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Patterns of Species Co-occurrence in the Antillean Bat Fauna

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in the Antillean Bat Fauna

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Summary. — The bat fauna of 25 Antillean islands is presented as a species presence-absence matrix, and used to construct a large population of randomized null-model matrices by Monte-Carlo simulation techniques. Comparison of the observed data matrix with the randomized population reveals a statistically significant departure from randomness which is interpreted as evidence of community structure. The Antillean bat fauna is marked by a pattern of high species co-occurrence, with endemics dominating in the northern Antilles and undifferentiated South American taxa dominating in the southern Antilles. The 'checkerboard' distributions which have been identified in the bird populations of some tropical archipelagoes are absent in Antillean bat fauna.

Résumé. — Les espèces de chauves-souris de 25 îles des Antilles sont, d'une part, récapitulées dans une matrice en présence-absence et, d'autre part, utilisées pour construire, au hasard, une longue série de matrices de distribution aléatoire. La comparaison de ces deux types de matrices montre que les données observées diffèrent de manière statistique-ment significative d'une répartition au hasard, ce qui est interprété comme une preuve de la structuration du peuplement.
La faune des chauves-souris des Antilles est marquée par un fort degré de coexistence des espèces, avec une dominance des endémiques dans les Antilles du nord et des taxons sud-américains indifférenciés dans les Antilles du sud. Les répartitions en damier qui ont été mises en évidence dans les populations d'oiseaux de quelques archipels tropicaux font défaut chez les chauves-souris des Antilles.

INTRODUCTION

The analysis of matrices of presence-absence data, based on lists of species from various islands, has usually been undertaken in one of two ways. In the first approach, plots of column totals (island species-richnesses) against island area and other physiographic parameters have been analysed statistically with linear and multiple regression models to investigate what has been called the species-richness/island area relationship (MacArthur and Wilson 1967 ; Connor and McCoy 1979). An earlier analysis of West Indian bats in a similar vein was undertaken by Koopman (1958), but without statistical treatment. Recently,

Lazell and Jarecki (1985) have attempted to identify « supersaturated » bat faunas on some very small islands within the British Virgin Islands.

The second approach to the analysis of presence-absence matrices involves the search for non-random patterns of positive and negative species associations (Simberloff 1978 ; Wright and Biehl 1982 ; Gilpin and Diamond 1982). The Gilpin and Diamond log-linear model was developed to overcome a problem inherent in earlier analyses by Connor and Simberloff (1979). In the Connor-Simberloff procedure, presence-absence matrices were shuffled and re-shuffled in multiple Monte-Carlo simulations to obtain 'randomized' matrices. The original data matrix was then compared to the population of computer-generated 'randomized' matrices and tested for statistically significant differences. Unfortunately, the Connor and Simberloff procedure, which reshuffles the matrix by locating and swapping elementary 2 × 2 submatrices, does not erase the checkerboard patterns of two or more species with mutually exclusive but geographically irregular distributions. Such patterns are characteristic of deterministic processes. If the 'null' model preserves the original checkerboard pattern then it will always be concordant with that pattern. Thus the Connor and Simberloff procedure is biased towards so-called Type II statistical errors.

Gilpin and Diamond (1982, 1984) solved this problem by developing a procedure based on incidence probabilities. Their technique is a powerful tool for illustrating community-wide trends of species co-occurrence.

I have used the Gilpin-Diamond technique to test the hypothesis that the co-occurrence of bat species in the Antilles is not random, but is structured by ecological 'assembly rules'. The data matrix consists of species lists for bats occuring on 25 Antillean islands.

METHODS

The probability that a given species will occur on a given island, its 'incidence probability', is defined by Gilpin and Diamond (1982) as

$$P_{ij} = R_i C_j / T$$

where P_{ij} is the probability that species i will occur on island j, R_i is the number of islands occupied by species i, C_j is the observed number of species on island j, and T is the observed total instances of species occurrences on the islands under study. Observed and expected numbers of shared islands for each possible pairwise species combination can be compared, and the standard deviate determined by the equation

$$D_{ik} = O_{ik} - E_{ik} / SD_{ik}$$

where O_{ik} is the observed number of islands shared by species i and k, E_{ik} is the expected number of islands shared by species i and k from the equation

$$E_{ik} = P_{ij} . P_{kj}$$

and SD_{ik} is the standard deviation of this estimate from the equation

$$SD_{ik} = P_{ij} . P_{kj} (1 - P_{ik} . P_{kj})$$

The null model in this procedure is a normal distribution of standard deviates (mean = O, standard deviation = 1) against which the observed distribution of standard deviates can be compared graphically and tested for non-conformity using the chi-squared statistic.

   The basic equations of Diamond and Gilpin (1982) were incorporated into
a microcomputer program written in GWBASIC (McFarlane 1987), and used
to analyse a data set consisting of 53 species on 25 islands (Appendix 1).
   The phytophagous bats (24 species on 25 islands), and the non-phytophagous
bats (29 species on 25 islands) were analysed as two seperate subsets.

RESULTS AND DISCUSSION

   The distributions of the observed and null model data from the analysis
of the data set and its two subsets are shown in Fig. 1, from which it is appears
that the observed distribution of standard deviates departs markedly from the
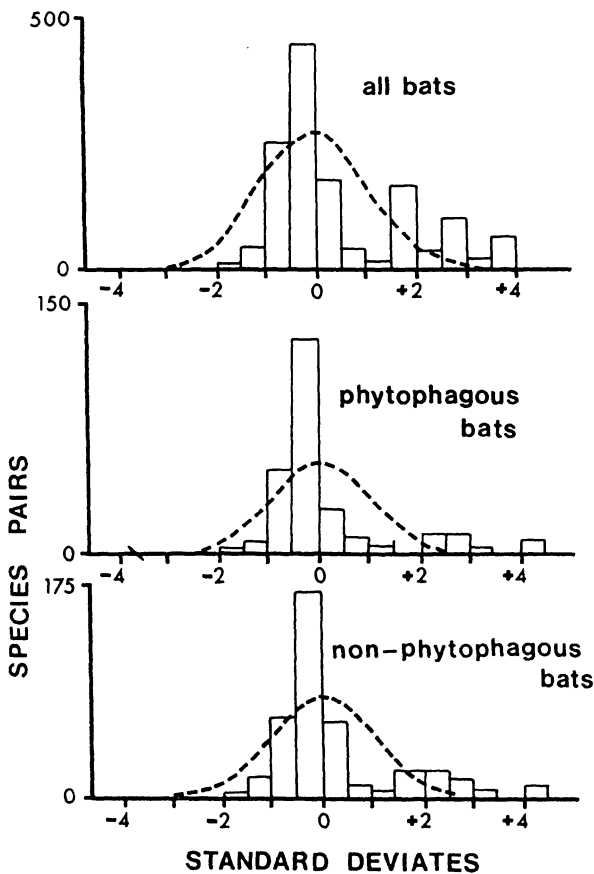

Fig. 1. — Observed (histogram) and null-model (curve) distributions of pairwise associations
   for Antillean bat species. Abscissa ; difference between the observed and expected
   number of islands shared by a species pair. Ordinate ; number of species pairs exhibi-
   ting such a difference.

null model in all three cases. Summary statistics (Table 1) show that the probabilities of drawing the observed distributions from the null model population are extremely small — in each case very much less than $P = 10^{-6}$. Table 2 provides examples of the 1378 possible pairwise combinations, selected to illustrate the range of biogeographic relationships.

TABLE 1. — Summary Statistics, Gilpin-Diamond Co-occurrence Analysis.

	# of Dik's	Chi-Squared	df	Probability
All extant	1378	17015	19	$< < 10^{-6}$ bats
Phytophagous	276	6168	19	$< < 10^{-6}$ species
Non-phytophagous	406	7709	19	$< < 10^{-6}$ species

Dik is the standard deviate of the difference between the observed and expected values according to the equation

$$D_{ik} = O_{ik} - E_{ik} / SD_{ik}$$

where O_{ik} is the observed number of islands shared by species i and k, E_{ik} is the expected number of islands shared by these species, and SD_{ik} is the standard deviation of this estimate.
    The probability values represent the likelehood of drawing the observed distributions from the null model distributions. Degrees of freedom (df) are also shown.

The data set and its two subsets show similar patterns ; a distribution with an elongate positive tail, shortened negative tail, and an excess of species pairs in the range of 0 to -0.5. This pattern corresponds to circumstances in which some species pairs occur very much more often than expected, whilst many more

TABLE 2. — Representative Taxa and Log-Linear Model Statistics.

	O_{ik}	E_{ik}	SD_{ik}	D_{ik}
Artibeus jamaicensis/ Brachyphylla cavernarum.	18	14.44	1.74	2.04
Carollia perspicillata/ Anoura geoffroyi.	1	0.05	0.22	4.24
Glossophaga longirostris/ Artibeus lituratus.	2	0.30	0.54	3.12
Phyllops haitensis/ Phyllops falcatus.	0	0.05	0.22	0.22
Carollia perspicillata/ Stenoderma rufum.	0	0.15	0.38	0.39
Artibeus lituratus/ Phyllonycteris aphylla.	0	0.10	0.31	0.31

For explanation of statistics, see text. Examples represent the following categories of biogeographic relationships : 1) Two widespread taxa. 2 and 3) Two undifferentiated South American invaders. 4) Two Greater Antillean endemics. 5 and 6) An undifferentiated South American invader with an Antillean endemic.

pairs occur slightly less often than expected. The majority of the taxa producing small negative distributions are closely related Greater Antillean endemics that show checkerboard patterns but have very restricted distributions. The endemic

Stenodermines *Ariteus, Stenoderma* and *Phyllops* are examples. Small negative deviations are also produced by pairwise combinations of some Antillean endemics with undifferentiated South American forms occurring on one or two of the southern Lesser Antillean islands, for example *Sternoderma* and *Carollia*.

High positive deviations are for the most part the result of the co-occurrence of taxa with only a single island distribution, but of more divergent taxonomic and ecological relationships — for example *Ariteus flavescens* and *Phyllonycteris aphylla* on Jamaica, or *Anoura geoffroyi* and *Carollia perspicillata* on Grenada. These high positive deviations reflect similarities in the origin or history of the species — high endemism on Jamaica, and recent immigration to Grenada.

In the data set and its two subsets, the absence of large negative deviations from the mean is marked. Large negative deviations would be expected to be produced by pairs of taxa which are both wide ranging and distributed in near-perfect checkerboard patterns. In contrast to the bird species of the Bismarck Archipelago (Gilpin and Diamond 1984), such taxa are conspicuously absent from the Antillean chiropterofauna. In the Caribbean region, checkerboard distributions are largely restricted to single island endemics. Wide ranging taxa such as *Artibeus jamaicensis* and *Brachyphylla cavernarum* exhibit high positive co-occurrence (Table 2).

Three conclusions can be drawn from this study :

1) The pattern of bat species co-occurrence in the Antilles is non-random, with many species pairs co-occurring much more often than is predicted by the null model.

2) Widely ranging species with checkerboard distributions are absent from the Antillean bat fauna.

3) The structure of bat assemblages on the Greater Antillean islands is dominated by the co-occurrence of single-island endemics, wheras a similar structure in the Lesser Antilles is dominated by the co-occurrence of undifferentiated South American taxa.

Appendix 1.

Presence-absence matrix for bats on 25 Antillean islands.

Compiled from literature sources through 1985; Baker and Genoways, 1978; Baker, Genoways and Patton, 1978; Jones, 1978; Lazell and Jarecki, 1985; Ottenwalder and Genoways, 1982.

Island Codes.

1 Jamaica	14 Barbuda
2 Cuba	15 St. Kitts
3 Hispaniola	16 Antigua
4 Puerto Rico	17 Montserrat
5 St. John	18 Guadaloupe
6 St. Thomas	19 Dominica
7 Tortola	20 Martinique
8 Anegada	21 St. Lucia
9 St. Croix	22 St. Vincent
10 Guana	23 Barbados
11 St. Martin	24 Grenada
12 Saba	25 Anguilla
13 St. Eustatius	

Species Codes.

1 Glossophaga longirostris
2 Glossophaga sorcina
3 Monophyllus plethedon
4 Monophyllus redmani
5 Anoura geoffroyi
6 Carollia perspicallata
7 Sturnira ludovici
8 Sturnira thomasi
9 Chiroderma improvisum
10 Artibeus cinereus
11 Artibeus jamaicensis
12 Artibeus lituratus
13 Ardops nichollsi
14 Phyllops falcatus
15 Phyllops haitensis
16 Ariteus flavescens
17 Stenoderma rufum
18 Brachyphylla cavernarum
19 Brachyphylla nana
20 Erophylla bombifrons
21 Erophylla sezekorni
22 Phyllonycteris obtusa
23 Phyllonycteris poeyi
24 Phyllonycteris aphylla
25 Peropteryx macrotis
26 Noctilio leporinus
27 Pteronotus parnelli
28 Pteronotus fuliginosus

29 Pteronotus macleayi
30 Pteronotus davyi
31 Mormoops blainvilli
32 Micronycteris megalotis
33 Macrotus waterhousii
34 Natalus stramineus
35 Natalus micropus
36 Myotis dominicensis
37 Myotis martiniquensis
38 Myotis nigricans
39 Eptesicus fuscus
40 Eptesicus guadaloupensis
41 Eptesicus lynni
42 Lasiurus borealis
43 Lasiurus intermedius
44 Nyticeius humeralis
45 Antrozous koopmani
46 Tadarida brasiliensis
47 Tadarida macrotis
48 Mormopterus minutus
49 Eumops auripendulus
50 Eumops glaucinus
51 Eumops perotis
52 Molossus molossus
53 Tadarida laticaudata
● 54 Mormoops megaphylla
● 55 Tonatia bidens
●● 56 Phyllonycteris major
● 57 Desmodus rotundus

● Not extant in the Antilles.   ●● Extinct taxon.

Phytophagous Species.   Remaining species.

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--------- ISLANDS -----------
SP1    00000 00000 00000 00010 01010      SP25  00000 00000 00000 00000 00010
SP2    10000 00000 00000 00000 00000      SP26  11111 11010 10011 11111 11110
SP3    00000 00000 00010 10110 11101      SP27  11110 00000 00000 00000 00000
SP4    11110 00000 00000 00000 00000      SP28  11110 00000 00000 00000 00000
SP5    00000 00000 00000 00000 00010      SP29  11000 00000 00000 00000 00000
SP6    00000 00000 00000 00000 00010      SP30  00000 00000 00000 00111 00010
SP7    00000 00000 00000 00011 11000      SP31  11110 00000 00000 00111 00010
SP8    00000 00000 00000 00100 00000      SP32  00000 00000 00000 00000 00010
SP9    00000 00000 00000 00100 00000      SP33  111F0 00000 00000 00000 00000
SP10   00000 00000 00000 00000 00010      SP34  11100 00000 01000 11010 00001
SP11   11111 11111 11111 11111 11111      SP35  11000 00000 00000 00000 00000
SP12   00000 00000 00000 00000 01010      SP36  00000 00000 00000 00010 00000
SP13   00000 00000 00100 01111 11000      SP37  00000 00000 00000 00001 00100
SP14   01000 00000 00000 00000 00000      SP38  00000 00000 00000 00000 00010
SP15   00100 00000 00000 00000 00000      SP39  01110 00000 00000 00000 00000
SP16   10000 00000 00000 00000 00000      SP40  00000 00000 00000 00100 00000
SP17   00011 10000 00000 00000 00000      SP41  10000 00000 00000 00000 00000
SP18   00011 10011 11110 11111 11101      SP42  11110 00000 00000 00000 00000
SP19   F1100 00000 00000 00000 00000      SP43  01000 00000 00000 00000 00000
SP20   00110 00000 00000 00000 00000      SP44  01000 00000 00000 00000 00000
SP21   11000 00000 00000 00000 00000      SP45  01000 00000 00000 00000 00000
SP22   00100 00000 00000 00000 00000      SP46  11111 00000 10111 11111 10000
SP23   01000 00000 00000 00000 00000      SP47  11000 00000 00000 00000 00000
SP24   10000 00000 00000 00000 00000      SP48  01000 00000 00000 00000 00000
                                          SP49  10000 00000 00000 00000 00000
F denotes occurrence only as a fossil.    SP50  11000 00000 00000 00000 00000
                                          SP51  01000 00000 00000 00000 00000
                                          SP52  11111 11011 10111 11111 11111
                                          SP53  01000 00000 00000 00000 00000
                                          SP54  0F000 00000 00000 00000 00000
                                          SP55  F0000 00000 00000 00000 00000
                                          SP56  000F0 00000 00000 00000 00000
                                          SP57  0F000 00000 00000 00000 00000
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