

# Papéis Avulsos de Zoologia

PAPÉIS AVULSOS ZOOL., S. PAULO, 29 (15): 95-109

12.IV.1976

---

DISTRIBUTION AND DIFFERENTIATION OF ANIMALS ALONG THE COAST AND ON CONTINENTAL ISLANDS OF THE STATE OF SÃO PAULO, BRASIL. 3. REPRODUCTIVE DIFFERENCES BETWEEN AND WITHIN *MABUYA CAISSARA* AND *M. MACRORHYNCHA* (SAURIA, SCINCIDAE)

P. E. VANZOLINI  
REGINA REBOUÇAS-SPIEKER

## ABSTRACT

*M. caissara* and *macrorhyncha* are closely related species that occur in a small area on the coast and islands of São Paulo. Sharp differences in reproductive strategies are found between and within the species, indicating very local and efficient control mechanisms, in a spatial and ecological scale much narrower than accepted by current ecological thinking.

## INTRODUCTION

In a previous paper (Rebouças-Spieker, 1974) it was shown that *Mabuya caissara* Rebouças-Spieker, 1974, is probably a direct descendant of *Mabuya macrorhyncha* Hoge, 1946, that differentiated on the northern half of the coast of São Paulo within the last 11.000 years, following the post-glacial rise of the sea level and the consequent changes in the topography of the coast line. The parent species remains on the southern half of the coast and on the coastal islands, even the northern ones. Besides showing marked morphological differences, the two species have diverged in habitat preference, *caissara* living in grass clumps and *macrorhyncha* in thickets of ground bromeliads. Further data on the area and on the species, as well as on the aims and methods of this research project will be found in Rebouças-Spieker (1974) and in Vanzolini (1973).

In the present paper we discuss some features of the reproductive biology of these two viviparous species that can be gathered from the collections made for the systematic work. We are of course aware that our analysis cannot replace adequate longitudinal studies; in fact

it was undertaken to provide guidelines for one such study, already under way. It happens that some of the results are striking, and involve materials not easy to collect again, and so we feel they deserve publication.

#### MATERIALS AND METHODS

The specimens used were the same that served for Rebouças-Spieker's 1974 paper. The localities are shown on Map 1.

The specimens were dissected under a stereomicroscope, and the reproductive condition of the females scored: I, yolked eggs (diameter around 3.5 mm); II, embryos well formed, but still without scales; III, embryos with complete scalation, well pigmented, undistinguishable from the smallest specimens captured in the wild or born in the laboratory. We were not capable of unambiguously identifying corpora lutea and atresic follicles.

Measurements and statistical treatment were the same as in Rebouças-Spieker (1974). Table 1 summarizes the data. In further tabulations of the results, either all samples are individually listed or, when preliminary treatment so advised, assembled in three groups: (i) *Mabuya caissara*, (ii) coastal and (iii) insular *M. macrorhyncha*.

#### BREEDING CYCLE

Table 2 indicates that, as it is often the case with viviparous lizards (Tinkle, Wilbur & Tilley, 1970: 67) both species breed once a year. It also suggests that *M. caissara* breeds earlier than *M. macrorhyncha*.

Stage III embryos of *M. caissara* (10 specimens from two Ubatuba females) vary from 25 to 28 mm, the distribution being strongly asymmetrical to the left, with mode 25 and mean 26.0 mm. The smallest juvenile female (Ubatuba, December) measures 29 mm, and there is also one 34 mm specimen from Ilhabela in November. We may thus accept as probable that this species gives birth at least from early November to late December. Yolked eggs were found in Bertioga in February, indicating that breeding cycles follow each other rather closely, or perhaps overlap. Of course, given the intra-specific variation described below, we must keep in mind that these may be characteristics of the northern populations of *caissara* only, not of the species as a whole.

Thirty three stage III embryos from 9 Peruíbe females taken in December and January vary from 26 to 33 mm, the distribution being fairly symmetrical, with mean 29.4 mm. No significant differences were found between the two months (16 and 17 specimens respectively). One single female (February, Mongaguá) contained one embryo of 32 mm, representing either a brood of one or a last sibling of a brood just delivered; although the first alternative is more probable, a definite decision cannot be made, since there was only one pregnant female in the sample. The smallest female juvenile measures 34 mm (Peruíbe, January). We may then take as probable that coastal *M. macrorhyncha* gives birth to young a little longer than 30 mm, from





December to February. That February is the end of the season is indicated by the fact that only one female in eight was found gravid in Mongaguá.

The difference in length between the stage III embryos of *M. caissara* and *M. macrorhyncha* is highly significant (we applied the median test, given the asymmetry of the *caissara* distribution;  $p = 0,0022$ , Fisher's exact test).

#### AGE AT FIRST BREEDING

In the absence of long-term studies we tried an indirect method to ascertain this parameter. We plotted (Graphs 1 and 2) body length of the smallest female and of the smallest gravid female against month of collection, for the three groups mentioned above (*caissara*, coastal and insular *macrorhyncha*). As the data for the two species are not exactly comparable, we used as the starting point for the abscissas for *caissara* the earliest inferred month of parturition (November) and for *macrorhyncha* the month (January) corresponding to the smallest female.

Graph 1 (*caissara*) is highly suggestive. It indicates that in February the females of the season are not yet mature, and that by June they are found pregnant. Pregnancy would thus occur within the first year and last from June (or May) to November-December.

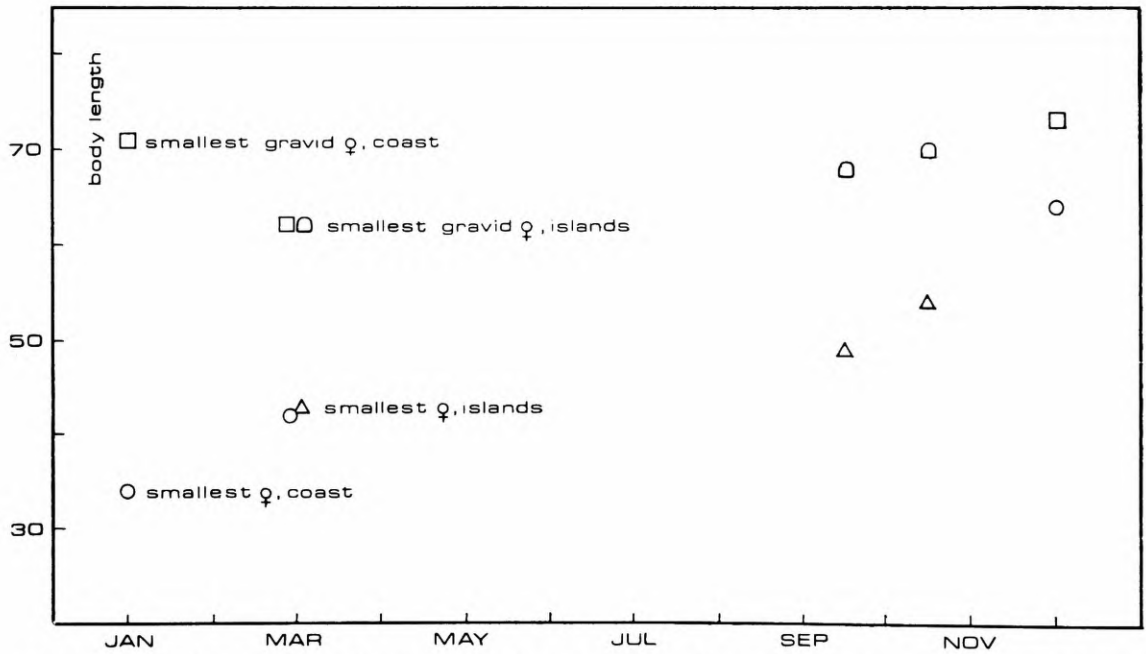
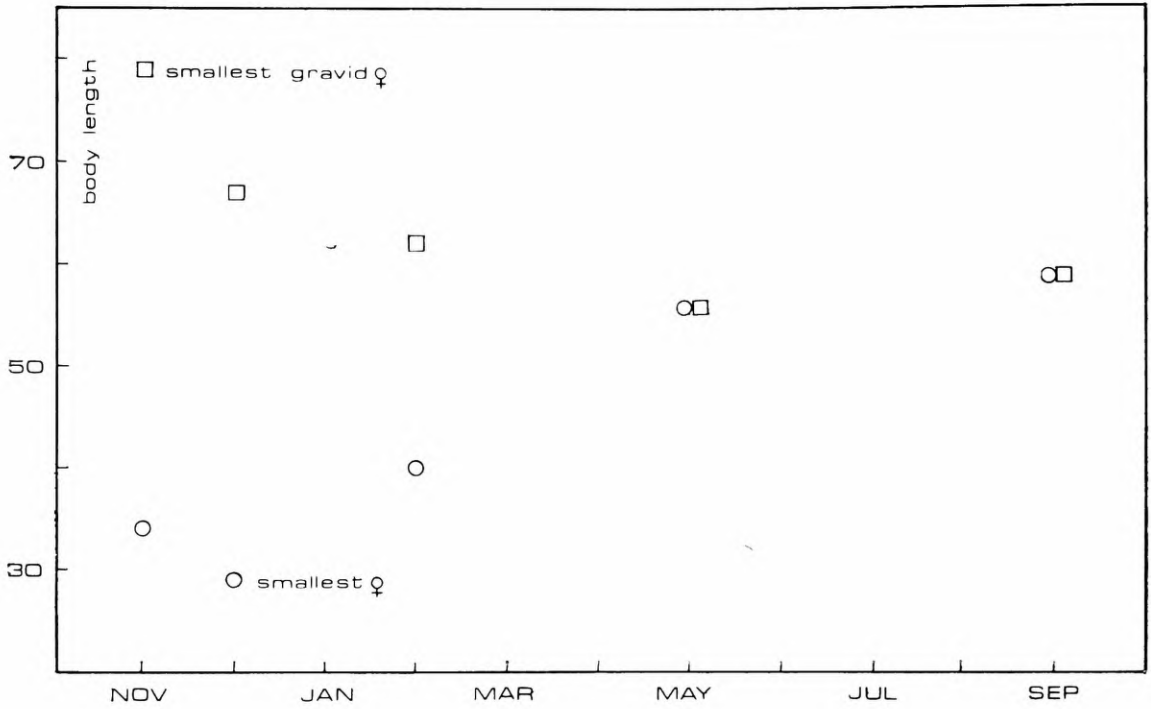
Graph 2 is much less clear, but suggests to us that *macrorhyncha* females do not breed in their first year, as in no month the smallest female (or one slightly larger) was found gravid. The alternative explanation, made possible by the presence of 60 mm pregnant females in March, would be an extremely short pregnancy; this would not be in good agreement with the data of Table 2. We are aware of the insufficiency of our *macrorhyncha* data to reach a definite conclusion, but it would seem clear that anyway a difference exists between the two species in this respect. On the other hand, it seems that there are no marked differences between coastal and insular *macrorhyncha*.

#### BROOD SIZE

In studying brood size we used females in all reproductive stages. This implies assuming that all eggs of stage I are viable, an assumption for which we have no definite evidence. However, comparison of the two Ubatuba samples, obtained in different months, shows that abortion rates must be low. Furthermore, the type and magnitude of the differences found are such that we are confident that our data, while not demographically perfect, are adequate to outline a complex and interesting situation.

#### Brood size vs female length

We found significant regressions of brood size on female body length in four samples of *Mabuya caissara*: Ubatuba, September and December, Caraguatatuba and S. Sebastião. The remaining *caissara*



Body length of smallest female and smallest gravid female, month by month. Graph 1, *Mabuya caissara*. Graph 2, *M. macrorsyncha*.

and all the *macrorhyncha* samples showed very definitely absence of regression. The data on the significant regressions are shown on table 3; the Ubatuba distributions and all the regressions lines are on Graph 3, and Graph 4 contains, for comparison, a typical *macrorhyncha* distribution, showing absence of regression.

In comparing regression lines one has to take into account the month of collection, since at least the young females grow steadily during pregnancy. This can be seen very clearly by comparing the two Ubatuba lines, of September, with young embryos, and of December, with embryos ready to be born. The two lines are parallel ( $t$  for the difference between the coefficients of regression being 0,92 for 13 degrees of freedom, probability between 0,4 and 0,3) but differ in elevation ( $t = 2.65$  for 14 degrees of freedom, probability close to 0.02).

The Caraguatatuba line agrees closely with the September Ubatuba regression. The two Ilhabela specimens do not permit a definite conclusion, but indicate presence of regression, and large broods.

The S. Sebastião line, however, differs markedly from all others. The difference in slope is clearly not related to the month of collection: if it were, it would be in the wrong direction, as the sample was collected in June, and should be above the other lines, not, as it is, considerably below. We take this to be a very real difference. When considering these regressions one must take separately the slope and the correlation. It is obvious that, as the regression coefficient decreases, the relationship between brood size and female length becomes less important as a reproductive strategy. Thus, S. Sebastião, with

Table 3

Data on regressions of brood size on female body length.

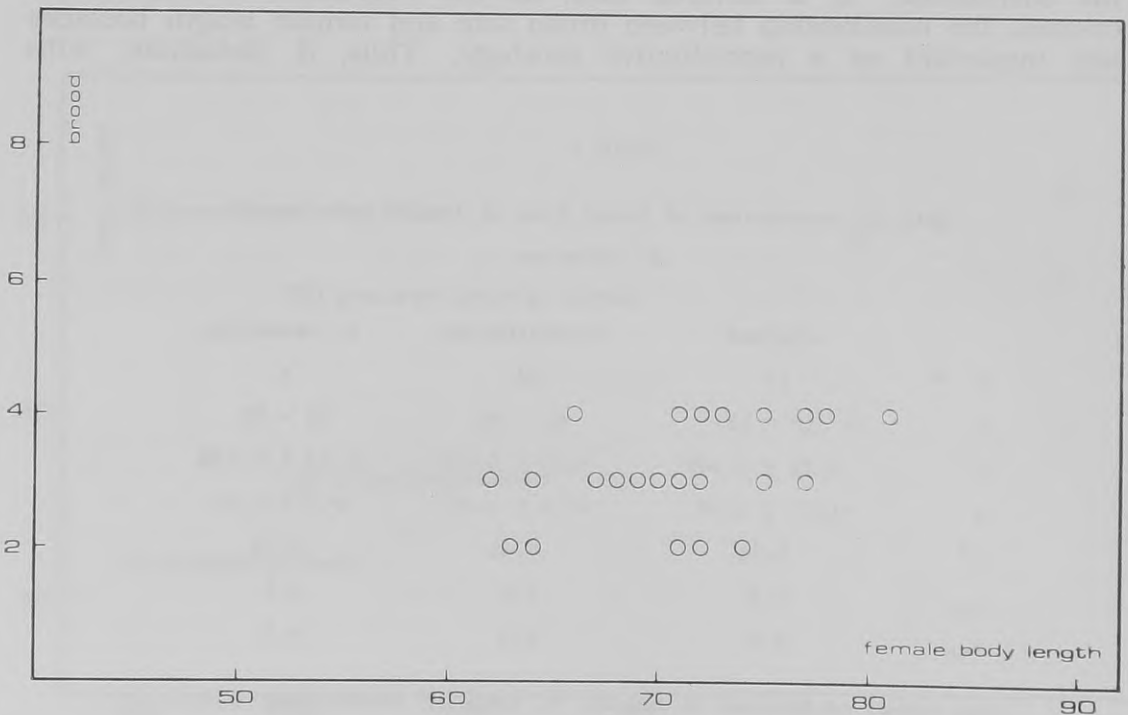
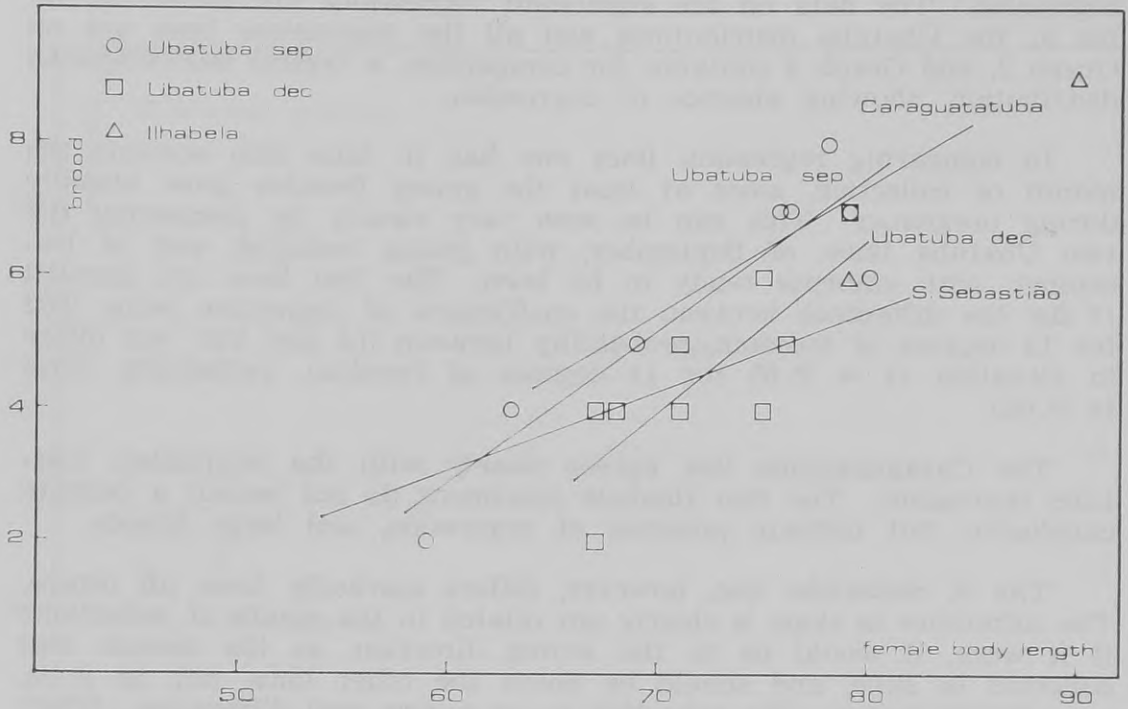
*M. caissara*

	Ubatuba	Caraguatatuba	S. Sebastião
N	17	14	9
R	59 - 83	65 - 84	55 - 81
b	0.25 ± 0.040	0.19 ± 0.049	0.12 ± 0.021
a	-12.7 ± 2.94	-7.8 ± 3.44	-4.1 ± 1.47
r <sup>2</sup>	0.71	0.56	0.80
y <sub>60</sub>	2.3	3.6	3.1
y <sub>90</sub>	9.6	9.3	6.7

N, number of females in sample. R, range of female body length.

b, coefficient of regression ± its standard deviation. a, regression constant ± its standard deviation. r<sup>2</sup>, coefficient of determination. y<sub>60</sub>, estimated brood size for female body length

60 mm. y<sub>90</sub>, ditto, body size 90 mm



Graph 3. *Mabuya caissara*. Regression of brood size on female body length. Graph 4. *Mabuya macrorhyncha*, Ilha dos Búzios. Scatter diagram of brood size on female body length.



its low regression coefficient, may be said to be intermediate between Ubatuba-Caraguatatuba and Bertioga. On the other hand, high correlations indicate that controls are strict, and this acquires still more importance in the case of low slopes, i.e., of small quantitative differences. This is what we mean by "efficient" controls in the context of this work: those associated with apparently small environmental changes or end results.

We show on Table 4 the distributions of frequencies of brood size in all samples. Some facts are evident, from the previous analysis, from inspection of Table 4 and from some further statistical elaboration.

Table 4

Distributions of frequencies of brood size

Brood	<i>M. caissara</i>					<i>M. macrorhyncha</i>						
	Ubatuba	Caraguatatuba	São Sebastião	Ilhabela	Bertioga	Coast			Islands			
						Enseada	Monaguá	Peruíbe	Vitória	Búzios	Alcatrazes	Queimada Grande
1							1	2				5
2	2		2			8		2	1	6	2	35
3	1	1	3		1	2		3	2	13	1	9
4	5	2	-		4	-		3	1	10		2
5	2	3	5		4	1		1	1			
6	2	4	2	1	3			1				
7	3	1		-								
8	2	1										
9		1		1								

#### Within *caissara*:

1. The northern *caissara* samples (Ubatuba and Caraguatatuba) agree in average size of brood, and have the largest broods of all, the average per female in the aggregate sample being 5.3 and the maximum observed 9.

2. The Ilhabela sample seems also to have large broods, as one of 9 was found in a sample of 2 females.

3. In S. Sebastião the maximum number found was 6. A chi square test between S. Sebastião and Bertioga gives a probability between 0.10 and 0.05; it is possible that fertility is about the same

in both localities, but better collections are needed. This is a geographical area that must be explored.

Within *macrorhyncha* on the continent:

4. Our materials afford only one reasonable comparison, between Enseada and Peruíbe, by the chi square test; in spite of the very striking asymmetry of Enseada, the difference is not significant ( $p$  between 0.20 and 0.10).

As for the insular samples:

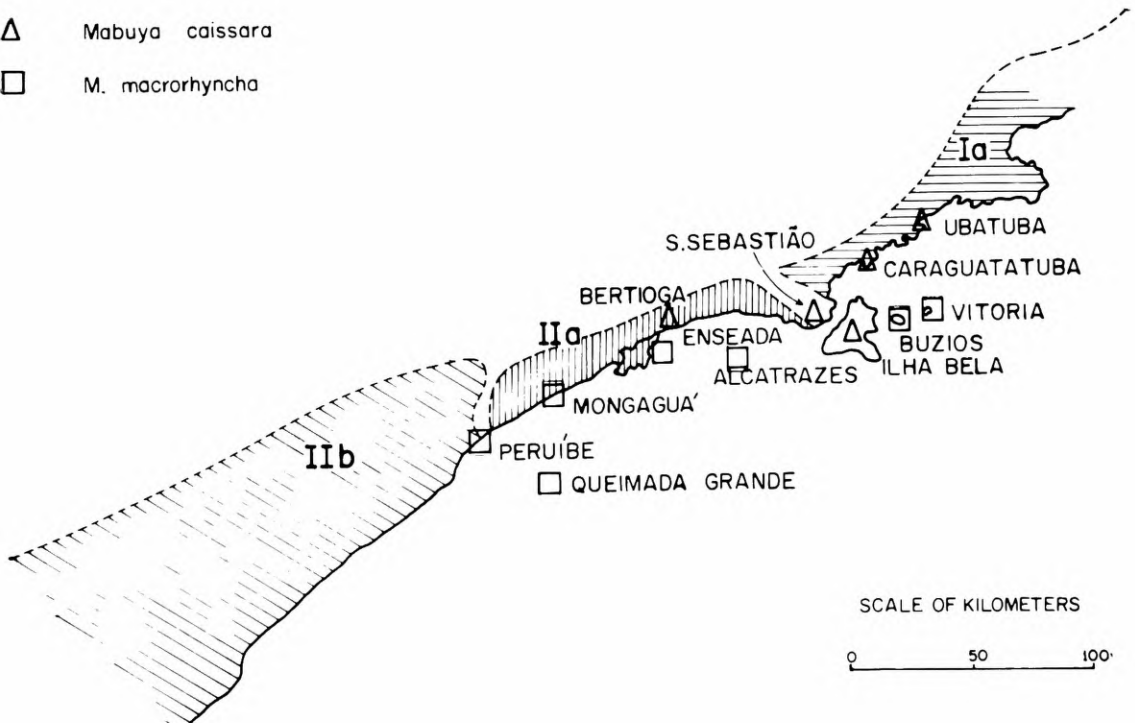
5. The Búzios and Vitoria averages are practically coincident, respectively 3.3 and 3.4.

6. Búzios and Vitoria agree with Peruíbe.

7. The difference between the northern islands and Queimada Grande is large, Queimada having the smallest broods of all samples studied.

△ *Mabuya caissara*

□ *M. macrorhyncha*



Localities of *Mabuya caissara* and *M. macrorhyncha* on the frame of Monteiro's (1973) climatic division of the São Paulo coast. Ia, area of predominance of equatorial and tropical air masses. II, area of predominance of tropical and polar air masses: a, northern segment; b, southern segment.

Finally, comparing *caissara* and *macrorhyncha*:

8. The most important comparison is that between Bertioga *caissara* and Enseada *macrorhyncha*. The chi square test affords a probability of less than 0.01, and it can be said that in general *caissara* has definitely larger broods than *macrorhyncha*. These two adjacent and sharply divergent populations are at present the subject of a continuing study.

#### ECOLOGICAL CORRELATES

Variation within *M. caissara*

As seen, the following intra-specific differentiation pattern was found in *M. caissara*:

1. The southernmost population, Bertioga, differs from the others in not showing correlation between brood size and female length. The next population to the north, S. Sebastião, approaches this condition in having a low regression coefficient. The two northern samples, Ubatuba and Caraguatatuba, have identical regressions, with high slopes.

2. Average brood size is consequently higher in the north than in the south: no significant difference was found between S. Sebastião and Bertioga, but this finding should be substantiated by further evidence. Anyway, either S. Sebastião equals in practice Bertioga in having small broods, or is intermediate between Bertioga and the northern populations.

3. The Ilhabela data are too few, but sufficient to indicate that average brood size there is larger than in adjacent S. Sebastião.

This geographic pattern shows that reproductive strategies can vary markedly within a very narrow geographic space. This is not, however, an ecologically homogeneous space, and it is possible to look for ecological correlates of the intra-specific variation.

The latest, and by far the best, analysis of the dynamic climatology of the state of São Paulo (Monteiro, 1973) contains much of interest to us. In what follows I quote freely from this work.

The coast of São Paulo is on the boundary between two climatic zones, the intertropical and the subtropical. The climates of the former are controlled by equatorial and tropical air masses, while in the latter control passes to tropical and polar masses. In Monteiro's chart 27 the boundary is seen to cut across S. Sebastião and Ilhabela.

On the northern part the participation of the polar masses in the causation of rainfall varies from 30 to 40%, the important connotation to us being that the area is much less subject to cold spells. The relief of the Serra do Mar, that is never far from the coastline and in many places reaches the sea, interacts primarily with the Tropical Atlantic mass, and as this has less moisture than the Polar mass, rainfall is inferior to that to the south.

The increase in rainfall does not follow latitude but rather the spatial arrangement of the relief and the direction of the coast line relative to the currents of the regional atmospheric circulation. In the area from Santos to S. Sebastião the coast describes a shallow arc with its chord almost dead East-West, and the Serra do Mar is perpendicular to the prevailing perturbed air currents from the South; this is the rainiest area in Brasil, with rainfall as high as 4.5 meters on the high slopes of the Serra.

We have then a parallel between rainfall and reproductive strategy in the northern (*caissara*) segment of the São Paulo coast; large broods, correlated with female body length, prevail in the northern, less humid part of the range, and smaller broods, unrelated to body sizes, in the southern part. It must be borne in mind that the actual differences are rather small when considered in the context of broad climatological patterns: Setzer's pioneer (1948) thermo-pluviometric data for the area, purely descriptive, and not related to the dynamics of the pluviometry, do not afford the insight of Monteiro's climatogenetic analysis. From the latter, however, it becomes quite clear that there may be present a temperature effect not revealed by the available summary climatological data: cold spells obviously are much more likely to happen in the area under control of the polar air mass than further north. Unfortunately, we have found no summarized data on cold spells in the literature, but latitudinal effects in this transitional zone (Monteiro, 1973, *supra*) should not be ignored.

The fact that Ilhabela resembles rather Ubatuba and Caraguatatuba than the neighboring S. Sebastião may be correlated to the fact that it lies in the same position relative to the open sea as the northern localities, while S. Sebastião is walled off by the broad and tall mass of the island (1300 m at the highest), and has significantly less rainfall (Setzer, 1946).

#### Variation within *M. macrorhyncha*

The fact that the only *M. macrorhyncha* population sampled that deviates from the norm is that of Queimada Grande looks especially interesting. Queimada Grande is an island made notorious by its endemic *Bothrops insularis*, a derivative of *B. jararaca*, not only differentiated on morphological grounds, but also in process of rapidly (on a scale of tens of years) developing a high percentage of intersexes (Hoge & al., 1961).

*Prima facie*, there is a strong argument in favor of the evolution of endemism in Queimada Grande. It lies 33 kilometers from Peruíbe, on the mainland, while Búzios is 7.5 km off the island of S. Sebastião (Ilhabela). Mere reduction of gene flow might seem to account for the Queimada peculiarities. It happens, though, that Búzios is only 7.5 km from the nearest *Mabuya* population, but that is *caissara*, not *macrorhyncha*, of which the nearest population to Búzios is Enseada, 110 km away as the crow flies, and with the bulk of the island of S. Sebastião on the way. Nevertheless, there must exist at Queimada some very peculiar set of circumstances, acting both on the differentiation of snakes and on the brood size of *Mabuya*. We must again look for very local and "efficient" controls at work.

### Differences between *caissara* and *macrorhyncha*

From the analysis above we may say that *caissara* (i) is born smaller, and (ii) earlier, (iii) has larger broods, (iv) probably matures earlier and (v) in part of its range shows correlation between brood size and female length. The matter of the later breeding season in the south (we have no adequate data on the islands) is probably correlated with the frequency of cold spells. For the other differences we find no obvious correlates.

The distribution of *macrorhyncha* presents some peculiar aspects. If it were considered on the mainland alone, it could be said that, while occupying part of the same pluviometric belt as southern *caissara* (Monteiro, 1973), the latitudinal distribution of cold spells might again be held responsible for the pattern observed. However, *macrorhyncha* is on Vitoria, Búzios and Alcatrazes, at the same latitude and very close to the island of S. Sebastião, which precludes any broad climatic common denominator. The only important feature in common remains the ancestral preference for ground bromeliads, in no way an explanation, but obviously a correlation.

### Summary

We have thus three patterns of geographical-systematic differentiation: (i) within *M. caissara*, an apparent direct correlation between climate and reproductive strategy; (ii) in Queimada Grande *M. macrorhyncha*, a clear endemism, parallel to that of *Bothrops insularis*, but so far without any identifiable correlates; (iii) in the remainder of *M. macrorhyncha*, an apparent uniformity, without a visible common denominator.

These three disparate patterns have however one thing in common: they can only be explained in terms of very local and efficient controls.

*M. caissara* and *M. macrorhyncha* are nowhere sympatric, although they very definitely differ in structural habitat (Rand, 1964). The divergence in habitat would seem especially designed to permit sympatry, especially in lizards with very restricted home ranges. However, *caissara* has not been able to gain a foothold in Búzios, Vitória or Enseada, across a few kilometers or less than one kilometer of sea, distances negligible to the pre-eminently seafaring *Mabuya*. The populations on both sides of such narrow gaps maintain strongly different reproductive strategies, just as it was the case with the intra-specific differentiation in either species. Again we must accept the presence of very local and efficient controls.

Evaluating these findings in the framework of current literature, one does not find any novelty in kind, but a striking one in geographical and ecological scale. The largest distance between localities in this study is 220 kilometers and, as said, contrasting patterns are found practically side by side. The climatic differences within the area of *caissara* have only recently been revealed, not on the basis of usual climatic parameters, but consequent on a detailed analysis of rhythms, differential participation of air masses and other refined techniques.

Equivalent phenomena have been usually ascribed to very broad ecological adaptations, mostly involving ample latitudinal contrasts, with frequent emphasis on tropical against temperate environments.

As an example, McCoy & Hoddenbach (1966) found differences in ovarian cycles and individual reproductive potentials between Colorado and Texas populations of *Cnemidophorus tigris* and concluded that they were responses to different climatic conditions. Tinkle (1969: 511) says, under the heading "Suggestions for further study": "Many more data are needed on age at first breeding in tropical and temperate species and particularly on wide ranging species that live under quite different environmental conditions in different parts of their ranges". The same line of thought is adopted by Tinkle, Wilbur & Tilley (1970) in their thorough review and re-elaboration of the literature, to which they add new data. Cody (1966: 183) goes as far as saying: "Predictions are made that all stable environments, the tropics, islands, coasts, will favor reduced clutches".

It has been brought to our attention (in fact we were not totally unaware) that these preliminary data of ours, the by-product of a taxonomic study, could be used, along the current lines of thought exemplified above, to frame predictions, or hypotheses to be tested, in the field (for instance) of K and r selection and related areas. That we choose not to do so reflects an informed bias, supported by the results of this analysis.

We think that the state of theoretical, predictive ecology, in what concerns tropical regions, demands at present not the verification of hypotheses, but rather experiments, in the words on the nineteenth century physiologist Claude Bernard, "pour voir".

It is not only that our finding an ample spectrum of reproductive strategies within such a narrow geographical and ecological compass indicates the need for looking for new parameters, or for so far neglected interactions between major parameters. It must be kept in mind that what are currently considered, albeit implicitly, cause-effect relationships, are nothing but examples of concomitance, accepted in the name of plausibility and based on very slim inductive basis, which can only be given significant weight by a broad spread of longitudinal studies.

As a corollary, it is obvious that there is no point in using the words "tropics" or "tropical" as if they had any precise or even approximate ecological meaning. The "tropics" are not a plot of convenient forest in Costa Rica; they are an enormous realm of patchiness, and any theoretical thinking based on presumed general properties is bound to become an ingroup exercise in short-lived futility.

#### ACKNOWLEDGMENTS

Aziz N. Ab'Saber and Carlos Augusto Figueiredo Monteiro have helped with geographical matters. E. E. Williams and J. F. Jackson have read the manuscript. The insular collections were made with help from the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP).

## REFERENCES

- CODY, M. L.  
1966. A general theory of clutch size. *Evolution* 20 (2): 174-184.
- HOGUE, A. R., H. E. BELLUOMINI, G. SCHREIBER & A. M. PENHA  
1961. Anomalias sexuais em *Bothrops insularis* (Amaral) 1921. (Serp. Crot.) Análise estatística da terceira amostra, desdobramento e comparações com as duas amostras anteriores. *An. Acad. Brasil. Ci.* 33: 259-264.
- HUECK, K.  
1966. *Die Wälder Südamerikas. Ökologie, Zusammensetzung und Wirtschaftliche Bedeutung.* xvii + 422 pp Stuttgart: Gustav Fischer Verlag.
- MCCOY, C. J. & J. A. HODDENBACH  
1966. Geographic variation in ovarian cycles and clutch size in *Cnemidophorus tigris* (Teiidae). *Science* 154 (3757): 1671.
- MONTEIRO, C. A. F.  
1973. *A dinâmica climática e as chuvas no Estado de São Paulo; estudo geográfico sob a forma de atlas.* 129 pp., 27 charts. S. Paulo: Instituto de Geografia da Universidade de São Paulo.
- RAND, A. S.  
1964. Ecological distribution in anoline lizards of Puerto Rico. *Ecology* 45 (4): 745-752.
- REBOUÇAS-SPIEKER, R.  
1974. Distribution and differentiation of animals along the coast and in islands of the state of São Paulo, Brasil. 2. Lizards of the genus *Mabuya* (Sauria, Scincidae). *Papéis Avulsos Zool.*, S. Paulo, 28 (12): 197-240.
- SETZER, J.  
1946. *Contribuição para o estudo do clima do Estado de São Paulo.* 239 pp., 130 tables, 87 diagrams, 23 maps. São Paulo: Departamento de Estradas de Rodagem.
- TINKLE, D. W.  
1969. The concept of reproductive effort and its relation to the evolution of life histories of lizards. *Amer. Nat.* 103 (933): 501-516.
- TINKLE, D. W., H. M. WILBUR & S. G. TILLEY  
1970. Evolutionary strategies in lizard reproduction. *Evolution* 24 (1): 55-74.
- VANZOLINI, P. E.  
1973. Distribution and differentiation of animals along the coast and in islands of the state of São Paulo, Brasil. 1. Introduction to the area and problems. *Papéis Avulsos Zool.*, S. Paulo, 26 (24): 281-294.

