On the bird faunas of coastal islands of Rio de Janeiro state, Brazil

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RESUMO. **Sobre as avifaunas das ilhas costeiras do Estado do Rio de Janeiro, Brasil.** A avifauna de dôze ilhas costeiras do Estado do Rio de Janeiro (áreas 0,01 a 169,6 km²) foi estudada entre 1983 e 1984. Oitenta e oito espécies foram registradas nas ilhas. A correlação entre o número de espécies de aves terrestres (S_t) e a área (A) das ilhas foi significativa (p < 0,01) apenas para os dados transformados logaritmicamente, sendo marginalmente não significativa (0,05 < p < 0,10) para os dados não transformados. Nenhuma correlação foi encontrada entre número de espécies de aves marinhas (S_m) e A, provavelmente porque as aves marinhas são menos dependentes dos recursos das ilhas que as terrestres. Para curvas $S_t \times A$, tanto o modelo da função potência como o exponencial mostraram um bom ajuste aos dados, o primeiro tendo sido apenas um pouco melhor. Em regressões bivariadas $S_t \times A$ e distância, DNLM (distância para a área maior mais próxima, seja ela uma ilha maior ou o continente) mostrou-se ligeiramente superior a DC (distância para a costa). Nas distribuições das espécies individuais, parece haver um limite mínimo de área (por volta de 1 km²) para a ocorrência de quase todas as aves terrestres, mas este limite não se aplica às aves marinhas e a algumas espécies associadas ao homem. Algumas espécies terrestres foram encontradas em quase todas as ilhas maiores que a área mínima. Quatorze espécies foram encontradas exclusivamente na maior das ilhas estudadas, a maioria delas sendo especialistas e/ou de grande porte. Estes padrões de ocorrência são discutidos dentro do contexto das "funções de incidência" descritas por J.M. Diamond.

PALAVRAS-CHAVE: aves, biogeografia de ilhas, padrões de distribuição, ilhas costeiras, Brasil.

ABSTRACT. Bird faunas of twelve coastal islands of Rio de Janeiro state (areas 0.01 to 169.6 km²) were studied between 1983 and 1984. Eighty-eight species were recorded on the islands. The correlation between number of species of terrestrial birds (S_t) and area (A) was significant (p < 0.01) only for log-transformed data, being marginally not significant (0.05 < p < 0.10) for the untransformed data. No correlation was found between the number of species of marine birds (S_m) and A, probably because the marine birds are less dependent on the resources of the islands than the terrestrial ones. For $S_t \times A$ curves, both the power function and the exponential models showed a good fit to the data, the former being only slightly better. For bivariate regressions $S_t \times A$ and distance, DNLM (distance to the nearest larger landmass, either a larger island or the continent) performed slightly better than DC (distance to coast). There seems to be a lower limit for the area (about 1 km²) needed for the occurrence of nearly all terrestrial birds, but this limit does not apply to marine birds and to some species associated with man. Some terrestrial species were found on nearly all islands larger than the minium area. Fourteen species were found exclusively on the largest of the islands studied, most of them specialists and/or large birds. These distributional patterns are discussed within the framework of the "incidence functions" described by J.M. Diamond.

KEY WORDS: birds, island biogeography, distributional patterns, coastal islands, Brazil.

Since the formulation of the theory of island biogeography by MacArthur and Wilson (1967), many studies have been undertaken to discover the factors influencing the number of bird species on islands (e. g.

Vuilleumier 1970, Abbott and Grant 1976, Abbott 1978, Case and Cody 1987, Brown and Dinsmore 1988) as well as the composition of insular bird communities (e.g. Diamond 1975, Connor and Simberloff 1979, Gilpin and Diamond 1982). In Brazil, there are few ornithological studies on islands, especially with respect to terrestrial bird faunas (Oren 1982, Maciel *et al.*

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1984); no comparative studies of species-area relationships or patterns of species occurrences among a group of islands has been attempted.

In 1983-1984 a general biological survey was conducted on twelve coastal islands of Rio de Janeiro state ("Insular-Rio" expedition). Birds were censused on all these islands. Besides extending the known distribution of some bird species, these data can be used for two kinds of analysis: a) a quantitative one, trying to evaluate the importance of some island characteristics in the determination of species richness in these communities; b) a qualitative one, relating the known distribution of some species among the islands to some of their biological attributes.

STUDY AREA AND METHODS

The twelve islands visited (figure 1) vary in area over five orders of magnitude, from less than 0.01 km² (ilha dos Trinta-Réis da Barra) to 169.6 km² (ilha Grande) (table 1). Distances from the coast vary from 0.2 to 18.4 km. Areas and distances were calculated from nautical charts at scales of 1:100,000 and 1:400,000, provided by the Department of Hydrography and Navigation of the Brazilian Navy. Ten islands are part of a drowned landscape formed through sea

transgression ("land-bridge islands"). The long-term variations in sea level at this part of the coast, as described by Martin and Suguio (1978), indicate that they have been isolated for at least 6,000-7,000 years. The other two islands were formed by processes of sedimentation from the continent: Convivência (a deltaic island) and Pombeba (a "spitz" of marine deposition).

The most widespread vegetation type on the coastal plains of southeastern Brazil, as well as on the islands studied, is "restinga". "Restinga" assumes many forms but generally is composed of shrubs of xeric appearance, at variable densities, intermixed with clearings. The soils are white sand derived from marine deposition. For description and floristic analysis, see Araújo and Henriques (1984) and Henriques *et al.* (1986). Some islands show particular characteristics as well. Trinta-Réis da Barra and Costa are rocky islands where only low halophytes are found. Convivência and Pombas, quite disturbed by human action, are covered with cultivated fields with few remnants of native vegetation. Cabo Frio has a drier climate than the other islands and a rather xeric vegetation, although there are some transitional areas of mixed restinga-mesic forest with some elements of the Atlantic Forest. Similar transitional areas are found in Jaguanum and Itacuruçá. However, extensive areas of Atlantic Forest occur only on the mountain slopes of ilha Grande.

The census trips took place between July, 1983 and March, 1984. In order to make the data comparable, no literature or museum records were used, even when avai-
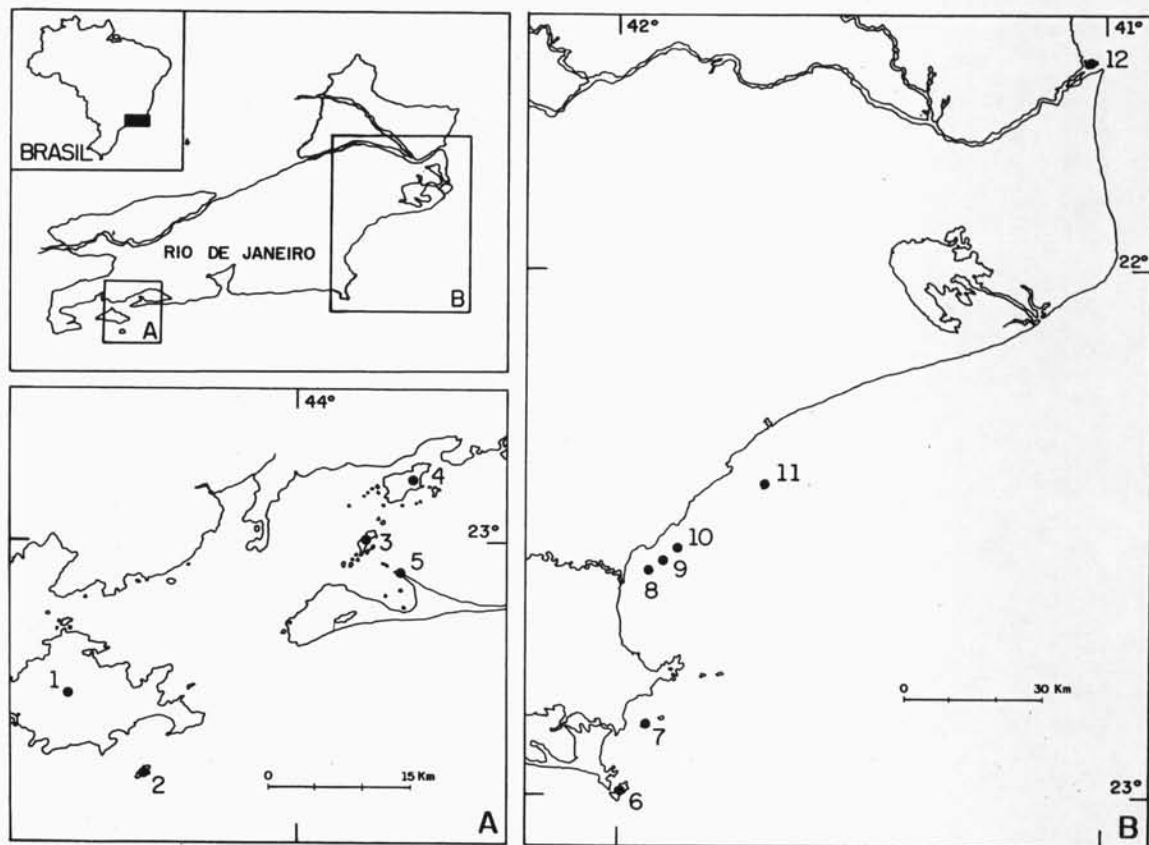

Figure 1. Islands surveyed: 1. Grande;   2. Jorge Grego;   3. Jaguanum;   4. Itacuruçá;   5. Pombeba;   6. Cabo Frio;
7. Comprida;   8. Trinta-Réis da Barra;   9. Pombas;   10. Costa;   11. Santana;   12. Convivência.

Table 1. Areas (A), minimum distances to coast (DC) and distances to the nearest larger landmass (DNLM), for the twelve islands visited in this study. DNLM is defined as the distance from a given island to either a larger island or the continent itself, whichever is nearer.

Island	A (km²)	DC (km)	DNLM (km)
Grande (1) [a]	169.6	3.6	3.6
Jorge Grego (2)	0.9	18.4	3.7
Jaguanum (3)	2.5	6.7	3.3
Itacuruçá (4)	8.3	0.8	0.8
Pombeba (5)	0.035	0.1	0.1
Cabo Frio (6)	5.6	0.4	0.4
Comprida (7)	1.2	2.8	2.8
Trinta-Réis da Barra (8)	0.01	0.65	0.35
Pombas (9)	0.03	0.2	0.2
Costa (10)	0.03	0.5	0.5
Santana (11)	1.0	7.0	7.0
Convivência (12)	0.6	0.2	0.2

[a] Numbers in parentheses refer to location of islands in figure 1.

lable for an island. One to seven days were spent on each island, depending on its size; birds were censused mainly by direct observation and captures with mist nets. In a few cases, it was necessary to shoot some individuals (mostly canopy birds) to allow a correct identification of the species. These individuals were deposited as voucher specimens in the Laboratory of Ornithology of UFRJ.

Because the sampling was short-term, it seems likely that the total numbers of species on the islands were higher than the numbers recorded, and that such bias was greatest in the case of the largest island, ilha Grande (two orders of magnitude larger than any of the other islands). As an attempt to reduce this problem, ilha Grande was excluded from the quantitative analysis. In the remaining eleven islands, total numbers of species seems to have been underestimated by a much smaller and more constant proportion, making their data more suitable — although admittedly not ideal — for quantitative analysis.

Three variables were measured for each island, in order to relate island characteristics to species richness (S): island area, in km² (A), minimum distance to coast, in km (DC) and minimum distance to the nearest larger land mass, in km (DNLM). DNLM is here defined as the minimum distance from a given island to either a larger island or to the continent itself, whatever is nearest. This definition implies that for coastal islands, DC and DNLM will coincide in several cases and therefore they are not independent variables.

The first two variables are the main determinants of species numbers on islands according to MacArthur and Wilson's (1967) equilibrium model. Distance to the nearest larger island (DNLI), an analog of DNLM, is also regarded as important by many authors since large islands at short distances may provide alternative sources of colonizing species (Vuilleumier 1970, Brown 1971, Schoener and Schoener 1983, Nilsson et al. 1988). However, for the case of islands along a coastline DNLI is not appropriate, because very often distances to the coast are much smaller than distances to any large island. DNLM, on the other hand, accounts for the nearest potential source of colonizing species.

The following statistics were calculated:
• Single correlations between S and A, S and DC, and S and DNLM.
• Single regression S × A by the power function model, log S = C + z. log A, and by the exponential model, S = C + z. log A. In both, C and z are fitted constants.

• Bivariate regressions S × A and DC and S × A and DNLM, in the form S = C + a.A + b.DC (or DNLM); C, a and b are fitted constants.

All analyses except for the single regressions were performed with both untransformed and log-transformed data (using Log 10). For the bivariate regressions, the log models consistently explained a greater part of the variance than their non-logarithmic analogs, so only their results are presented here.

Migratory species that clearly do not reproduce in the islands were excluded in the quantitative analysis. They are, however, included in the species list. The remaining species were also divided into two subsets, terrestrial birds and marine birds. Marine bird species were recorded for an island only when actually observed on the ground, rather than just flying over the island. Quantitative analysis were attempted both for the number of terrestrial bird species (S_t) and number of marine bird species (S_m). This separation is based on the assumption that number of species of marine birds, which forage over the ocean or along the shore, may relate to island variables in a different way than for terrestrial birds. The separate analysis of the two subsets aims to compare the roles of the variables in both cases as well as to test whether the assumed difference is true.

RESULTS

A total of 88 bird species, belonging to 14 orders and 32 families, were recorded on the islands; their distributions are shown in table 2. Four species (Charadrius semipalmatus, Arenaria interpres, Actitis macularia and Sterna maxima) were regarded as non-breeding migrants. Of the remaining species 78 were terrestrial (including waterfowl) and 6 were marine birds.

The correlation between S_t and A was high but non-significant for untransformed data (r = 0.583, 0.05 < p < 0.10). However, when logarithm transformations were applied, a highly significant correlation was found between either log S_t and log A (r = 0.928, p < 0.01) or S_t and log A (r = 0.857, p < 0.01). As the power function and the exponential

Table 2. Species recorded on the study islands. Nomenclature according Sick (1985).

Species	Trinta-Réis-da-Barra	Costa	Pombas	Pombeba	Convivência	Jorge Grego	Santana	Comprida	Jaguanum	Cabo Frio	Itacuruçá	Grande
Podiceps dominicus							+					
Sula leucogaster (M)			+	+		+	+	+		+		+
Fregata magnificens (M)		+	+		+	+	+	+	+	+	+	+
Ardea cocoi				+								
Casmerodius albus				+	+							
Egretta thula		+			+							
Florida caerulea					+							
Butorides striatus					+							
Nycticorax nycticorax				+			+		+			
Dendrocygna viduata		+										
Coragyps atratus					+							+
Cathartes aura				+	+	+	+	+	+	+	+	+
Buteo magnirostris						+	+	+	+	+	+	+
Leucopternis lacernulata											+	+
Milvago chimachima				+		+	+	+	+		+	+
Polyborus plancus												+
Laterallus viridis					+							
Rallus nigricans						+	+					
Aramides cajanea						+	+		+	+		
Haematopus palliatus (M)	+	+	+									
Charadrius semipalmatus (NB)					+							
Charadrius collaris					+							
Arenaria interpres (NB)	+			+								
Actitis macularia (NB)	+	+	+	+								
Larus dominicanus (M)	+	+		+	+	+	+	+	+		+	+
Sterna hirundinacea (M)	+	+		+	+				+	+	+	+
Sterna maxima (M,NB)	+	+							+		+	
Sterna eurygnatha (M)			+									
Columbina minuta					+					+	+	
Columbina talpacoti								+	+	+		+
Leptotila sp.							+			+		+

Table 2 (continued)

Species	Trinta-Réis-da-Barra	Costa	Pombas	Pombeba	Convivência	Jorge Grego	Santana	Comprida	Jaguanum	Cabo Frio	Itacuruçá	Grande
Amazona amazonica						+	+	+			+	
Piaya cayana												+
Crotophaga ani			+	·	+		+		+	+		+
Guira guira							+	+		+		+
Athene cunicularia										+		
Ceryle torquata					+		+	+	+	+	+	+
Chloroceryle americana					+		+			+	+	+
Colaptes campestris					+		+					
Furnarius rufus												
Synallaxis cinerascens												+
Lochmias nematura												+
Thamnophilus punctatus										+		+
Myrmotherula axillaris												+
Formicivora serrana										+		+
Drymophila squamata										+		+
Pyriglena leucoptera												+
Procnias nudicollis												+
Chiroxiphia caudata												+
Manacus manacus									+			+
Fluvicola nengeta							+	+	+	+	+	+
Machetornis rixosus									+		+	+
Megarhynchus pitangua									+			+
Myiodynastes maculatus			+						+			+
Myiozetetes similis			+									+
Pitangus sulphuratus					+	+	+	+	+	+	+	+
Myiarchus ferox									+			
Cnemotriccus fuscatus												
Hirundinea ferruginea												
Elaenia flavogaster							+		+	+	+	+
Camptostoma obsoletum							+		+	+	+	+
Tyrannus melancholicus									+	+		+

Table 2 (continued)

Species	Trinta-Réis-da-Barra	Costa	Pombas	Pombeba	Convivência	Jorge Grego	Santana	Comprida	Jaguanum	Cabo Frio	Itacuruçá	Grande
Progne chalybea		+										+
Notiochelidon cyanoleuca				·	+		+		+			+
Stelgidopteryx ruficollis												+
Thryothorus longirostris		+	+									+
Troglodytes aedon		+			+		+	+	+	+	+	+
Turdus rufiventris									+			+
Turdus amaurochalinus					+		+					
Anthus lutescens												
Vireo olivaceus							+		+	+	+	+
Parula pitiayumi							+				+	+
Geothlypis aequinoctialis						+		+	+		+	+
Coereba flaveola						+	+	+	+	+	+	
Conirostrum speciosum									+			
Euphonia chlorotica							+		+		+	+
Thraupis sayaca							+		+		+	
Thraupis palmarum								+				+
Ramphocelus bresilius					+	+	+	+	+	+	+	+
Tachyphonus coronatus							+				+	+
Thlypopsis sordida						+	+					
Saltator sp.						+						
Volatinia jacarina								+		+		
Sporophila caerulescens									+			
Sicalis flaveola								+				
Zonotrichia capensis									+	+	+	
Passer domesticus												+
Estrilda astrild												+
Total 78	7	10	9	10	20	14	29	18	35	25	27	49
Terrestrial birds 71	0	4	5	5	16	11	26	15	30	22	22	45
Marine birds 7	5	6	4	5	3	3	3	3	4	3	4	3

M = Marine bird   NB = Non-breeding migratory bird

Table 3. Results of the regression analysis for terrestrial birds. Symbols for the variables are: S_t, number of species of terrestrial birds; A, area (in km^2); DC, minimum distance to coast (in km); DNLM, distance to the nearest larger landmass (in km). Symbols for significance of values are:**, highly significant (p < 0.01).

a) single regressions $S_t \times A$

Power function model:

$\log S_t = 1.186 + 0.328 \log A$

$r^2 = 0.861$
$F = 49.71**$

Exponential model:

$S_t = 17.997 + 8.752 \log A$

$r^2 = 0.734$
$F = 22.10**$

b) bivariate regressions $S_t \times A$ and D (DC or DNLM)

$\log S_t = 1.183 + 0.313 \log A + 0.037 \log DC$

$r^2 = 0.867$
$r^2 (A) = 0.820$
$r^2 (DC) = 0.043$
$F = 22.88**$

$\log S_t = 1.196 + 0.311 \log A + 0.076 \log DNLM$

$r^2 = 0.885$
$r^2 (A) = 0.860$
$r^2 (DNLM) = 0.173$
$F = 27.02**$

models are based in regressions between log S and log A and between S and log A respectively, and the bivariate regression models used were logarithmic ones (see above), it was found appropriate to carry on the regression analysis for the case of terrestrial birds. For marine birds, in contrast, the correlation between S_m and A was found to be very low, not significant (r = 0.011, p > 0.50), and after logarithm transformations of either S_m or A or both the correlation remained always not significant. Therefore, marine bird species richness was found to be not related at all with area and no regression model was tested for S_m.

Analysis of the single regression models (table 3) showed that both the power function and the exponential models performed well in fitting the data for terrestrial species. The power function model was slightly better than the exponential in explaining the variance ($r^2 = 0.861$ and $r^2 = 0.734$, respectively); nevertheless both regressions were highly significant. The slope of the species-area curve in the power function model, the "z" parameter (which expresses the rate by which species numbers increase with the increase in area) was 0.328, falling within the range of values usually found for species-area curves for islands (0.18 − 0.35, according to Diamond and May 1976).

A bivariate regression using DNLM as the second independent variable explained a proportion of the variance only marginally greater than one using DC ($r^2 = 0.885$ and $r^2 = 0.867$, respectively); in both cases the regressions were highly significant and

explained a slightly higher proportion of the variance than the univariate models (table 3). Partial r^2's for A were always higher than the ones for either DC or DNLM.

DISCUSSION

Quantitative patterns. The non-significance of the correlation between number of terrestrial bird species and area may be due to the relatively small number of islands sampled; the value found for r (0.583) is quite high, yet even higher values of the correlation coefficient are required to produce statistical significance when only eleven points are available. Nevertheless, the same correlation was highly significant for log-transformed data, and the single regressions between S_t and A produced highly significant regression equations. Therefore, it seems justifiable to conclude that a species-area relationship was found for terrestrial birds, as one should expect, since the existence of such relationships is a recurrent pattern in ecology (Diamond and May 1976). However, there is much disagreement on the form of the species-area curve that best represents the relationship. The two models tested here have been the most often used for this purpose, although their relation to causal explanations are not clear; given this lack of a causal link, the recurrent forms of species-area curves should be considered an empirical pattern that has not yet been well explained (McGuinness 1984). As pointed out by

McGuinness, there is no unique "correct" model but both (or alternative ones) can give the best description of the species-area relationship in different particular situations. In the present study, the power function model showed a small advantage over the exponential, but what seems more important is that both described the relationship quite well.

In sharp contrast with the pattern found for terrestrial birds, for marine birds no relationship was found between number of species and area. This is probably because marine birds do not depend on the islands themselves for feeding, as they forage mainly in the surrounding sea. So island area should not be a crucial factor for the diversity of marine birds.

No significant correlation was found between bird species richness and distance to the coast, either for terrestrial of for marine birds. These results are not in agreement with the predictions of McArthur and Wilson's (1967) insular equilibrium model. The model predicts not only a positive correlation between species richness and area but also a negative correlation between species richness and distances to coast. The two following hypotheses are suggested to explain not finding a correlation with distance. 1) All the distances are so short that they are not a barrier at all to the dispersal of most birds. In this case, a correlation $S_t . \times D$ should not be expected even if the distances found may be an effective barrier to a minority of the species (see discussion on Formicariidae below). 2) Because the range of areas is greater than the range of distances, any correlation that could exist between S_t and distance would be obscured by the effects of the stronger simultaneous correlation with area. Area is usually found to explain a much larger proportion of the variation in species richness than distance does (Gilbert 1980); this is consistent with the partial correlation coefficients found for the bivariate regression equations (table 3). To separate perfectly the effects of the two variables A and D (DC or DNLM) is possible only in systems where there are many islands at varying distances within each range of areas; this is not the case in the present study.

However, there is some circumstantial evidence that distance may be related in some way to S_t, since the bivariate models including either A and DC or A and DNLM performed slightly better than the univariate $S_t \times A$ models. The replacement of DC by DNLM improved slightly the fit of the model, suggesting that for small islands, a large island closer than the continent provides an additional source of colonizing species.

Several variables not taken into account in our analyses surely influence numbers of species on these islands, for example degree of human disturbance and climate. The number of species of terrestrial birds on Cabo Frio (the island with driest climate) was lower than the expected value for all the four models tested, although the deviation was only 1.1 species for both bivariate models. However, it is noteworthy that the most sucessful model (bivariate with A and DNLM) explained over 88% of the variance in S_t; less than 12% remains to be explained by variables not in the equation. This result shows the robustness of such models, which help to understand much of the pattern regardless of the considerable local variation found among these islands.

There has been criticism of the use of data on patterns (e.g. parameters of species-area curves) rather than on processes (e.g. immigration and extinction rates) to discuss the validity of the MacArthur and Wilson model in particular situations (review in Gilbert 1980). There are alternative explanations for most of the patterns which have been proposed in the past as validations of the equilibrium model. For example, for the slope of the power function S × A curve the range of values $0.18 < z < 0.35$ has been declared consistent with the insular equilibrium model (e.g. Diamond and May 1976), and yet this range is to be expected for other reasons as well, even on purely statistical grounds (Connor and McCoy 1979). Critical tests of the insular equilibrium model must be based on data on the processes involved, that is, immigration and extinction rates. For birds, data on these rates are difficult to obtain because the time scales involved are very large (Gilbert 1980). Therefore, while our data may allow comparisons between models describing the patterns found in the relationships between number of species, areas and distances, they do not allow conclusive determination of whether these coastal islands are in a situation of insular equilibrium or not.

Qualitative patterns. Marine birds comprised a much larger proportion of the avifaunas on some of the smallest islands, with an area of less than 1 km² (Trinta-Réis da Barra, Costa e Pombeba; see table 2). This size seems to be below the minimum threshold necessary to maintain a viable population of most terrestrial birds. However, for marine birds this limitation does not seem to apply. Marine birds not only have a smaller dependence on the resources of the island itself, as stated above, but also may find especially good nesting sites on those small rocky islands. For example, *Sterna hirundinacea* and *Larus dominicanus* nested only on the smallest island, Trinta-Réis da Barra. It is noteworthy that some terrestrial birds which also feed on fish, the kingfishers (family Alcedinidae), were not recorded on the small islands although *Ceryle torquata* occurred on almost every island larger than 1 km² and *Chloroceryle americana* was also found on three large islands. This pattern may be related to avoidance of competition with marine birds such as *Sterna* spp. which occur in very great numbers on small rocky islands, or to

different preferences of nesting places (kingfishers nest on cliffs), or both.

The highest numbers of species of herons (family Ardeidae) are found on the intermediate-sized islands of Convivência (4 species) and Pombeba (3 species). Because Convivência is estuarine and Pombeba is separated from the coast by a natural channel, both are partially surrounded by slow-flowing, shallow waters, very suitable for the foraging techniques used by herons.

Some species distributions may be better understood if related to the concept of incidence functions developed by Diamond (1975). Diamond argued that among birds of the Bismarck archipelago each species had a characteristic pattern of occurrence related to the species richness of the bird community as a whole. Some species occurred only on very small, species-poor islands (supertramps); others occurred in communities with richness from intermediate to high (tramps); still others occurred only on the richest islands (high-S). These incidence functions seem to be related to certain biological attributes of the respective species. For instance, supertramps tend to be generalists and often quite vagile species, while high-S species tend to be those of large size, high trophic level and/or habitat or feeding specialists, which could not maintain viable population sizes in the smallest and simplest island communities (Diamond 1975).

In the present study no species corresponding to Diamond's supertramps was found. Supertramps have an upper limit to the complexity of communities where they can occur, but in our case even the marine birds which have often been found on the smallest islands, as stated above, were found on some of the largest as well (see table 2).

Many species were not found on any small islands, but occurred on some islands of an intermediate size and were found in almost every island above this size (e.g. the above mentioned *Ceryle torquata*, as well as *Vireo olivaceus*, *Coereba flaveola* and *Ramphocelus bresilius*; see table 2). The incidence function of these species is similar to the tramp pattern described by Diamond; they are common on islands with areas above 1 km^2. Such areas (or their corresponding species richness, as both variables are correlated) seem to be a minimum requirement for some terrestrial species. Islands of this size or greater present a vegetation roughly similar to that on the mainland, allowing the persistence of many bird species that depend on this vegetation.

Some birds are ubiquitous, being found on islands of almost any size; the most conspicuous examples of this pattern are synanthropic species such as *Pitangus sulphuratus* and *Troglodytes aedon*. Their distribution may be explained by the widespread human influence on these islands, rather than by any particular characteristic of the biological systems themselves.

Examples of high-S species might be found among the birds that occur only on ilha Grande, which is the most species-rich island, the largest, and by far the most complex. During this study fourteen species were found only on ilha Grande. Some of these species have biological attributes similar to those one would expect to find in high-S species. Examples are the hawk *Leucopternis lacernulata* (a top predator), the bellbird *Procnias nudicollis* (which requires large areas of continuous forests) and *Lochmias nematura* (a habitat specialist restricted to the vicinity of rivers, where it nests). Other species may be restricted to ilha Grande by more subtle ecological requirements.

The distribution patterns of some species may be related to biological attributes other than resource utilization. This may be the case of the antbirds (family Formicariidae). The antbirds found in this study (*Thamnophilus punctatus*, *Myrmotherula axillaris*, *Formicivora (serrana) littoralis Drymophila squamata* and *Pyriglena leucoptera*) were restricted to islands very close to the coast (Cabo Frio, 0.4 km, and Itacuruçá, 0.8 km) and to ilha Grande (table 2). This distribution may be related to their poor dispersal capacity (MacArthur *et al.* 1972) which may make it difficult for them to recolonize any distant island once the local population has gone extinct. Their distribution today probably corresponds to a few islands where such a replacement was possible, and ilha Grande where the large area would have allowed the continuous maintenance of populations after the isolation of the island by sea transgression.

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