

A COMPARISON OF BAT ASSEMBLAGES FROM PHYTOGEOGRAPHIC ZONES OF VENEZUELA

MICHAEL R. WILLIG AND MICHAEL A. MARES

ABSTRACT—The distributional status of Venezuelan bats was obtained from Handley (1976) and used to assess faunal relationships among the phytogeographic zones of the country. Species presence or absence from each zone was used to construct phytogeographic zone similarity matrices, whereas the inclusion or exclusion of a particular zone from the distribution of each bat species was used to construct species similarity matrices. In either case, both Jaccard's and simple matching coefficients were analyzed using UPGMA clustering algorithms. A strict consensus tree between phenograms based on the two different similarity coefficients was calculated to determine groups of phytogeographic zones with similar faunal compositions. Bats also were classified into feeding guilds for each phytogeographic zone. Trophic structure (relative number of species per guild) of zones within groups defined by the clustering procedures then were compared using Contingency Chi-square analysis. In general, bats do not have distributions limited to a particular phytogeographic zone; moreover, bat assemblages cannot be used to define Tropical, Premontane, Lower Montane, or Montane sets of life zones. Little congruence is obtained between the floral zones of phytogeographers and the distributional limits of bats. Gallery forest bat faunas that occur along the river systems in many phytogeographic zones probably contribute to this phenomenon, especially in more arid regions. Moreover, bats may not respond to environmental gradients in the same manner as the dominant floral elements. Our analyses suggest six clusters of phytogeographic zones that are taxonomically related in terms of bat composition, and for the only cluster of phytogeographic zones with sufficiently large species pools in each zone, bat trophic structure was indistinguishable for the component phytogeographic zones.

Biogeographers and ecologists have endeavored to quantify how faunal assemblages relate to each other in overall taxonomic composition. One approach, direct gradient analysis, relates faunal composition to environmental variables such as temperature, precipitation, or altitudinal relief. Two difficulties exist with this approach for bat assemblages: each species is assumed to respond linearly to measured environmental variables, and few studies of bat distribution include relevant data for location along the environmental gradient. Indirect gradient analysis, or ordination, positions assemblages in multidimensional space based upon actual species composition. The Euclidean distance between assemblages is then a measure of faunal similarity. Such an approach has been used for bats from the Antilles (Baker and Genoways, 1978) and from North Africa and the Middle East (Qumsiyeh, 1985); indirect ordination is commonly used by phytogeographers and plant community ecologists (see Kershaw, 1973, and Gauch, 1982).

Bats are frequently viewed as organisms of great vagility and wide habitat tolerance. Yet the way in which tropical bats are allocated among habitats or phytogeographic zones has not been adequately described. Neotropical bats are particularly intriguing because high species richness and trophic

diversity characterize many areas of Central and South America (see Willig and Selcer, 1988, and Willig and Sandlin, 1989). Whether particular suites of species characterize one or more of the varied phylogeographic zones of the Neotropical Region is not yet clear.

Venezuela is a country with broad habitat diversity, although contained entirely within the tropics. Lowland rain forest, tropical deciduous forest, grassland, thorn scrub, montane rain forest, and alpine scrubland characterize the country that has a diverse bat fauna of 134 species (Handley, 1976). In this paper, we examine the distribution of bat species and their allocation among the major phylogeographic zones of this tropical country, and assess whether any of these zones are characterized by particular bat species. We also examine the patterns of distribution and habitat selection of the bats, relating these patterns to the history and geography of the habitats.

MATERIALS AND METHODS

Bat species lists for phylogeographic zones of Venezuela (Ewel and Madriz, 1968, and Table 1) were obtained from Handley (1976) and organized into a 14 by 134 phylogeographic zone-species matrix; phylogeographic zones in which bats were not found (Tropical scrub forest, Lower Montane dry forest, Montane dry forest, Montane humid forest, Montane very humid forest, Subalpine paramo, and Subalpine rainy paramo) were excluded from analyses. Two kinds of comparisons were performed using the above matrix. The similarity between phylogeographic zones was estimated using the presence or absence of species in the zones as classificatory variables. Two similarity indices, Jaccard's coefficient (S_j —Jaccard, 1908; Sneath, 1957) and the simple matching coefficient (S_{sm} —Sokal and Michener, 1958), were calculated for each kind of comparison. Jaccard's coefficient is given by

$$S_j = a/(a + u),$$

where a is the number of positive matches (shared species) and u is the number of mismatches (sum of the unshared species) between the two groups (phylogeographic zones). It does not consider that the absences shared by two groups contribute to overall similarity. The simple matching coefficient is given by

$$S_{sm} = m/(m + u),$$

where m (number of matches) equals a (the number of shared presences) plus the number of shared absences (species known from the fauna of Venezuela but not present in either of the compared phylogeographic zones), and u is the number of mismatches. It does consider shared absences in assessing overall similarity. These and other similarity indices are discussed in more detail by Sneath and Sokal (1973).

Each set of similarity coefficients produced a triangular matrix, the data from which were subjected to the unweighted pair-group arithmetic

TABLE 1.—*Phytogeographic zones of Venezuela (Ewel and Madriz, 1968) in which bats have been recorded (Handley, 1976). Phytogeographic zones that are members of the same consensus cluster based upon UPGMA of Jaccard's and simple matching coefficients are indicated parenthetically by identical letters.*

Abbreviation	Phytogeographic zone
me-T	Tropical thorny forest (F)
bms-T	Tropical very dry forest (D)
bs-T	Tropical dry forest (E)
bh-T	Tropical humid forest (E)
bmh-T	Tropical very humid forest (E)
me-P	Premontane thorny forest (F)
bs-P	Premontane dry forest (D)
bh-P	Premontane humid forest (E)
bmh-P	Premontane very humid forest (E)
bp-P	Premontane rain forest (C)
bh-MB	Lower Montane humid forest (A)
bmh-MB	Lower Montane very humid forest (B)
bp-MB	Lower Montane rain forest (C)
bp-M	Montane rain forest (C)

averaging cluster algorithm (UPGMA) in order to define associations among species or phytogeographic zones (Sneath and Sokal, 1973; Rohlf *et al.*, 1974). Cophenetic correlation coefficients between the resultant phenogram and the original similarity matrix estimate the degree to which the relationships suggested by clustering are representative of the actual relations among elements in the original similarity matrix. Consensus between phenograms based upon the simple matching and Jaccard's coefficient indicate the group relationships in common to both analyses, and has been produced following the methodology of strict consensus trees used in systematic studies (Sokal and Rohlf, 1981*b*).

Bats from each phytogeographic zone were categorized into feeding guilds based upon the work of Wilson (1973), Gardner (1977), and Willig (1982). Eight guilds were recognized: aerial insectivores, molossid insectivores, foliage-gleaning insectivores, nectarivores, frugivores, piscivores, sanguinivores, and omnivores. The resultant trophic structure (number of species per guild) was compared via Contingency Chi-square tests (Sokal and Rohlf, 1981*a*) for each consensus group that was defined from the cluster analyses.

RESULTS

In terms of bat species composition, clustering algorithms based upon Jaccard's (Fig. 1A) and simple matching (Fig. 1B) coefficients attain consensus concerning the existences of six groups of phytogeographic zones (Fig. 2A). Tropical thorny forest and Premontane thorny forest form a thorny forest cluster (group F in Fig. 2). Tropical very dry forest and Premontane dry forest form a dry forest cluster (group D in Fig. 2). Premontane rain forest, Lower Montane rain forest, and Montane rain

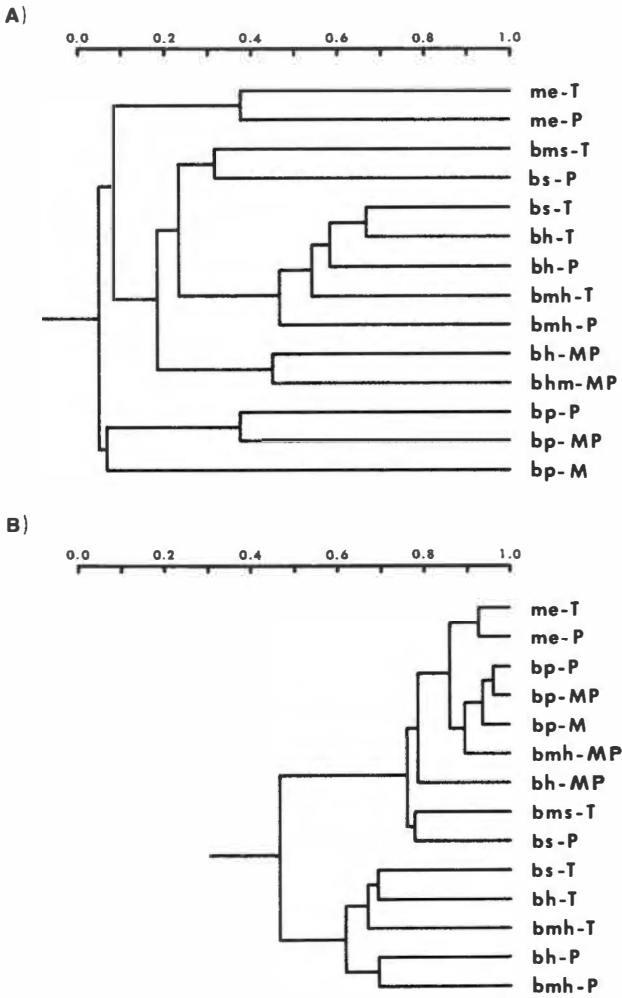
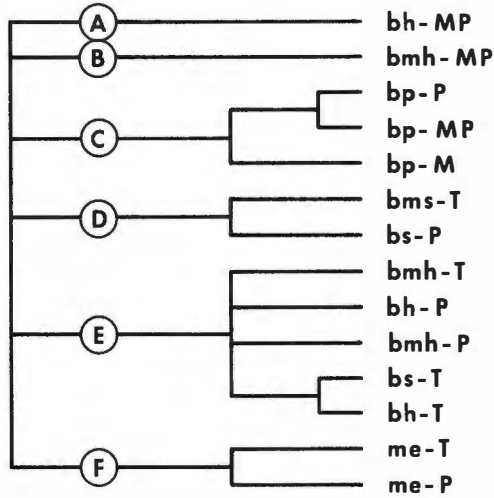


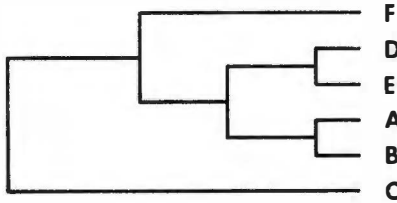
FIG. 1.—Phytogeographic zone phenograms based upon UPGMA clustering algorithms performed on Jaccard's (A) and simple matching (B) coefficients. Phytogeographic zone codes are as in Table 1. The cophenetic correlation coefficient for clustering based on the Jaccard's (0.94) and simple matching (0.88) coefficient indicate little distortion in either phenogram. The degree of similarity between zones may be obtained with reference to the scale above each phenogram.

forest constitute a rain forest cluster (group C in Fig. 2). Lower Montane humid forest (group A in Fig. 2) and Lower Montane very humid forest (group B in Fig. 2) each represents a distinct group. The final consensus cluster (group E in Fig. 2) consists of five phytogeographic zones: Tropical dry forest, Tropical humid forest, Premontane very humid forest, Tropical very humid forest, and Premontane humid forest. Differences in clustering at higher levels (compare Fig. 2B with 2C) is related to the differential sensitivity of the simple matching coefficient to shared absences wherein

A)



B)



C)

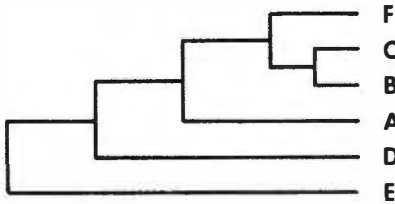


FIG. 2.—A consensus tree (A) for the phenograms in Figure 1; the single capital letters indicate consensus groups (see text for details). Phytoecographic zone codes are as in Table 1. The relationship of consensus groups (capital letters in the phenogram) based upon Jaccard's (B) and simple matching (C) coefficients cannot be further resolved based upon the method of strict consensus.

depauperate faunas will be viewed as similar because of the joint absence of many species from both zones.

Phenograms of species clusters using Jaccard's and the simple matching coefficients are complex and show little consensus beyond identifying subsets of species that in some cases link various phytoecographic zones

into groups. The thorny forest cluster (F) consists of two phylogeographic zones with depauperate faunas, linked primarily by the joint occurrence of four bat species, *Lasiurus cinereus*, *Rhogeessa minutilla*, *Leptonycteris curasoae*, and *Glossophaga longirostris*. *Eumops nanu* and *Myotis larensis* are species found only within the Tropical thorny zone. Within group E, Tropical dry forest and Tropical humid forest are linked by the joint occurrence of seven species, *Saccopteryx naso*, *Diclidurus ingens*, *Noctilio albiventris*, *Lonchorhina orinocensis*, *Molossops paranus*, *M. planirostris*, and *Molossus aztecus*. Four species, *Eptesicus dimidiatus*, *Eumops auripendulus*, *E. dabbenei*, and *Promops centralis*, have distributions restricted to Tropical dry forest. The Tropical humid forest contains nine species (*Diclidurus isabellus*, *Tadarida laticauda*, *Eumops amazonicus*, *Molossops greenhalli*, *M. abrasus*, *Glyphonycteris sylvestris*, *Tonatia carrikeri*, *Lichonycteris degener*, and *Scleronycteris ega*) that only occur within that phylogeographic zone. Nonetheless, a large number of species defines links between various subsets of the entire cluster of five phylogeographic zones within group E. Seven species are uniquely found in each of these five zones; they include *Peropteryx macrotis*, *Trachops cirrhosus*, *Chrotopterus auritus*, *Vampyressa bidens*, *Chiroderma trinitatum*, *C. villosum*, and *Artibeus concolor*. Like the Thorny forest group, both the dry forest group (D) and the rain forest group (C) each contains phylogeographic zones that are linked by the lack of whole suites of species; no species is unique to either cluster. Neither of the Montane humid forests (A or B) contains bat species with distributions that are limited to those zones.

Reliable Chi-square tests require 1) all expected cell values to be greater than or equal to one, and 2) less than 20 percent of the expected cell values to be less than five. These requirements were only satisfied within group E (bs-T, bh-T, bmh-T, bh-P, and bmp-P) after combining omnivore, sanguinivore, and piscivore guilds into a single category. The nonsignificant statistical result ($X^2 = 19.70$, $df = 20$, $0.50 > P > 0.10$) indicates that all five phylogeographic zones within group E have indistinguishable trophic structures.

DISCUSSION

Faunal relationships among Venezuelan phylogeographic zones are complex. In general, distinct subsets of the fauna do not characterize phylogeographic zones or consensus groups. With the exception of Tropical humid forest (nine species), Tropical dry forest (four species), and Tropical thorny forest (two species), bat species do not have distributional ranges limited to single phylogeographic zones. Interestingly, over two-thirds of the species that are phylogeographic zone specialists are insectivores. Although the New World fruit-eating bats (Phyllostomidae) reach their highest diversity in the tropics (Wilson, 1973; McCoy and Connor, 1980), few species are limited to particular phylogeographic zones. This is opposed

to the popular belief that South American mammals are stenotopic (see Mares, 1986, 1987; Patterson, 1987). Moreover, unique assemblages of bats cannot be used to define Tropical, Premontane, Lower Montane, or Montane life zones. Our analyses suggest that there is little congruence between the floral zones as defined by phytogeographers and the bat species frequenting those zones. Few of the defined zones have even one or two bat species that characterize them.

Nevertheless, as Figure 2 indicates, some distinct associations of phytogeographic zones can be obtained based upon bat species composition. The phenograms in Figure 1 can be reconciled into the consensus phenogram of Figure 2A. Each of the six clusters thus defined, although not perfectly distinct from each other, does in fact share a mix of species, and in some cases, is delimited by species that occur in all zones of the cluster. This figure may be considered as a model to determine from which zone a particular species was obtained. In most cases, a single individual cannot, with certainty, be assigned to a particular zone. But, as more species are obtained from an area, the probability of ascertaining the proper phytogeographic zone with which the area should be associated increases greatly.

The absence of bats from a number of phytogeographic zones in Venezuela may, in part, be affected by the precipitous decline of bat diversity above elevations of 1000 meters. The depauperization of high altitudes recapitulates hemispheric trends of reduced bat species richness at high latitudes (Wilson, 1973; McCoy and Connor, 1980), and may similarly involve physiological constraints associated with low temperatures and reduced food abundance (McNab, 1969, 1983).

In general, the absence of characteristic species from particular phytogeographic zones suggests that bats are not life zone specialists but rather are eurytopic. Bat distributions may fail to show patterns that reflect phytogeographic zones for a variety of reasons. Perhaps different species of bats respond in different ways to abiotic and biotic gradients such that distinct assemblages that correspond to phytogeographic zones are not obtained. In a different context, Terborgh (1970) found most of the avifauna of the Codillera Vilcabamba in Peru to have distributions that are relatively unaffected by competitive exclusion or habitat discontinuities. Over half of the bird species had distributional limits that were determined by factors in the environment that vary continuously and in parallel with the altitudinal gradient. This also resulted in the absence of pervasive avifaunal associations within floral zones because the location of the density optima of species varied randomly along the environmental gradient. The complexity of faunal relationships among phytogeographic zones also may be an artifact of using presence-absence data in lieu of species abundances. If bats have different densities in different life zones, which is a realistic assumption, then our methods may not detect life zone specialists, if they exist, because the quantitative information on abundance is not accurate.

For example, a particular species may be abundant in the Tropical dry forest but only rarely found in Tropical humid forest, Premontane dry forest, and Lower Montane rain forest. An analysis using only presence-absence information would consider the species equally characteristic of all four phytogeographic zones. Alternatively, the salient features used by phytogeographers to characterize life zones may not reflect the critical components defining the niche limitations of particular bat species. In fact, the Ewel and Madriz classification, like the Holdridge system, is primarily based upon temperature and precipitation, and does not take into account other edaphic factors. Although substantial tracts of gallery forest parallel the many rivers that occur north of the Orinoco, the land is homogeneously classified as "bosque seco." The species composition of these gallery forests shows great affinity with multistratal rain forest and substantially contributes to the species richness of areas in central Venezuela north of the Orinoco. Moreover, the extensive distribution of such riverine habitats and their associated faunas would tend to diminish the chance of detecting unique bat associations within phytogeographic zones.

ACKNOWLEDGMENTS

We thank J. Braun for expert rendering of the figures and R. Owen for statistical and technical advice in the use and interpretation of NT-SYS programs. M. Ybarra aided with all aspects of data compilation. P. Jones typed the manuscript. Much of the early work on this research was conducted while Willig was supported by a Mellon Fellowship from the University of Pittsburgh; later work was completed while Willig was supported by the Department of Energy Faculty Participation Program administered by Oak Ridge Associated Universities and the Center for Energy and Environment Research (Terrestrial Ecology Division) in Puerto Rico. Critical evaluations of an earlier draft of the manuscript by J. Eisenberg, B. Fox, and D. Morris greatly improved the final version. We also benefited from discussions with participants at the Fourth International Theriological Congress and the Pymatuning Symposium on Mammalian Biology in South America.

LITERATURE CITED

- BAKER, R. J., AND H. H. GENOWAYS. 1978. Zoogeography of Antillean bats. Pp. 53-97, in *Zoogeography of the Caribbean* (F. G. Gill, ed.), Spec. Publ. Acad. Nat. Sci., Philadelphia, 13:iii+1-128.
- EWEL, J. J., AND A. MADRIZ. 1968. Zonas de vida de Venezuela. Ministerio Agric. y Cria., Caracas, Venezuela, 265 pp.
- GARDNER, A. L. 1977. Feeding habits. Pp. 295-350, in *Biology of bats of the New World family Phyllostomatidae. Part II* (R. J. Baker, J. K. Jones, Jr., and D. C. Carter, eds.), Spec. Publ. Mus., Texas Tech Univ., 13:1-364.
- GAUCH, H. G., JR. 1982. *Multivariate analysis in community ecology*. Cambridge Univ. Press, Cambridge, 298 pp.
- HANDLEY, C. O., JR. 1976. Mammals of the Smithsonian Venezuelan projects. Brigham Young Univ. Sci. Bull., 20:1-89.
- JACCARD, P. 1908. Nouvelles recherches sur la distribution florale. Bull. Soc. Vaud. Sci. Nat., 44:223-270.
- KERSHAW, K. A. 1973. *Quantitative and dynamic plant ecology*. American Elsevier Publ. Co., Inc., New York, 308 pp.

- MARES, M. A. 1986. Conservation in South America: problems, consequences, and solutions. *Science*, 233:734-739.
- . 1987. Species loss (response). *Science*, 234:1311-1312.
- MCCOY, E. D., AND E. F. CONNOR. 1980. Latitudinal gradients in the species diversity of North American mammals. *Evolution*, 34:193-203.
- MCNAB, B. K. 1969. The economics of temperature regulation in Neotropical bats. *Comp. Biochem. Physiol.*, 31:227-268.
- . 1983. The physiological ecology of South American mammals. Pp. 187-207, *in* *Mammalian biology in South America* (M. A. Mares and H. H. Genoways, eds.), Spec. Publ. Ser., Pymatuning Lab. Ecol., Univ. Pittsburgh, 6:1-539.
- PATTERSON, B. D. 1987. Species loss. *Science*, 234:1311.
- QUMSIYEH, M. B. 1985. The bats of Egypt. *Spec. Publ. Mus., Texas Tech Univ.*, 23:1-102.
- ROHLF, F. J., J. KISHPAUGH, AND D. KIRK. 1974. NT-SYS: Numerical taxonomy system of multivariate statistical programs. The State Univ. New York at Stony Brook, 74 pp.
- SNEATH, P. H. A. 1957. Some thoughts on bacterial classification. *J. Gen. Microbiol.*, 17:184-200.
- SNEATH, P. H. A., AND R. R. SOKAL. 1973. *Numerical taxonomy*. W. H. Freeman and Co., San Francisco, 573 pp.
- SOKAL, R. R., AND C. D. MICHENER. 1958. A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull.*, 38:1409-1438.
- SOKAL, R. R., AND F. J. ROHLF. 1981*a*. *Biometry*. W. H. Freeman and Co., San Francisco, 2nd. ed., 859 pp.
- . 1981*b*. Taxonomic congruence in Leptodomorpha re-examined. *Syst. Zool.*, 30:309-325.
- TERBORGH, J. 1971. Distribution on environmental gradients: theory and a preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology*, 52:23-40.
- WILLIG, M. R. 1982. A comparative ecological study of Caatingas and Cerrado chiropteran communities: composition, structure, morphometrics, and reproduction. Unpublished Ph.D. dissertation, Univ. Pittsburgh, 324 pp.
- WILLIG, M. R., AND E. A. SANDLIN. 1989. Gradients of species density and β -diversity in New World bats: a comparison of quadrat and band methodologies. *In* *Latin American mammals: their conservation, ecology, and evolution* (M. A. Mares and D. J. Schmidly, eds.), Univ. Oklahoma Press, Norman, in press.
- WILLIG, M. R., AND K. W. SELCER. 1988. Bat species density gradients in the New World: a statistical assessment. *J. Biogeog.*, in press.
- WILSON, D. E. 1973. Bat faunas: a trophic comparison. *Syst. Zool.*, 22:14-29.
- WILSON, J. W., III. 1974. Analytical zoogeography of North American mammals. *Evolution*, 28:124-140.