment, that takes care of eventual interactions between broods (implicating geography or genetics) and sex, and that makes better use of the available degrees of freedom, consists of applying a two-criteria analysis of variance, followed, if so be the case, by a multiple comparison test (Kramer or Tukey; Zar, 1999). This much for broods. In the case of the general samples, however, parametric methods should be avoided, given the heterogeneity of the materials. We have applied to them the Mann-Whitney U teste, as explained and exemplified by Siegel (1956, 1975) or by Zar (1999).

Body length

The two alternative ways of dealing with brood data outlined above have been employed in the analysis of the broods. Table 8 shows the results of the application of the t test. In only one case there is a significant difference (Brood 10), and this only at the 5% level.

Analysis of variance applied to the same data resulted in

Source	df	Sum of squares	Mean square	F
Broods	8	48416.0	6052.0	55.350 ***
Sex	1	980.5	980.5	8.967 *
Interaction	8	549.5	68.687	0.628 ns
Error	106	11590.0	109.33	

As already indicated, we do not take in this context the 5% level as decisive, but nevertheless we did apply Kramer's test tp the data. We found no difference beteween the sexes of any same brood.

In the case of the geneeral samples, the results of the Mann-Whitney U teste are shown on Table 9, where no significant differences are found.

We thus find no sexual differences in body length, neither in neonates nor in general samples.

Total length

Very similar results arise from the study of total length. Application of the t test to the broods (Table 10) shows 7 cases of not significant and 2 conflicting cases of highly significant differences -- Brood 3 with larger females, Brood 7 with larger males. Not surprisingly, analysis of variance does not show a significant effect of sex:

Source	df	Sum of squares	Mean square	F
Broods	8	58328.0	7291.0	57.281 ***
Sex	1	0.66	0.66	0.0052 ns
Interaction	8	1009.34	126.17	0.991 ns
Error	105	3365.0	127.29	

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
Campo Grande	M	9	321 - 1267		0.798 ns
	F	11	325 - 1297		
Colina	M	8	596 - 892		0.145 ns
	F	13	550 - 832		
Curitiba	M	6	800 - 1157	10 ns	
	F	5	300 - 1273		
Foz de Iguaçu	M	9	306 - 905		1.800 ns
	F	5	322 - 1234		
Goiandira	M	8	626 - 1076		0.733 ns
	F	5	805 - 1045		
Goiânia	M	7	334 - 1287	12 ns	
	F	4	513 - 1039		
Guanambi	M	11	540 - 1310		1.609 ns
	F	11	452 - 1170		
Ilha Solteira	M	24	416 - 1045		0.311 ns
	F	39	430 - 1046		
Itaipu	M	6	682 -116	14 ns	
	F	5	760 -1056		
Ivaiporã	M	8	303 -935	21 ns	
	F	6	460 - 1198		
Ouvidor	M	5	674 - 945	15 ns	
	F	8	421 - 1041		
Petrolina	M	10	340 - 1385		1.160 ns
	F	16	292 - 1461		
Rio Verde	M	9	341 - 1322		1.722 ns
	F	9	372 - 1252		
Salvador	M	16	304 - 1333		0.493 ns
	F	31	373 - 1121		
São Luís	M	12	344 - 1435		1.183 ns
	F	7	406 - 1058		
Tapurah	M	5	698 - 942	7 ns	
	F	7	836 - 964		

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	

Among the general samples the Mann-Whitney U test (Table 11) did not reveal any significant differences either. Total length and body length agree.

Comments. In the literature there is aparently no statistical treatment of sexual differences in the size of rattlesnakes, but we have found some papers that include data amenable to analysis.

Fitch (1949) has data on body ("head and body") *oreganus* from central California. The Mann-Whitney test showed z = 6. 931 *** (males longer).

Klauber (1956: 302) has a histogram of lengths of male and female *Crotalus v. viridis* from Platteville, Colorado, from which it is possible to read the actual frequencies and to apply the Mann-Whitney test. Klauber nowhere mentions whether he is dealing with body or total length; a note in an earlier paper (Klauber, 1943: 7), however, convinces us that "length over-all", not SVL, is meant. The test shows the males to be decidedly larger: $z = 3.078$, $p < 0.01$.

Fitch & Glading (1947, *C. viridis oreganus* form Central California) have also a table from which it is possible, by back-reading, to compute Mann-Whitney's U statistics for sexual differences in body length. One obtains $z = 4.420$ ***, males larger.

Heyrend & Call (1951) present a table of body lengths of the population of *C. viridis lutosus* from Woodbury's Utah den, already cited. Again males are significantly longer: z = 5.104 ***.

Seigel (1986), working with *Sistrurus catenatus* from Missouri, applied Mann-Whitney's U test to the differences in body length, and found no significant sexual difference. This absence of dimorphism justifies his applying the same test to tail length — and finding highly significant differences in favor of the males. He also applied regression analysis to the tail length data, and found longer tails in males (no further data).

Macartney *et al*. (1990) have data on body length of three age classes, broods, one and two year old snakes. We computed t tests for the differences between the means of sexes, and no one was significant.

Brown (1991) has also histograms of the distributions of frequencies of body (SVL) length of *Crotalus horridus* in northeastern New York state. Males are larger: $z = 2.807$ ** (Mann-Whitney U test).

Timmerman (1995) has a table (on food habits) in which are cited the body lengths of 14 male and 3 female *C. adamanteus* from northeastern Florida. The Mann-Whitney test did not detect any significant differences; the sample is anyway very small.

From Beaupre et al.'s (1998) graphs (*C. atrox*, Arizona) it is possible to recover the raw data and to apply Mann-Whitney's U test to body lengths; males are significantly longer (z = 5.004 ***).

Solórzano & Cerdas (1988) have data on the total length of broods of Costa Rican *Crotalus durissus* (Table 12). It is a confusing situation: in 1 case there is no dimorphism, in 3 cases the males prevail, in 1 case the females are longer. We think one cannot speak of dimorphism in the usual sense.

Finally, Mann-Whitney's U test applied to Vanzolini's (1991) samples of *Bothrops moojeni* did not reveal any sex dimorphism (for body length z = 0.230, for total length z = 0.652).

On the *Bothrops* side, there are four relevant papers, three on Costa Rican and one on southern Mexican snakes. Solórzano (1988) found in broods of *B. nummifer* no dimorphism in body length ($t = 0$) and strong dimorphism in total length ($t = 3.934$, 68 df). This means of course strong sexual dimorphism in tail length from birth, males already prevailing. Solórzano & Cerdas

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		

Table 11. Continued.

Sample		N	R	U	z
Rio Verde	M	9	378 - 1438		1.7219 ns
	F	9	398 - 1336		
Salvador	M	16	334 - 1472		0.2661 ns
	F	22	400 - 1199		
São Luís	M	11	377 - 1725		1.1055 ns
	F	6	430 - 9240		
Tapurah	M	5	774 - 1048	10 ns	
	F	5	907 - 1039		
Toriba	M	13	442 - 1135		0.2003 ns
	F	9	540 - 1112		
Transvaal	M	6	346 - 1274	10 ns	
	F	6	549 - 1092		
Valença	M	5	516 - 800	5 ns	
	F	5	722 - 1066		
Vazante	M	27	282 - 1091		0.9897 ns
	F	14	269 - 1270		
Vitória da Conquista	M	8	719 - 1287		2.5253 *
	F	14	400 - 1096		
Xingu	M	5	343 - 1188	11 ns	
	F	6	348 - 1215		

Table 12. *Crotalus durissus*, Costa Rican broods, statistics of the distributions of frequencies of total length (Solórzano & Cerdas, 1988).

		N	R	m	t
Brood 1	M	14	33.5 - 40.6	38.0 ± 2.26	5.920 ***
	F	11	32.6 - 39.1	36.1 ± 1.85	
Brood 2	M	14	33.4 -37.2	36.2 ± 1.10	4.559 ***
	F	14	32.8 - 37.3	35.2 ± 1.24	
Brood 3	M	6	31.4 - 43.0	39.7 ± 4.10	0.204 ns
	F	12	36.8 - 42.0	39.6 ± 1.55	
Brood 4	M	11	27.5 - 37.5	34.8 ± 3.40	3.082 **
	F	13	34.4 - 37.1	35.8 ± 0.70	
Brood 5	M	17	37.3 - 40.0	38.7 ± 0.70	5.291 ***
	F	11	35.2 - 39.1	37.7 ± 1.00	

(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 13. *Crotalus,* broods, statistics of the regression of tail length on body length.

		N	R (x)	R (y)	b	a	F	r^2
Brood 1	M	4	287 - 312	26 - 28	0.046 ± 0.1343		0.120 ns	
	F	4	300 - 316	20 - 26	0.220 ± 0.1506		0.135 ns	
Brood 2	M	9	265 - 343	28 - 34	0.072 ± 0.022	8.95 ± 0.767 ***	10.751 ***	0.6057
Brood 3	M	10	320 - 335	31 - 37	0.148 ± 0.0845		3.072 ns	
	F	13	300 - 357	25 - 30	0.076 ± 0.0242	1.75 ± 0.662 *	9.772 *	0.4704
Brood 4	M	4	292 - 324	25 - 32	0.189 ± 0.0428	-30.08 ± 1.655 ***	19.452 *	0.9068
	F	7	303 - 317	20 - 24	0.187 ± 0.0913		4.188 ns	
Brood 5	M	5	303 - 314	27 - 30	0.251 ± 0.0660	-48.40 ± 1.300 ***	14.366 *	0.8272
	F	7	302 - 321	21 - 23	-0.013 ± 0.0691		3.350 ns	
Brood 6	M	5	272 - 300	28 - 31	-0.007 ± 0.0558		1.778 ns	
	F	4	288 - 310	22 - 24	0.053 ± 0.0580		0.873 ns	
Brood 7	M	9	292 - 303	27 - 30	0.024 ± 0.0894		0.073 ns	
	F	5	296 - 303	20 - 23	0.344 ± 0.2073		2.758 ns	
Brood 8	M	4	310 - 345	28 - 38	0.207 ± 0.1057		3.834 ns	
Brood 9	M	12	323 - 374	30 - 34	0.061 ± 0.0172	11.35 ± 0.458 ***	12.501 *	0.5556
	F	10	333 - 387	22 - 26	0.068 ± 0.0318		4.516 ns	
Brood 10	M	9	289 - 298	27 - 30	0.092 ± 0.0525		3.092 ns	
	F	8	290 - 313	18 - 23	0.088 ± 0.0836		1.099 ns	

Table 14. *Crotalus* , general samples, statistics of the regression of tail length on body length.

Sample		N	R (x)	R (y)	b	a	F	r^2	db	da
Afranio	M	14	337 - 1530	30 - 146	0.110 ± 0.0110	-7.66 ± 10.386 ns	101.031 ***	0.8938	ns	*
	F	20	905 - 1296	67 - 102	0.74 ± 0.0140	3.75 ± 2.744 ns	27.819 ***	0.6071		
Apucarana	M	7	564 - 1004	54 - 106	0.089 ± 0.0183	9.29 ± 6.046 ns	23.817 ***	0.8265	ns	*
	F	7	481 - 1189	32 - 92	0.84 ± 0.0068	-11.85 ± 8.137 ns	149.964 ***	0.9677		
Araçatuba	M	10	250 - 1193	22 - 122	0.109 ± 0.0050	-3.31 ± 11.534 ns	479.060 ***	0.9836	*	
	F	12	322 - 1216	19 - 80	0.069 ± 0.0027	0.47 ± 7.198 ns	661.533 ***	0.9851		
Brasília	M	18	320 - 1115	34 - 115	0.113 ± 0.0066	-7.80 ± 6.442 ns	291.982 ***	0.9480	*	
	F	19	345 - 1188	23 - 95	0.074 ± 0.0058	-3.14 ± 4.838 ns	166.267 ***	0.9072		
Campo Grande	M	9	321 - 1267	29 - 148	0.114 ± 0.0073	-7.13 ± 14.467 ns	243.360 ***	0.9720	**	
	F	11	325 - 1297	21 - 84	0.066 ± 0.0048	1.74 ± 6.965 ns	186.735 ***	0.9540		
Colina	M	8	596 - 892	57 - 102	0.142 ± 0.0284	-30.74 ± 6.558 **	25.011 ***	0.8065	***	
	F	13	550 - 832	34 - 59	0.059 ± 0.0132	7.32 ± 1.918 **	19.868 ***	0.6436		
Curitiba	M	6	800 - 1157	83 - 123	0.111 ± 0.0157	-2.55 ± 6.817 ns	49.876 **	0.9258	ns	*
	F	5	300 - 1273	25 - 104	0.074 ± 0.0107	-0.13 ± 14.613 ns	47.306 **	0.9404		
Goiandira	M	8	626 - 1076	63 - 116	0.088 ± 0.0097	17.74 ± 4.792 **	82.277 ***	0.9320		
	F	6	739 - 1045	56 - 88	0.064 ± 0.0273		5.453 ns			

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		

they are found to differ, the analysis is over. If, on the contrary, they agree, the two lines are reduced to a joint coefficient, and the new intercepts compared.

In every case where comparison was possible, males were found to have proportionately longer tails, either by a difference in slope ("db" on Table 11, 14 cases) or in intercept ("da" on Table 14, 18 cases). In the first instance, the difference increases with growth; in the second a fixed arithmetic difference is maintained.

Among the 47 samples with significant regression, the intercept did not differ significantly from zero in 43 — tail length in these may be represented by the ratio (actually the slope, *b*, of tail length on body length. This varies, in males, from 0.08 to 0.13 (mean 0.11) and in females from 0.05 to 0.09 (mean 0.07). Thus, in these cases, a majority, the tail of males may be said to be on the average 10% of body length, that of females 7%. This difference is large enough to permit visual sexing of the snakes.

The cases in which the regression of tail length in broods is not significant may be handled by parametric methods, as done with body length. In all cases males had longer tails.

As to other data on *Crotalus*, Klauber (1956: 156 *seq*.) has a brief discussion of sexual dimorphism in tail length of rattlesnakes, including *C. durissus terrificus*, name under which he grouped all South American rattlers. He has a table (his Table 4: 3, p. 158) of "average tail length of adults, expressed as a percentage of length over-all", having in mind the use of the character in systematics. The conceptual basis for this treatment was established in a previous paper (Klauber, 1943), on sexual dimorphism of tail length in snakes in general, with a special section on *Crotalus*. In this paper Klauber made convoluted calculations to obtain comparable estimates of relative tail length of adults. He made some use (as far as possible in his day) of regression analysis, and clearly acknowledged and discussed the dangers of "spurious correlation", i.e., the regression of a part on the whole. His data are not amenable to re-analysis, and are flawed by his adherence to "spurious correlation", but the differences come through clearly: males have longer tails than females. Beyond this it is not possible to go.

Unfortunately, Klauber's unsatisfactory method of dealing with body proportions has had a strong following. It is not always easy to retrieve from the North American literature data on relative tail length. For instance, Greene & Oliver (1965) have potentially very interesting data (sexual differences in tail length within broods of *Sistrurus catenatus tergeminus*), but the only information given is that the tails of males measure from 10.3 to 11.0 % of total length (average 10.7), while those of females vary from 7.4 to 9.3 (average 8.5).

Seigel (1986), as commented above, applied regression analysis to the tail length of *Sistrurus catenatus* from Missouri, and found significant differences, but did not publish the details.

Brown & Lillywhite (1992) present measurements of two broods of *C. c. cerastes* from the Mojave Desert. We computed the regression of tail length on body length for the sexes (broods combined). They are significant:

	b	a	F
Males	0.122 ± 0.0202	-4.33 ± 1.084	36.672 **
Females	0.021 ± 0.0068	6.96 ± 0.241	9.986 *

and the slopes differ significantly (*t* = 5.563 ***). The intercepts differ significantly from zero, so it is not legitimate to apply ratios.

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.

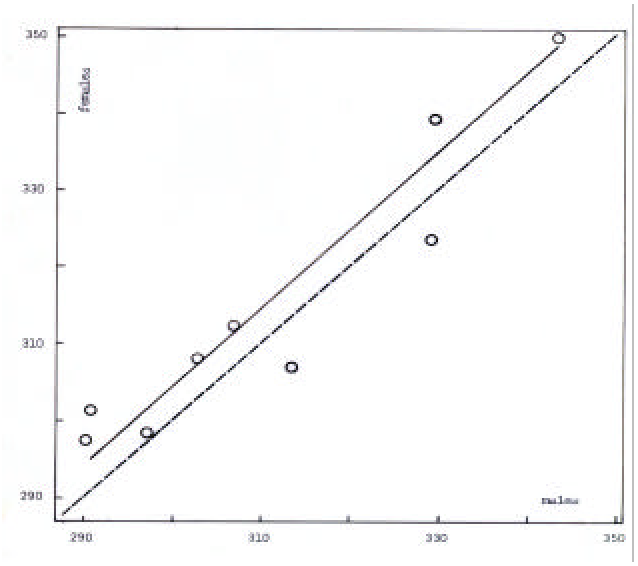
In the case of total length (Graph 3), *b* does not differ significantly from 1, but *a* differs from zero. Notwithstanding, the line of regression falls exactly on the line of evenness. Previous conclusions about this character are confirmed, but an easy and intuitive measure of dimorphism does not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

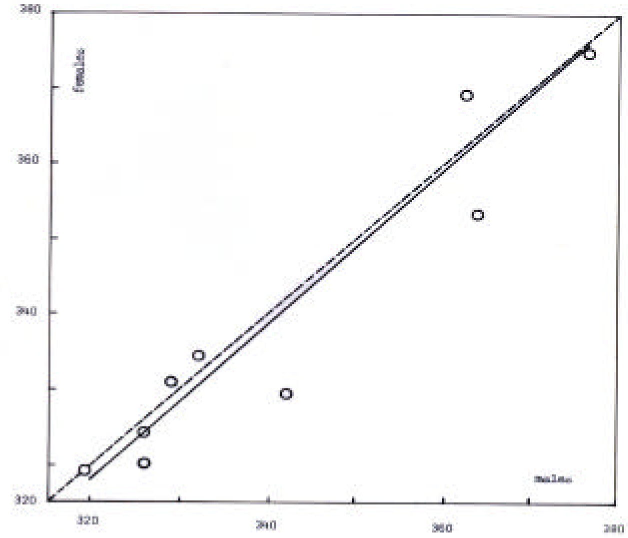
Table 15. *Crotalus*, broods, statistics of the regression of female on male means.

	N	b	a	F
Body length	61	1.015 ± 0.1100	-0.03 ± 3.214 ns	85.255 ***
Total length	61	1.046 ± 0.1107	-16.84 ± 3.534 ***	89.278 ***
Tail length (a)	61	0.944 ± 0.1706	-4.81 ± 1.002 ***	30.598 ***
(b)	57	1.140 ± 0.1221	-11.08 ± 0.769 ***	87.168 ***

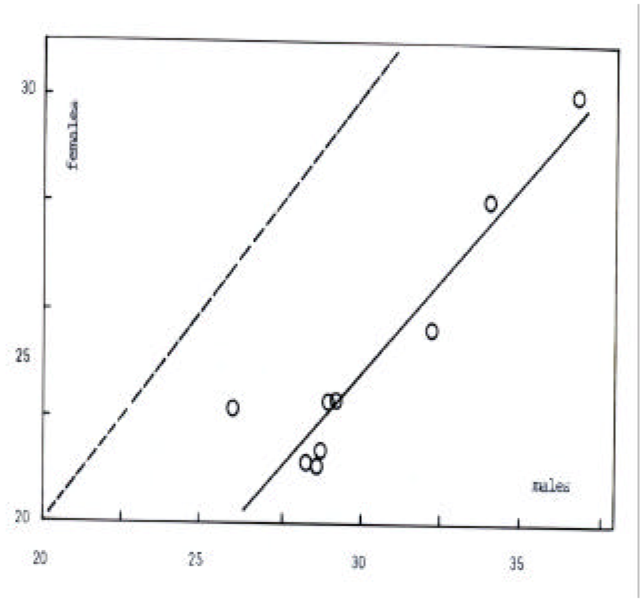
(a) all broods included. (b) brood 1 excluded.



Graph 2. *Crotalus*, broods, body length, regression of female on male means.



Graph 3. *Crotalus*, broods, total length, regression of female on male means.



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

Table 16. *Crotalus*, statistics of the distributions of frequencies of the number of young per brood.

	N	R	m	s	V
Klauber (1956)					
viridis caliginis	7	1 - 4	2.6 ± 0.37	1.0	38.0
lepidus klauberi	14	2 - 8	3.9 ± 0.44	1.7	43.0
mitchelli pyrrhus	10	4 - 8	5.5 ± 0.45	1.4	26.1
ruber lucasensis	15	3 - 12	5.7 ± 0.73	2.8	49.8
t. triseriatus	8	2 - 12	5.8 ± 1.15	3.2	56.4
p. pricei	6	4 - 7	5.8 ± 0.48	1.2	20.0
m. molossus	13	3 - 13	6.4 ± 1.00	3.6	56.7
viridis nuntius	10	3 - 10	7.0 ± 0.82	2.6	36.9
c. catenatus	57	2 - 14	7.8 ± 0.38	2.9	36.6
miliarius barbouri	15	2 - 18	7.3 ± 1.10	4.3	58.2
viridis lutosus	38	3 - 13	7.8 ± 0.47	2.9	37.3
viridis oreganus	79	1 - 15	7.9 ± 0.49	4.3	54.8
s. scutulatus	21	5 - 13	8.1 ± 0.48	2.2	27.3
viridis helleri	12	2 - 16	8.7 ± 1.19	4.1	47.5
r. ruber	28	3 - 20	8.7 ± 0.73	3.9	44.7
mitchelli stephensi	6	6 - 10	8.7 ± 0.67	1.6	18.8
cerastes laterorepens	27	5 - 16	8.9 ± 0.56	2.9	32.9
atrox	33	4 - 21	9.0 ± 0.66	3.8	41.9
unicolor	6	6 - 14	9.2 ± 1.14	2.8	30.4
horridus atricaudatus	7	7 - 11	9.7 ± 0.52	1.4	14.2
c. cerastes	10	7 - 18	10.0 ± 0.98	3.1	28.6
h. horridus	44	5 - 17	10.1 ± 0.45	3.0	29.6
v. viridis	307	4 - 21	11.4 ± 0.19	3.4	29.6
adamanteus	19	8 - 21	14.8 ± 1.01	4.4	29.0
Present work	8	7 - 17	10.8 ± 1.16	3.3	30.6

Table 17. *Crotalus*, data from the literature, brood size.

	N	R	m	s	V	source
durisus, Costa Rica	15	15 - 35	23.0 ± 1.48	5.7	24.9	(1)
triseriatus, Mexico	3	6 - 14	10.7 ± 1.96	3.4	31.8	(15)
vegrandis, zoo	4	3 - 6	4.0			(2)
zoo	6	2 - 8	5.0 ± 1.10	2.7	53.7	(3)
zoo	1	13				(4)
c. catenatus, Illinois	5	5 - 14	9.4 ± 1.60	3.6	30.1	(5)
Pennsylvania	4	5 - 7	6.3 ± 0.48	1.0	15.3	(6)
Missouri	17	4 - 10	6.4 ± 1.87			(7)
c. tergeminus, Texas/Kansas	7	3 - 11	5.3 ± 0.99	2.6	49.7	(8)
atricaudatus, S. Carolina	16	10 - 16	12.6 ± 0.52	2.1	16.7	(9)
horridus, Wisconsin	16	6 - 10	8.4 ± 0.29	1.1	13.7	(10)
t. triseriatus, Mexico	3	6 - 14	10.7 ± 3.40			(11)
viridis, California	35	4 - 25	10.0 ± 0.80	4.4	44.5	(12)
California	23	5 - 16	9.2 ± 0.63	3.0	32.9	(13)
British Columbia	28	2 - 8	4.6 ± 0.31			(14)

Sources: (1) Solórzano & Cerdas, 1988. (2) Murphy & Mitchell, 1979. (3) Carl, Peterson & Hubbard, 1982. (4) Muir, l984. (5) Wright, l941. (6) Reinert, 1981. (7) Seigel, l986. (8) Greene & Oliver, l965. (9) Gibbons, 1972. (10) Keenlyne, 1978. (11) Ramirez-Bautista et al., 1995. (12) Fitch, 1949. (13) Aldridge, 1979. (14) Macartney & Gregory,1988. (15) Ramirez-Bautista et al.,1995.

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.

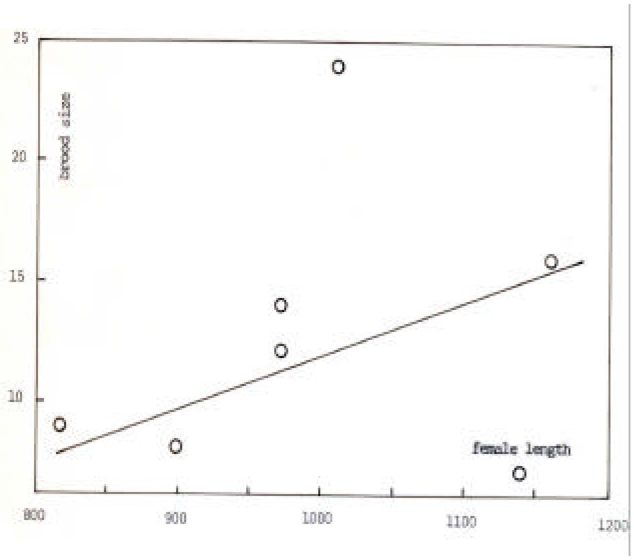
The available data on *Bothrops* are shown on Table 18.

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.

Table 19. *Crotalus*, statistics of the regression of brood size on mother length.

	N	R (x)	R (y)	b	a	F	r^2
Body length							
all broods	9	817 - 1160	7 - 24	0.009 ± 0.0177		0.263 ns	
expurgated	6	817 - 1160	9 - 17	0.026 ± 0.00067	-13.10 ± 1.37	14.537 *	0.7842
Total length							
all broods	8	878 - 1244	7 - 24	0.010 ± 0.018		0.330 ns	
expurgated	6	878 - 1244	8 - 17	0.024 ± 0.0058	-13.67 ± 1.37	17.554 *	0.8144

We offer these data not only as a first approach to an until now barren field, but also to stress the need for careful sampling, and to make clear the nature of our raw data.

The literature contains few data on this aspect.Wrigh (1941) has measurements of the mothers of 5 broods of *Sistrurus catenatus* from Illinois; the regression of brood size on mother length is not significant. Fitch & Glading (1947) have data on the number of embryos in 13 autopsied *C. viridis oreganus* from central California; there was no relatinship between mother length and number of young. Gibbons (1972) failed also to find regression in 16 *C. horridus atricaudatus* from South Carolina (embryos and enlarged follicles). Aldridge (1979) has a graph of the number of eggs against female body length of *C. viridis* from several (unspecified) localities in New Mexico. It is possible to recover the raw data from the graph and compute a regression, which turns out to be barely significant at the 5% level: F = 6.176, r^2 = 0.2192.

Comments

Sex ratio

No definite pattern emerges from the data on sex ratio of North American rattlesnakes. In 4 species males undoubtedly predominate; in the other 25 forms investigated there is no statistically significant predominance of either sex.

An extremely interesting fact, one that deserves better study, is variation of sex ratios in time (Berish, 1998; Hirth & King, 1968). The change observed by Berish occurring within the same year, was probably due to differences in vulnerability of males and females, caused by circumstances in the respective reproductive cycles. The change report by Hirth & King happened over a period of years; as proposed by the authors, it was probably due to differential predation on the two sexes by man, and thus would differ from the previous case as reflecting a real change in ratios, not a sampling bias.

In our materials there is no doubt about the evenness of the ratio; they thus conform to the general reptilian pattern (Parker & Plummer, 1987).

Size dimorphism

Except for the trivial matter of tail length, we found no dimorphism in size. On the North American side, reliable data are available on three subspecies of *C. viridis (viridis, lutosus* and *oreganus*), on *C. horridus* 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 added adequate databases and suitable statistical procedures.

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