

Papéis Avulsos de Zoologia

DISTRIBUTION AND DIFFERENTIATION OF ANIMALS ALONG THE COAST AND IN CONTINENTAL ISLANDS OF THE STATE OF S. PAULO, BRASIL. I. INTRODUCTION TO THE AREA AND PROBLEMS

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The general lowering of the sea level caused by the last glaciation uncovered a broad expanse of the continental shelf of southern Brasil, bringing the coast line considerably to the east of its present position. The succeeding post-glacial marine ingression flooded again the shelf and transformed into islands numerous mountains and hills arising from the generally flat and gently sloping platform.

These islands very much resemble, in physiography and vegetation, the outlying hills of the Serra do Mar, the long fault escarpment that parallels the coast. The fauna of each island is thus a sample of the general fauna of the area at the time of marine ingression, modified by contemporaneous intrinsic conditions, or by subsequent evolution, or both. The study of these insular faunas, compared among themselves and with the fauna of the mainland, must, therefore, afford insight into several evolutionary mechanisms, especially rates of evolution and the control of diversity, essential to the understanding of the processes that have determined the formation of complex tropical biotas.

Such comparative studies, having as raw materials natural situations not modifiable by the observer, must take advantage of similarities and differences between areas. In the present case the relevant features are climate, age, area, ecological diversity within islands, ecological similarity and diversity among islands, and accessibility from sources of immigrants.

In what follows I'll present a brief informal discussion of these aspects, both for the coast and for the islands. The pertinent literature will be the subject of an individual section.

THE COAST

The coast of southern Brasil is dominated by the fault escarpment of the Serra do Mar. This is composed of resistant gneisses, which have been little dissected by rivers, and thus the Serra appears as a rather even wall, usually some 800-900 m high, but somewhat lower to the South.

Our area of study, roughly from 23°15' to 24°30'S, is not physiographically homogeneous; two main regions may be discerned,

north and south of Santos. On the northern half the escarpment is very close to the sea, and sends forward spurs, very aptly described as "crab claws", enclosing small, steep beaches, backed by narrow alluvial plains. The coast line has a "drowned" appearance, and the islands are closer to it.

South of Santos the Serra recedes towards the interior, from 20 to 40 km, and thus the coast line is a series of long, gently sloping sand beaches. The islands are farther away than in the north.

In areas where the coastal plain is well developed one finds three parallel lines of sand ridges. The innermost, older and better consolidated, dates probably from the height of the Flandrian transgression. The intermediate ridge, poorly consolidated, coffee-colored, corresponds to the regression of the Flandrian transgression and is capped in places by old fixed dunes. The outermost ridge, Dunkirkian in age, is formed by very low (1-1,5 m), ill-defined and unstable dunes. Between the ridges the land is usually marshy.

CLIMATE

The climate of the southern Brazilian coast belongs, in Strahler's genetic classification, to the group of "climates controlled by tropical and polar air masses", and more specifically to the type "humid climates of the eastern and subtropical parts of continents, largely dominated by maritime tropical masses". The predominant air masses are the Tropical Atlantic and the Polar Atlantic.

Descriptively, the climate of the coast is a tropical humid climate (Köppen's Af), with rainfall of the driest month above 60 mm, average temperature of the warmest month above 22°C and that of the coldest month above 18°C. Table 1 shows data (from Setzer, 1946) from three evenly distributed coastal stations.

As one goes up the Serra do Mar, the precipitation rises dramatically, to above 4000 mm on the ridge, the heaviest rainfall in Brasil, not matched even in Amazonia.

VEGETATION

The escarpment of the Serra do Mar is, even today, fully covered by rain forest. This is part of the general Atlantic Forest, that extends approximately from 7° to 29°S. It is in this area a medium tall forest (10-20 m), closely canopied, with little undergrowth.

In the littoral zone three types of vegetation are found: (i) the customary open beach flora; (ii) on the sand ridges, a "restinga" vegetation, a dense tangle of small trees (maximum 15 m) and shrubs; (iii) fresh water swamps and marshes; (iv) mangrove.

THE ISLANDS

AGE

Age, or the duration of the latest period of isolation, is obviously relevant to the study of rates of evolution. In older and more isolated islands it would be also relevant to the general

Thermo-pluviometric data for selected localities on the S. Paulo coast

Locality	Itanhaem	Santos	S. Sebastião	Ubatuba	Ilha da Moela
Latitude	24°11'	23°56'	23°49'	23°26'	24°03'
Longitude	46°47'	46°19'	45°25'	45°04'	46°16'
Temperature (° C)					
Coldest month	Sep	Jun	Jul	Jul	Jul
	18.9°	18.6°	18.7°	18.1°	
Warmest month	Jan-Feb	Feb	Jan-Feb	Feb	
	25.0°	25.2°	25.3°	24.6°	
Year average	21.4°	21.9°	22.0°	21.4°	
Rainfall (mm)					
Driest month	Jul	Jul	Jul	Jul	Jul
	95	103	53	79	62
Wettest month	Feb	Mar	Feb	Jan	Mar
	239	298	214	289	178
Year total	1921	2232	1456	2295	1356

composition of the fauna, but in our case there are no grounds for expecting any noticeable amount of adaptive radiation.

Considering the relative evenness of the sea floor and the rapidity of the post-Wisconsin rise of the sea level, these islands may be considered as contemporaneous, and about 11,000 years old. This absolute datum permits to compare rates of evolution of a number of taxa in a given setting, and to evaluate the influence of varying conditions of the rate of evolution of a single taxon.

CLIMATE

We have no temperature data for the islands. For one of them (Moela) we have pluviometric records, that show that precipitation (1356 mm) is considerably less than on the coast.

GENERAL ECOLOGY

As said, these islands, with the exception of some low, flat-topped, wave-washed rocks, closely resemble the outlying disarticulated hills and spurs of the Serra do Mar. This means that they are peaks or ridges, predominantly gneissic, the forest-covered areas usually showing a deep mantle of regolith. There are no sand beaches or alluvial plains, only cliffs and strongly sloping wave-cut platforms. The outline of their coast is characteristically crenulated, and largely fringed with wave-cut blocks. This is not a favorable coast for the landing of rafted animals.

Several meters above sea level there are occasional benches, covered with vegetation similar to that of the restinga on the coast.

Forest in the islands is of the general Atlantic Forest type. Depending on topography and presumably soils, there are lower, more xeric, more intricate woods. In all islands there are sizable areas that have been cleared and are now covered with tall, dense grass (chiefly *Imperata brasiliensis*). Ground bromeliads, forming thickets on soil or bare rock, are extremely abundant, and so are cacti, growing mostly on bare rock slopes and cliffs. The only crop plant extensively cultivated is manioc, with some maize and a little sugar cane coming next.

The amount of deforestation caused by man has in no case resulted in complete clearing of an island. There is not much need for wood, as the sea brings in plenty, and many slopes are too steep for agriculture, besides, a local tradition exists of protection of springs.

AREA

The islands vary in area from a few tens of thousands to about 7.5 million square meters. It is important to notice that variation within this broad range may be practically isomorphic, small islands being replicas of large ones, with the same environments and general physiography. In such cases, effects of area on the fauna will be probably intrinsically such, and not indirect effects of area on the vegetation.

ACCESSIBILITY

The accessibility of an island to rafted animals depends on its distance from sources of immigrants, i.e., the coast or other islands, and on the pattern of surface currents. It is an important feature of any island, as it affords an estimate, however rough, of the intensity of gene flow.

Distances in this group of islands vary from less than 1 km to about 40 km. There is no set pattern of inshore currents. The Brasii Current flows well to the east of the outermost islands, but it may be important in long range dispersal. The rivers that run to the sea on this coast are very small, given the nearness of the escarpment. Thus any rafting to and from the coast must depend on the wind. From this viewpoint, the most important are SE post-frontal winds, that blow along vast fetches and pile up large amounts of water against the coast, being thus contrary to rafting to the islands.

As the position of the islands relative to the coast is reasonably uniform, accessibility to rafted animals would then seem to be mostly a function of distance. The same can be said for land birds, which also depend on distance and winds.

LITERATURE

The coverage of the geographical and biological aspects of this area is thin, and some of the publications obscure. However, the information exists, is generally competent, and the publications, once noticed, are not hard to find. By South American standards this is a fortunate area with regard to literature.

The works listed below deal with the general problems of the area; I have based on them (with a supplement of personal experience) the notes above. They contain the basic documentation or afford easy access to it. Data in individual islands will be found in the next chapter.

Very good geographical information on the whole coast and on the northern islands is found in the volumes of the geographical explorations of the state of S. Paulo in the first quarter of the century (see, in the bibliography, "S. Paulo, Estado — Comissão Geográfica e Geológica"). The charts, on the scale of 1:50,000, are very accurate, and there are good photographs and some ecological information.

The geomorphological evolution of the area is well covered in chapter 2, by A. N. Ab'Saber, of volume 1 of "A Baixada Santista", a geographical survey of the coastal plain around the city of Santos (Azevedo, 1965). Additional relevant geomorphological information is given by Ab'Saber (1962) and by Almeida (1953).

The best general work on the climate of Brasil and specifically of the southern coast is chapter 3, by C.A.F. Monteiro, of volume 4, part 1, of the geography of Brasil published by the National Geographical Council (see "Brasil — Conselho Nacional de Geografia"). Setzer (1946) discusses the climate of the state of S. Paulo, and presents many useful tables of temperature and rainfall averages. A good analysis of the dynamic climatology of the S. Paulo

coast is given by Occhipinti (1963), which contains an account of prevalent and dominant winds.

Information on the currents in the area is given by Luedemann (1970), Luedemann & Rock (1971) and Mascarenhas, Miranda & Rock (1971).

Hueck (1966) describes adequately the Atlantic forest. The vegetation of the coast of S. Paulo is covered by Andrade & Lamberti (in Azevedo, 1965). The fluctuations of sea level and their dates are discussed by Bigarella (1965). Soundings off the S. Paulo coast, necessary for dating the islands, are shown in the Brazilian Navy charts (see, in the bibliography, "Brasil — Marinha do Brasil").

EXPLORATION

Zoological collections have been made in several islands. The collections are very uneven, reflecting the varying composition and interests of the collecting parties and the length of their stay; with a few exceptions they are small.

These are difficult islands. None of them has anything remotely resembling a harbor. The only approach is by canoe, and the landing directly on boulders or on a grillwork of poles set on the rocks. The canoe has to be rapidly beached on the crest of an incoming wave (photo in Mertens, 1955a), or to stand by, the cargo being thrown ashore (photo in Hoge, 1950). This makes the transportation of equipment difficult and hazardous. Additionally, any amount of turbulence in the sea makes the approach impossible, even for the islanders, who are master canoemen. Thus large parties and extended stays become difficult, since even in the inhabited islands no provisions can be had locally, and in the uninhabited islands drinking and cooking water is always a problem.

The terrain is difficult, very steep, rocky or covered with tall, dense, slippery grass or with forest, the latter affording very insecure footing. In the inhabited islands the natives are good collectors, and satisfactory samples can be obtained in a relatively short time, given a favorable season. In the uninhabited islands a good representation can be had only after a series of visits. Thus, negative evidence on the presence of forms, very important in the study of faunas composed of few species, can be considered as reasonably reliable in the former case, but much less so in the latter.

Materials are available in Brazilian collections from the following islands.

SÃO SEBASTIÃO

This island differs in kind from the others here considered. It is not a flooded mount, but a complex horst. Its area, 336 km², is much larger than that of the others, and its separation from the continent minimal: the channel is, at the narrowest, 2 km wide, and in general very shallow, rarely reaching 4.5 m; its deep (13.5 to 46 m) part varies in width from 250 to 500 m.

There are no really comprehensive collections from the island; the published accounts (Luederwaldt, 1929, 1929a; Müller, 1968) reveal meager materials.

QUEIMADA GRANDE

Position: 24°30'S, 43°42'W; 33 km ESE of the nearest point on the coast, Ponta do Arpoador. *Area:* 430,000 m². *Highest point:* ca. 200 m. *Occupation:* formerly inhabited by lighthouse keepers and their families, abandoned in the twenties because of snake hazard (*Bothrops insularis*). *Expeditions:* a) from 1914 to 1920 the lighthouse keepers sent snakes to Instituto Butantan; b) A. Amaral (Instituto Butantan), 8 days in April and 10 in November, 1920 (Amaral, 1922); c) Instituto Butantan parties (A. R. Hoge, pers. comm.): April, 1947; October, 1947; April, 1948; July, 1948; March, 1952; January, 1953; June, 1953; November, 1953; March, 1954; July, 1954; September, 1959; June, 1966; d) A. R. Hoge (Instituto Butantan) and R. Mertens (Senckenberg Museum) November 23 to 26, 1954 (Mertens, 1955).

Accounts: Amaral (1927); Hoge (1950); Mertens (1955); all are general descriptions, Hoge and Mertens presenting good photographs and ecological notes. Photographs also in Leão (1950).

QUEIMADA PEQUENA

Position: 24°23'S, 46°48'W, 16 km SE of the nearest point of the coast, Praia de Peruíbe. 18 km NW of Queimada Grande. *Area:* ca. 80,000 m². *Highest point:* 67 m. *Occupation:* None. *Expeditions:* a) Instituto Butantan party, 3 days in September-October 1947 (Leão, 1950); b) A. R. Hoge (Instituto Butantan) and R. Mertens (Senckenberg Museum) November, 27, 1954 (Mertens, 1955a).

Accounts: Mertens (1955a), a very short account of a landing and one photograph.

THE ALCATRAZES GROUP

This is a group composed of: one large island, Alcatrazes proper; two islets, Paredão and Sapata; and some rocks, not considered here.

ALCATRAZES

Position: 24°06'S, 45°42'W, 35 km S of the nearest point on the coast, Ponta do Saí; 35 km SW of the island of S. Sebastião. *Area:* 1,352,000 m². *Highest point:* 266 m. *Occupation:* Formerly inhabited by lighthouse keepers; abandoned before 1920. *Expeditions:* a) party from Museu Paulista, October 6 to November 4, 1920 (Luederwaldt & Fonseca, 1923); b) Instituto Butantan party, February, 1948.

Accounts: Luederwaldt and Fonseca (1923) present a very good description, with excellent ecological and botanical data, but without illustrations. The 1915 map of the S. Paulo Comissão Geographica e Geologica contains also good descriptions and a wonderful photograph of the whole archipelago.

PAREDÃO

Position: ca. 3 km NW of Alcatrazes. *Area:* ca. 30,000 m². *Highest point:* 50 m. *Occupation:* None. *Expeditions:* Instituto Butantan party, February, 1948.

SAPATA

Position: ca 3.5 km NE of Alcatrazes. *Highest point:* ca. 20 m. *Occupation:* None. *Expeditions:* Instituto Butantan party, February, 1948.

BÚZIOS

Position: 23°48'S, 45°08'W, 7.5 km E of the island of S. Sebastião. *Area:* 7,550,000 m². *Highest point:* 426 m. *Occupation:* a small settlement on the north side. *Expeditions:* a) A. R. Hoge (Instituto Butantan) and R. Mertens (Senckenberg Museum) November 28 to December 4, 1954 (Mertens, 1955a); b) party from the Departamento de Zoologia, S. Paulo, October 16 to November 2, 1963; c) ditto, March 28 to April 4, 1964. *Note:* A low islet, Sumitica (ca. 120,000 m²), 1.2 km to the south, has not been visited.

Accounts: A first and interesting report is that of Euclides da Cunha for a newspaper in 1904 (republished 1944). Mertens (1955a) gives a good description and photos. Bjornberg & Ellert (1955) discuss the geology. The 1915 volume of the Comissão Geographica e Geologica has a topographical description.

VITÓRIA

This is practically a double island, the two subequal members being joined by a narrow, low neck.

Position: 23°45'S, 45°00'W; 26 km SE of the nearest point on the coast, Serra da Lagoa; 1 km ENE of Búzios. *Area:* 2,213,000 m². *Highest point:* 240 m. *Occupation:* a small settlement on the north half. *Expeditions:* a) party from the Departamento de Zoologia, S. Paulo, March 15 to 28, 1964; b) ditto, March 29 to April 6, 1965. *Note:* One small island, Pescadores (ca. 145,000 m²), separated from the north half of Vitória by a narrow channel (minimum width 40 m) was briefly visited in 1964; its vegetation is very peculiar. An islet, Ilhote das Cabras (ca. 60,000 m²), 500 m to the west of Pescadores, remains unexplored.

Accounts: There is nothing published on Vitória, except for a laconic note in the 1915 volume of the Comissão Geographica e Geologica. Botanical notes of the late José Correa Gomes are kept in this Museum, and will be eventually published.

OTHER ISLANDS

Among the islands not yet explored zoologically, some 6 to 8 belong in the same class as the ones described above. Of these, Monte de Trigo is especially interesting. It measures about 1.3 million m², rises to 289 meters, and is 11 km S of the coast. It is inhabited by a highly inbred human population.

ZOOLOGICAL PROBLEMS

THE ISLANDS

A first approach to the problems whose investigation is made possible by the special features of these islands is the definition, for individual groups of animals, of the segment of the general

fauna represented in each island, and the comparative study of different islands and animal groups in this respect.

The fauna of small islands is usually, but not always, impoverished relative to the mainland, and the relationship may vary from group to group of animals. On the other hand, there are, in many cases, striking, and autoecologically unexplained differences in faunal composition between neighboring islands. This is usually attributed to accidents of colonization and extinction (species turnover). Features that can be profitably explored in this connection are the total area of the island, ecological diversity, and accessibility.

Also extremely important, but again not so easy to investigate, is the problem of the ecological niche of individual species, since insular niches may be broader, narrower or displaced relative to the mainland norm.

Among the more obvious and attractive problems posed by insular faunas is that of rates of evolution. These can be very favorably studied in reptiles, by using their many convenient quantitative characters. A number of forms of reptiles occur in more than one island, and from their comparative study one may expect valid information. The relevant factors here are those that determine population size (total area, area of favorable habitats; presence of competitors, predators and prey) and genetic isolation (as measured by accessibility).

With regard to this problem, an important point, both of concept and method, must be made: analysis of insular populations should not aim at simply demonstrating differences between them and the nearest mainland populations, but at examining the insular isolates against the pattern of differentiation of the species (or species group) on the continent.

An insular population that became isolated because of a sea level rise was, until the time of the rise, part of a general continental pattern. The contribution of insularity to the divergence should thus be assessed against the type of differentiation between continental populations, at least along a relevant coastal belt. Only differences above and beyond those found on the continent may be safely attributed to isolation in the island.

This has not been standard procedure, and the literature is cluttered with meaningless subspecies, insular and continental, as a monument to defective methods and insufficient information. Of course, methods are easy to improve, but information is a different matter.

From the viewpoint of coverage of broad ranges, there are not at present many species of which sufficient materials can be assembled, after pooling the collections of many institutions, to guarantee that adequate samples are available from all the territory. From the viewpoint of ecological information, the lack is still greater. Few museum samples are accompanied by natural history data; these, when present, refer usually to general habitat preferences, or, incidentally, to predator-prey relationships. Significant data can only be obtained by means of specific research, often through the collaboration of many individuals; the coverage of large areas is naturally labor and time-consuming.

It is thus obvious that ideal cases are few, and that much personal judgment will be involved in deciding whether a particular

problem is worth investigating, in view of its limitations. In our case, a reasonable amount of information is available for several species, and this can always be supplemented by further field work, since the more immediately relevant areas are not very large and are easily accessible.

In analyzing the geographical differentiation of species or species groups, I have for some time (Vanzolini, 1951; Vanzolini & Williams, 1970) preferred a character-by-character study of the available samples, searching for areas of stability and of steep change in individual characters and for common denominators among characters. This method usually provides intelligible patterns of differentiation, and points to problems amenable to experimental approach, and to the critical or favorable areas for that.

In the case of insular animals, however, a further step would be extremely useful. Gene flow to and from islands differs much in character from that between neighboring mainland populations. There is not a belt of terrain across which gradients of adaptation or introgression can be established, permitting great versatility in the relationships between formerly isolated or differently adapted gene pools. Islands receive genetic material by short, infrequent spurts, across an all-or-nothing barrier. Furthermore, the relationship must be, except on very special cases, a highly asymmetrical one, since the impact of island genes on the much larger continental pool should be obviously much less than the contrary. The geographical and demographic limits of an insular population are, it is obvious, much sharper than those of usual continental populations.

Thus it would be very important to have an aggregate measure of divergence between insular and continental areas. The problem is theoretically simple, consisting essentially in the determination of a system of distances in a space of n dimensions (for n characters), and many models are presently available. If all relevant characters were metric, or could be assimilated to metric characters, several methods of multivariate analysis could be used. However, many characters cannot be adequately quantified, not even by the tolerant standards of numerical taxonomists, who have notorious faith in the robustness of their methods; we must face the reality that no satisfactory mathematical tool exists to estimate numerically the total degree of divergence between biological populations. More than in the field of phylogenetic relationships, the need for a mathematical model is urgent in the study of insular differentiation.

THE COAST AND PALEOCLIMATES

The ideal coast for this type of work would be an ecologically homogeneous one, included in a "core area" (Vanzolini & Williams, 1970) of character stability. This is not our case. We have three major causes of inhomogeneity to contend with.

One is the matter of the different relationships between the Serra do Mar and the coast line in the northern and southern halves of the area. The numerous "crab claws" of the northern segment result in a large number of small complex compartments; in the southern plain the types of environment run in strips parallel to sea and escarpment. It is obvious that these differences in topography must have important consequences to a number of species.

A second factor of inhomogeneity is climatic. As mentioned above, this is a transitional zone: some species, both belonging to northern and southern groups, have here their distributional limits. As of course the limits of the several forms are not coincident, but staggered, interactions between species must per force vary from place to place.

Finally we have to reckon with patterns of distribution and differentiation largely independent from present ecological conditions. It has been shown for Amazonia (Haffer, 1969; Vanzolini & Williams, 1970) that striking patterns of differentiation may occur within largely homogeneous areas, as a consequence of historical events, specifically paleoclimatic cycles. Present large continuous forests, such as the Amazonian, have in the past been reduced to a number of refuges separated by stretches of semi-arid open formations. The animals confined in these refuges differentiated during isolation; with the amelioration of the climate in the wetter part of the cycle, the refuges coalesced again into continuous forest, and the former isolates, brought into contact, interacted in many ways (Vanzolini, 1970).

In the case of the coast of southern Brasil, recent and drastic climatic cycles are well documented. For instance, two well defined pediments are found along most of the Serra do Mar, indicating erosion under semi-arid climates (Bigarella & Ab'Saber, 1964). That these pediments show local interruptions (Vanzolini, 1970), strongly indicates the presence of refuges at the times of pediment sculpture.

Conversely, we are now witnessing, in the present area of study, differentiation, and very fast, in open formation refuges. During the last dry episode (some 2600 years ago), an essentially continuous belt of sand dunes extended from the La Plata estuary to at least the northern coast of Rio de Janeiro. Lizards of the genus *Liolaemus* followed the northward spread of the dunes. At present, in the wet part of the cycle, there are some remnant dune areas on the coast of Rio de Janeiro. These are inhabited by *Liolaemus* that have diverged from the southern populations to the point of being considered good and unmistakable species (Vanzolini & Ab'Saber, 1968).

None of these aspects, climatic, geomorphological, ecological, evolutionary, has been adequately studied in our area. Thus, the analysis of insular phenomena has to follow *pari passu* with the necessary investigations on the continent. It is also to be expected that the latter will uncover problems deserving study on their own merits. In fact, some studies that have been completed along these lines confirm the expectations based on general grounds.

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