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Donald A. McFarlane

*Claremont McKenna College; Pitzer College; Scripps College*

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# Patterns of Species Co-occurrence in the Antillean Bat Fauna

by D.A. MCFARLANE

*Section of Birds and Mammals, Natural History Museum of Los Angeles County,  
900 Exposition Boulevard, Los Angeles CA 90007, U.S.A.*

*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 statistiquement 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  $2 \times 2$  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 occurring 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

$$E_{ik} = P_{ij} \cdot P_{kj}$$

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

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

The null model in this procedure is a normal distribution of standard deviates (mean = 0, 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 separate 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

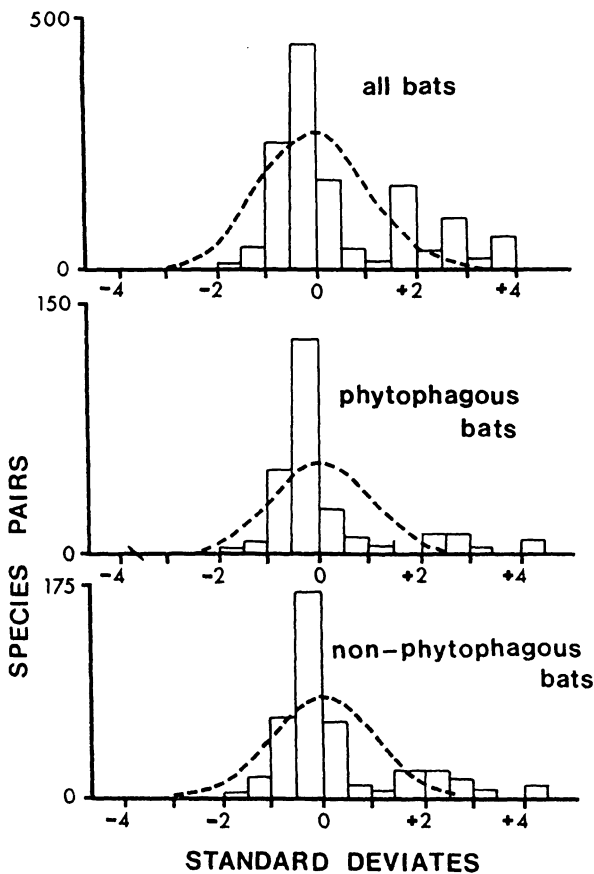


Fig. 1. — Observed (histogram) and null-model (curve) distributions of pairwise associations for Antillean bat species. Abscissa; difference between the observed and expected number of islands shared by a species pair. Ordinate; number of species pairs exhibiting such a difference.

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 likelihood 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, whereas 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 Guadeloupe
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	<u>Glossophaga longirostris</u>	29	<u>Pteronotus macleayi</u>
2	<u>Glossophaga sorcina</u>	30	<u>Pteronotus davyi</u>
3	<u>Monophyllus plethedon</u>	31	<u>Mormoops blainvilli</u>
4	<u>Monophyllus redmani</u>	32	<u>Micronycteris megalotis</u>
5	<u>Anoura geoffroyi</u>	33	<u>Macrotus waterhousii</u>
6	<u>Carollia perspicillata</u>	34	<u>Natalus stramineus</u>
7	<u>Sturnira ludovici</u>	35	<u>Natalus micropus</u>
8	<u>Sturnira thomasi</u>	36	<u>Myotis dominicensis</u>
9	<u>Chiroderma improvisum</u>	37	<u>Myotis martiniquensis</u>
10	<u>Artibeus cinereus</u>	38	<u>Myotis nigricans</u>
11	<u>Artibeus jamaicensis</u>	39	<u>Eptesicus fuscus</u>
12	<u>Artibeus lituratus</u>	40	<u>Eptesicus guadaloupensis</u>
13	<u>Ardops nichollsi</u>	41	<u>Eptesicus lynni</u>
14	<u>Phyllops falcatus</u>	42	<u>Lasiurus borealis</u>
15	<u>Phyllops haitiensis</u>	43	<u>Lasiurus intermedius</u>
16	<u>Ariteus flavescens</u>	44	<u>Nycticeius humeralis</u>
17	<u>Stenoderma rufum</u>	45	<u>Antrozous koopmani</u>
18	<u>Brachyphylla cavernarum</u>	46	<u>Tadarida brasiliensis</u>
19	<u>Brachyphylla nana</u>	47	<u>Tadarida macrotis</u>
20	<u>Erophylla bombifrons</u>	48	<u>Mormopterus minutus</u>
21	<u>Erophylla sezekorni</u>	49	<u>Eumops auripendulus</u>
22	<u>Phyllonycteris obtusa</u>	50	<u>Eumops glaucinus</u>
23	<u>Phyllonycteris poeyi</u>	51	<u>Eumops perotis</u>
24	<u>Phyllonycteris aphylla</u>	52	<u>Molossus molossus</u>
25	<u>Peropteryx macrotis</u>	53	<u>Tadarida laticaudata</u>
26	<u>Noctilio leporinus</u>	● 54	<u>Mormoops megaphylla</u>
27	<u>Pteronotus parnelli</u>	● 55	<u>Tonatia bidens</u>
28	<u>Pteronotus fuliginosus</u>	●● 56	<u>Phyllonycteris major</u>
		● 57	<u>Desmodus rotundus</u>

● Not extant in the Antilles.

●● Extinct taxon.

## Phytophagous Species.

## Remaining species.

----- ISLANDS -----

SP1	00000	00000	00000	00010	01010
SP2	10000	00000	00000	00000	00000
SP3	00000	00000	00010	10110	11101
SP4	11110	00000	00000	00000	00000
SP5	00000	00000	00000	00000	00010
SP6	00000	00000	00000	00000	00010
SP7	00000	00000	00000	00011	11000
SP8	00000	00000	00000	00100	00000
SP9	00000	00000	00000	00100	00000
SP10	00000	00000	00000	00000	00010
SP11	11111	11111	11111	11111	11111
SP12	00000	00000	00000	00000	01010
SP13	00000	00000	00100	01111	11000
SP14	01000	00000	00000	00000	00000
SP15	00100	00000	00000	00000	00000
SP16	10000	00000	00000	00000	00000
SP17	00011	10000	00000	00000	00000
SP18	00011	10011	11110	11111	11101
SP19	F1100	00000	00000	00000	00000
SP20	00110	00000	00000	00000	00000
SP21	11000	00000	00000	00000	00000
SP22	00100	00000	00000	00000	00000
SP23	01000	00000	00000	00000	00000
SP24	10000	00000	00000	00000	00000

F denotes occurrence only as a fossil.

SP25	00000	00000	00000	00000	00010
SP26	11111	11010	10011	11111	11110
SP27	11110	00000	00000	00000	00000
SP28	11110	00000	00000	00000	00000
SP29	11000	00000	00000	00000	00000
SP30	00000	00000	00000	00111	00010
SP31	11110	00000	00000	00111	00010
SP32	00000	00000	00000	00000	00010
SP33	111F0	00000	00000	00000	00000
SP34	11100	00000	01000	11010	00001
SP35	11000	00000	00000	00000	00000
SP36	00000	00000	00000	00010	00000
SP37	00000	00000	00000	00001	00100
SP38	00000	00000	00000	00000	00010
SP39	01110	00000	00000	00000	00000
SP40	00000	00000	00000	00100	00000
SP41	10000	00000	00000	00000	00000
SP42	11110	00000	00000	00000	00000
SP43	01000	00000	00000	00000	00000
SP44	01000	00000	00000	00000	00000
SP45	01000	00000	00000	00000	00000
SP46	11111	00000	10111	11111	10000
SP47	11000	00000	00000	00000	00000
SP48	01000	00000	00000	00000	00000
SP49	10000	00000	00000	00000	00000
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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