The species-genus relationship in Antillean bat communities

by D.A. McFARLANE

Section of Mammalogy, Natural History Museum of Los Angeles County, 900 Exposition Boulevard, Los Angeles, CA 90007

Summary. — The ratio of the number of species to the number of genera in an island community has long been recognised as a potential proxy indicator of competitive interaction. An analysis of this relationship in the bat fauna of the Antillean archipelago demonstrates that the observed species-genus ratios are significantly depressed below null-model expectations, and that the magnitude of this depression is inversely proportional to the log of the appropriate island area. These observations are consistent with the hypothesis that interspecific competition may play an important role in structuring Antillean bat communities.

Résumé. — La proportion du nombre d'espèces par rapport au nombre des genres dans une communauté insulaire a été reconnue comme un indicateur d'interactions compéti-tives. Une analyse de cette relation dans la faune des chauves-souris de l'archipel des Antilles montre que les proportions d'espèces/genres que l'on observe sont réduites de manière significative par rapport à l'hypothèse du modèle et que l'importance de cette réduction est inversement proportionnelle au log. de la surface de l'île. Ces observations concordent avec l'hypothèse que la compétition interspécifiques peut jouer un rôle impor-tant dans la structuration des communautés de chauves-souris antillaises.

INTRODUCTION

Several authors (Elton 1946 ; Grant 1966) have noted the apparent decrease in the average number of species per genus in island communities when compared with their mainland equivalents. According to Darwin (1878 : 59) : « As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competi-tion with each other, than between species of distinct genera ». If this is the case, then as Harvey *et al.* (1983) have noted, competitive exclusion might be expected to distance congeneric taxa so that local communities should exhibit

species-genus ratios lower than those observed in the regional fauna as a whole. Furthermore, this effect should be strongest on small islands where extinction rates are high and the 'distancing' of congeneric taxa in niche space implies the extinction of one or more species.

The validity of this phenomenon has been questioned by Simberloff (1970) who noted that a decrease in the species-genus ratio must accompany a decrease in the number of species in the sample. In the most extreme case of an island with only a single species, the species-genus ratio must equal unity. The examination of 22 data sets, including assemblages of vertebrates, invertebrates, and plants, led Simberloff to conclude that in most instances the reported decrease in the species-genus ratio did not significantly exceed that predicted by null models generated from Monte-Carlo simulations. Simberloff also reported several instances of species-genus ratios in impoverished communities being higher than those predicted by the null models.

In this analysis I have tested the hypothesis that the observed species-genus ratios for Antillean island bat communities are lower than the ratios predicted by a null model generated by Monte-Carlo drawings from a regional species pool. I have also tested the hypothesis that the magnitude of the depression of the species-genus ratios is correlated with the size of the islands.

METHODS

A presence-absence data matrix of 56 species of bats extant on 25 Antillean islands was used to provide the regional species pool for the null model (Appendix 1). This species pool includes all taxa known to occur in the Antillean archipelago, sensu Baker and Genoways (1978), drawn from the literature through 1988. The 25 islands include all major and many minor members of the archipelago, with sizes ranging over 5 orders of magnitude.

Null-model species assemblages of sizes equal to each observed assemblage size were generated by randomized drawing without replacement from the species pool. For each observed species-assemblage size, 1000 Monte-Carlo simulations were performed and the mean and standard deviation of the mean number of genera were tallied. The probability of obtaining a value equal to or greater than the observed number of genera was determined directly by tallying the number of occurences in the simulation distribution ($N = 1000$).

RESULTS

The 25 islands included in this analysis support 14 different species-assembla sizes. Islands supporting assemblages of equal size also support assemblages wi identical species compositions, with two exceptions. The two islands supporti 12 bat species each, Grenada and Dominica, host 10 and 12 genera respective The two islands supporting 9 species each, St. Vincent and Montserrat, h 8 and 9 genera respectively. Table 1 summarizes the observed assemblage siz

the number of observed genera in these assemblages, the mean and standard deviation of the predicted number of genera derived from 1000 Monte-Carlo simulations, and the probability of equalling or exceeding the observed number of genera by chance alone.

In all instances, the observed number of genera exceeds the number of genera predicted by the null model (Fig. 1). A Wilcoxon Signed Rank test (Sokal and Rohlf 1981) of the differences between observed and predicted counts of genera demonstrates that the probability of obtaining this pattern by chance alone is very small (n = 25, T_s = 0, P < < 0.005). Similarly, a Paired t-test (Sokal and Rohlf, 1981) demonstrates that the observed and predicted numbers of genera are significantly different (t = 7.81, df = 24, P < < 0.0005).
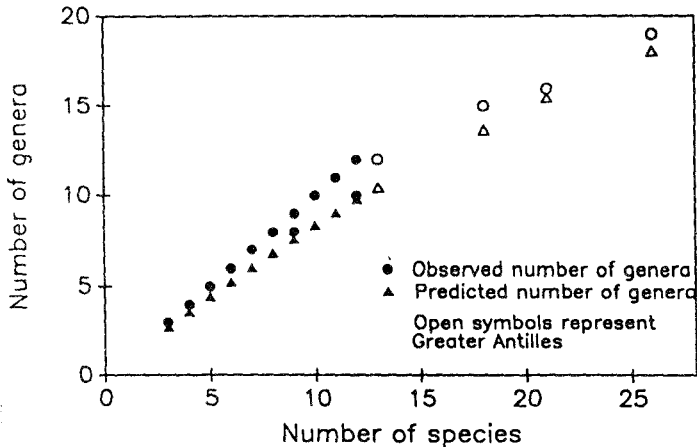

Fig. 1. — Relationship between observed and expected numbers of bat genera on Antillean islands of differing species-richness.

For assemblage sizes with only a single observed occurrence, the probabilities of obtaining the observed number of genera by chance do not fall below the 0.05 significance leve. For assemblage sizes with multiple observed occurrences in the archipelago, overall probabilities range from 0.055 to 0.068. Furthermore, Fisher's multiple probability test (Sokal and Rohlf 1981) demonstrates that the archipelago-wide observed pattern departs significantly from the null model (Fisher's statistic = 52.72, df = 32, P < < 0.025). Figure 2 illustrates the relationship between the species-genus ratio and the log of island area for the 25 islands. A simple linear regression analysis of this relationship demonstrates a significant slope (t = 5.10, P < 0.0005) and dependence of the ratio on island size (F = 25.99, P < 0.0005, r^2 = 0.531). However, the relationship is clearly curvilinear and is better fit by a third-order polynomial regression (r^2 = 0.738). The relationship between the observed number of genera on an island and the species assemblage size on that island is even stronger (linear regression statistics ; a = 1.64, b = 0.727, r^2 = 0.968, F = 686.69, p < < 0.0005). However Figure 1 illustrates that the size of the deviation between observed and expected numbers of genera increases with assemblage size in the Lesser Antilles, but declines in the Greater Antilles.

TABLEAU 1. — Summary statistics of the Monte-Carlo simulations. S = species richness (assemblage size). O = observed number of genera. M = mean expected number of genera based on 1000 Monte-Carlo simulations. SD = standard deviation of the mean expected number of genera. P = probability of equalling or exceeding the observed number of genera by chance. Island area data from Lack (1976) and Lazell and Jarecki (1985).

| Island	Area (Km2)	S	O	M	SD	P
Cuba	114,000	26	19	18.08	1.587	0.398
Jamaica	11,400	21	16	15.47	1.478	0.488
Hispaniola	80,000	18	15	13.66	1.414	0.277
Puerto Rico	9000	13	12	10.42	1.170	0.175
Dominica	800	12	12	9.787	1.120	0.052
Grenada	310	12	10	9.787	1.120	0.630
Guadeloupe	1500	11	11	9.062	1.078	0.076
Martinique	1100	10	10	8.337	1.009	0.113
Montserrat	100	9	9	7.590	0.969	0.176
St. Vincent	350	9	8	7.590	0.969	0.565
Gr. Cayman	180	8	8	6.823	0.887	0.235
St. Lucia	600	8	8	6.823	0.887	0.235
Antigua	280	7	7	6.050	0.847	0.329
Barbados	430	6	6	5.259	0.742	0.417
Barbuda	160	6	6	5.259	0.742	0.417
St. John	49	6	6	5.259	0.742	0.417
St. Martin	85	5	5	4.439	0.632	0.511
Anguilla	90	5	5	4.439	0.632	0.511
St. Eustatius	21	5	5	4.439	0.632	0.511
St. Thomas	70	5	5	4.439	0.632	0.511
St. Kitts	180	4	4	3.584	0.568	0.623
St. Croix	210	4	4	3.584	0.568	0.623
Guana	3	3	3	2.710	0.495	0.730
Tortola	54	3	3	2.710	0.495	0.730
Saba	12	3	3	2.710	0.495	0.730

14
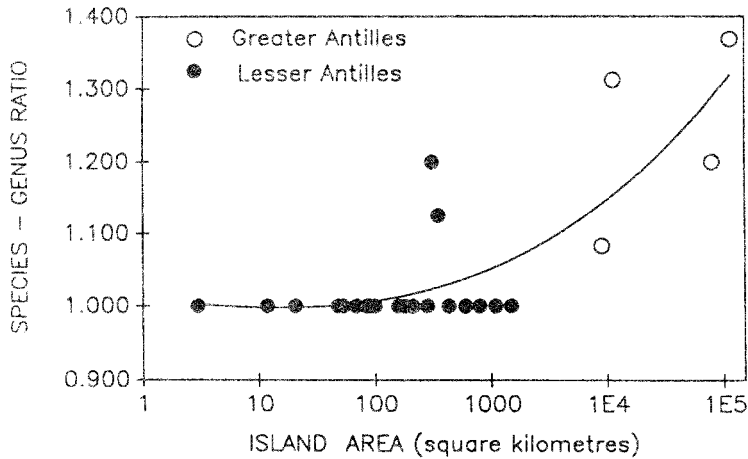
Fig. 2. — Relationship between the species-genus ratio and island area for the bat faunas of 25 Antillean islands.

DISCUSSION

The archipelago-wide pattern of bat species-genus relationships in the Antilles is consistently and significantly depressed below null-model expectations. Although individual island assemblages do not deviate from the null model at the 95 % significance level, this is to be expected with sample sizes of one. Hopf and Brown (1986) have addressed this general problem and emphasized the necessarity of examining multiple assemblages of differing species richnesses. The Fisher multiple probability test, the Wilcoxon Signed Rank test, and the Paired t-test (Sokal and Rohlf 1981) leave no doubt that the Antillean archipelago exhibits a highly non-random pattern of species-genus relationships.

Drawing biological conclusions from deviations in null models requires some confidence in the appropriateness of the regional species pool from which the null model is constructed. If the species pool is an amalgam of two or more discontiguous groups of species, null model species-genus ratios will be depressed. This would have the effect of reducing the probability of obtaining a significant difference between the observed and null model patterns (a Type II error ; Zar, 1984), which has not been a problem in this study.

It is also worthwhile to address potential differences between species assemblages, which are simply lists of bats occurring on an island, and communities which are assemblages of species spatially and temporally coexisting on an island. On small islands these terms will usually be synonomous, but on larger and higher islands that support multiple phytogeographic zones this may not always be the case. The effect of merging several island communities into one assemblage would be to raise the observed species-genus ratio, increasing Type II error in one tailed tests. As I have already noted, the Antillean bat data are not handicapped by Type II error.

Although depressed species-genus ratios may be considered concordant with Darwin's hypothesis of interspecific competition, Grant and Abbott (1980) have noted that many other forces or processes might be involved. A fauna with a long history of coexistence might contain a number of highly convergent taxa with similar niche requirements but generically distinct identities. Such taxa would have the potential for high levels of interspecific competition but would be characterized by a low species-genus ratio. It is possible that the smaller deviations between the observed and expected numbers of genera in the Greater Antilles, relative to the Lesser Antilles, may relate in part to this phenomena.

The adoption of Varona's (1974) conservative classification would reduce the endemic stenodermine taxa from four monotypic genera *(Ariteus, Stenoderma, Phyllops* and *Ardops)* to a single genus *(Stenoderma)* and correspondingly raise the species-genus ratios of simulated species assemblages. However, since the endemic stenodermines are distributed in a perfect checkerboard pattern (sensu Diamond, 1975), the species-genus ratios of the observed data sets would not be affected and the result would be to increase the dichotomy between the observed pattern and the null model.

The pattern of archipelago-wide depressed species-genus ratios exhibited by the Antillean bat fauna is counter to the generalized observations of Simberloff (1970), but is in accord with the specific case studies of the Galapagos Island finches, *Geospiza sp.* (Connor and Simberloff 1978 ; Simberloff 1984). Although there is little agreement as to the processes structuring the Galapagos avifauna, Harvey *et al.* (1983) have noted that on small islands with a narrow spectrum of resources competitive interaction should be enhanced and the species-genus ratios increasingly depressed. The demonstration in this study that the magnitude of the species-genus ratio shift in Antillean bats is indeed inversely correlated with island size provides some circumstantial support for Darwin's interspecific competition hypothesis. Taken together with evidence for a pattern of highly structured species co-occurrence in Antillean bat assemblages (McFarlane 1989), the argument that interspecific competition plays a significant role in the structuring of the Antillean bat fauna becomes increasingly persuasive.

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