NEOTROPICAL-NEARCTIC LIMITS IN MIDDLE AMERICA AS DETERMINED BY DISTRIBUTIONS OF BATS

JORGE ORTEGA AND HÉCTOR T. ARITA

Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510, México, D. F., Mexico (JO)
Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 27-3 (Xangari), CP 58089, Morelia, Michoacán, México (HTA)

The Neotropical-Nearctic transition in Middle America was analyzed using distributional patterns of bats. The 169 non-insular bat species of Middle America were classified into four categories: shared with North and South America, shared only with North America, shared only with South America, and endemic. A theoretical biogeographic index was developed and compared with null frequency distributions based on the multivariate hypergeometric model. A total of 1,054 half-by-half-degree quadrats were used to determine the biogeographic zone (Nearctic, Neotropical, or transitional) of sites in Mexico and Central America. The null distribution allowed statistical assessment of each quadrat, permitting the quantitative determination of the limit between the two biogeographic regions. Results showed a pattern that coincided with previous studies in the position of the southern limits for the Nearctic region but differed in locations of Neotropical areas, and in the extent of the transitional zone, which was much broader in the present study.

Key words: bats, biogeography, hypergeometric distribution, Nearctic, Neotropical

Candolle (1820) divided the globe in biogeographic regions, proposing 20 botanical provinces based on distributions of indigenous plants. Later, Sclater (1858) and Wallace (1876) proposed a system of six zoogeographical regions (Nearctic, Neotropical, Palearctic, Oriental, Ethiopian, and Australian) based on distributional patterns of birds and mammals. Sclater's (1858) system elicited much controversy about the placement of regional boundaries because limits for different plant and animal groups did not coincide. Eventually, however, the original lines were adopted widely by scientists and are still in use today (Nelson and Platnick, 1984).

The limit between Neotropical and Nearctic regions is located in Middle America (Brown and Gibson, 1983; Cox and Moore, 1985; Darlington, 1957), causing Mexico and Central America to be areas of high diversity and endemism. Mexico, for example, is considered a megadiverse country because its mammalian fauna includes more species than expected for a country of its size (Arita, 1997; Ceballos and Navarro, 1991; Fa and Morales, 1993; Mittermeier, 1988; Mittermeier and Mittermeier, 1992). Similarly, a high proportion of volant and nonvolant mammals are endemic to Mexico and Central America (Arita and Ortega, in press; Ceballos and Brown, 1995; Ceballos and Rodríguez, 1993).

Several authors have tried to establish the location of the limit between the New World biogeographic areas based on distributions of plants (Rzedowski, 1978; Takhtajan, 1969), insects (Halffter, 1964), *Sceloporus* lizards (Smith, 1940), and mammals (Goldman and Moore, 1946). Although there is agreement that the line lies somewhere in Mexico, its exact location varies depending on the group under study (Alvarez and de Lachica, 1974). All those studies are based on the comparison of distributional patterns of taxa that are considered Neotropical or Nearctic, using different indices of similarity, but no attempt has been made to test the statistical significance of the proposed lines.

As with other biogeographic analyses, determination of the limit between two regions is based on distributional patterns of species (Myers and Giller, 1988). The range of a species is not a random pattern because species respond in different ways to factors such as latitude, longitude, altitude, environmental heterogeneity, and productivity (Brown et al., 1996; Gaston, 1990; Gaston and Blackburn, 1996; Lawton et al., 1994; Mönkkönen, 1994). Any of those climatic or topographic factors can produce barriers to distributions of organisms because species are normally adapted to a limited range of environmental conditions (Brown, 1984; Brown and Maurer, 1989; Cox and Moore, 1985; Simpson, 1964, 1965).

Mammals have been used frequently for biogeographic analyses. This is because the species-level taxonomy of the group is comparatively well established and, in the New World, general distributional patterns of species also are well known (Ceballos and Navarro, 1991; McCoy and Connor, 1980; Pagel et al., 1991; Simpson, 1964; Wilson, 1974).

Distributional patterns of bats differ from those of nonvolant mammals. The latitudinal pattern of mammalian species richness in the New World is in great part determined by distributions of bats because tropical bat faunas are much richer than temperate ones (McCoy and Connor, 1980; Willig and Sandlin, 1991; Willig and Selcer, 1989; Wilson, 1974). Recent data suggest that distributions of bats have a strong influence on the latitudinal pattern, but they are not entirely responsible for the gradient, because the pattern is better understood if volant and nonvolant groups of mammals are considered (Kaufman, 1995). Bats are a group with morphological, physiological, and ecological adaptations for flight (Arita and Fenton, 1997; Norberg and Rayner, 1987), and their particular responses to geographical barriers differ from those of nonvolant mammals.

In this paper we use an index, with an associated statistical test, to propose a line between the Neotropical and Nearctic regions based on distributions of bats. We choose that group because chiropteran species contribute strongly to latitudinal patterns of mammalian diversity in North America. Additionally, because of their high vagility, bats have large distributional ranges that are suited to the types of analyses that we performed. Finally, most bat species in the New World can be allocated easily into categories of Neotropical or Nearctic origin, facilitating design of quantitative analyses.

Materials and Methods

We compiled a list of bat species from Middle America (Mexico and the seven countries of Central America—Arita and Ortega, in press), based primarily on Koopman (1993) but including nomenclatural changes reviewed by Ramírez-Pulido et al. (1996; Appendix I). Information to draw distributional maps for all species was obtained from Hall (1981) and updated with new records and taxonomic changes through 1993 (Arita and Ortega, in press; Arita et al., 1997). We overlaid a grid of 1,054 half-by-half-degree quadrats on maps to build a distributional database that was complemented with taxonomic information for each species. Our maps included only mainland distributions of species, so *Myotis findleyi*, a bat restricted to the Tres Marías Islands in western México (Wilson, 1991), was not considered in analyses.

Based on their distribution, species were classified into one of four biogeographic categories: species shared with North America north of Mexico (United States and Canada); species shared with South America (i.e., occurring beyond the Panamanian–Colombian border); species shared with North and South America; and species that are endemic to Middle America. To quantify species composition of a given quadrat in terms of similarity with Nearctic or Neotropical locations, we developed a biogeographic index:

$$I_i = \frac{\dfrac{NT_i}{NT_p} - \dfrac{NA_i}{NA_p}}{\dfrac{NT_i}{NT_p} + \dfrac{END_i}{END_p} - \dfrac{NA_i}{NA_p}},$$

where I_i was the value of the index for quadrat i, END_i was the number of species in quadrat i that were either endemic or shared with both North and South America (categories E and AM; Appendix I), NT_i was the number of species shared with South America (category NT; Appendix I), and NA_i was the number of species shared with North America north of Mexico (category NA; Appendix I). $END_p = 40$, $NT_p = 104$, and $NA_p = 25$ were the number of species in each category for the pool of species (i.e., the total Middle American fauna; Appendix I).

The index was developed as an extension of Simpson's index of similarity to the case of more than two sites, and values were weighed with the proportion of species in the pool to account for the effect of the unequal number of species in each category. The equation implicitly assigned a positive value to species shared with South America, a negative value to species shared with North America, and a value of zero to endemic species and to those shared both with North and South America. Theoretical values of the index ranged from −1.0 (totally Nearctic localities) to +1.0 (completely Neotropical), with values close to zero corresponding to transitional sites.

We assessed the statistical significance of our index using the multivariate hypergeometric distribution (Freund and Walpole, 1987). This statistical distribution is applicable when sampling without replacement from a finite population divided in more than two categories. We wrote a BASIC program to generate all possible combinations of species for a given sample size and to establish the 95 and 99% *CI* confidence intervals on extreme lower and higher points for new values (Table 1). After defining those limits, we classified quadrats as Nearctic, with significantly ($P < 0.01$) negative values of the index; transitional, with non-significant values; or Neotropical, with significant ($P < 0.01$) positive values.

TABLE 1.—*Critical values for the lower and upper 95 and 99%* CI *of values of the biogeographic index for selected sample sizes. For example, for a fauna of 10 species of bats, a value of 0.61 would be a significantly positive value, meaning a predominance of Neotropical influence.*

	95% *CI*		99% *CI*	
Sample size	Lower limit	Upper limit	Lower limit	Upper limit
5	−0.48	—	−0.72	—
10	−0.36	0.60	−0.49	0.77
12	−0.34	0.53	−0.50	0.80
14	−0.32	0.49	−0.43	0.69
16	−0.33	0.45	−0.45	0.62
18	−0.30	0.43	−0.39	0.60
20	−0.29	0.36	−0.40	0.55
25	−0.26	0.32	−0.35	0.49
30	−0.23	0.29	−0.32	0.44
35	−0.21	0.27	−0.29	0.39
40	−0.19	0.24	−0.27	0.36

RESULTS

The bat fauna of Middle America consisted of 170 species classified in nine families (Appendix I). Excluding the insular *Myotis findleyi,* 25 Middle American species were shared with North America, 104 were shared with South America, nine were shared with both North and South America, and 32 were endemic to Middle America. At the family level, Noctilionidae, Mormoopidae, Phyllostomidae, Natalidae, Furipteridae, and Thyropteridae were considered of Neotropical origin. Emballonuridae and Molossidae had a pantropical distribution, although some species of the latter family were found in subtropical environments. Vespertilionidae had a worldwide distribution, but their probable site of origin was the Old World (Koopman, 1976). The analysis at the species level provided a better resolution and a clearer evidence for distributional limits than did the family level, because of variation in distributional patterns in some families.

Our biogeographic index performed as expected. We carried out exploratory analyses generating theoretical distributions for several sample sizes and found that the weighting with the total for the total produced frequency distributions that were

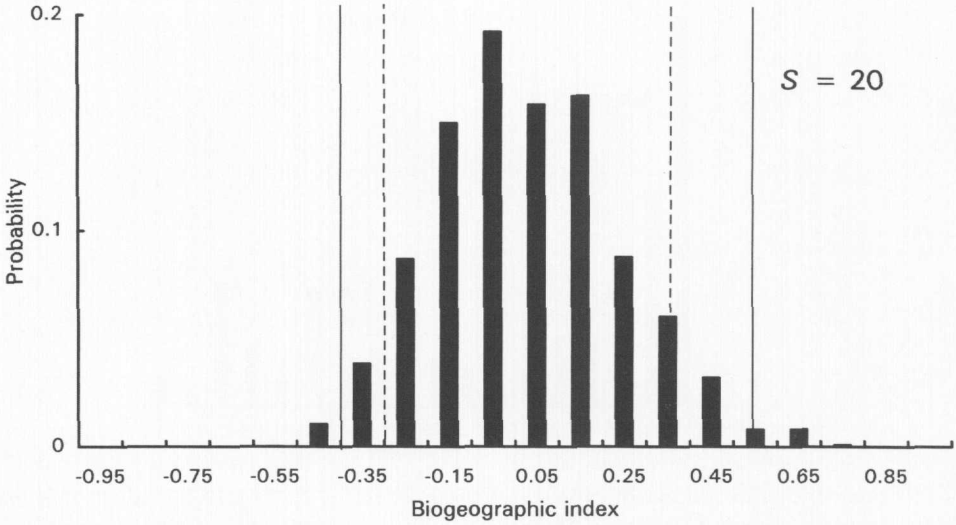

FIG. 1.—Probability distribution for values of the biogeographic index for samples of 20 species. Distribution is based on the probabilities of the 231 possible samples of 20 species from three categories (shared with North America, shared with South America, and endemic or shared with both North and South America). Probabilities are calculated from a multivariate hypergeometric distribution. Lines mark the lower and upper *CI* on the mean for the prediction of new values (dashed lines: 95% *CI*, continuous lines: 99% *CI*).

nearly normal with a mean of 0.0 (Fig. 1). Although probabilities of obtaining values of −1.0 or +1.0 are very low, those values were theoretically possible when all species of a given quadrat were Nearctic ($I_i = -1.0$) or Neotropical ($I_i = +1.0$).

Frequency distribution of values of the index for the 1,054 quadrats differed from the theoretical probability distribution (Fig. 2). About one-half of the quadrats (532, 50.5%) were considered Nearctic because they had significantly ($P < 0.01$) negative values of the index; 181 quadrats (17.1%) were Neotropical with significantly ($P < 0.01$) positive values; and 342 (32.4%) were transitional with nonsignificant values.

By mapping quadrats, we found a distinct pattern that allowed the establishment of the line between the two biogeographic regions in Middle America (Fig. 3). The Nearctic zone encompassed all of the Baja California Peninsula, most of the Mexican Plateau, and highlands of the Eastern and Western Sierras Madre, areas covered with forests of oak (*Quercus*) and pine (*Pinus*). The zone also included large parts of the Sonoran and Chihuahuan deserts in northern Mexico, characterized by xerophytic vegetation and grasslands (Rzedowski, 1978). Bat faunas of that area were characterized by low species richness and were dominated by vespertilionids, with a minor percentage of molossids (e.g., *Tadarida brasiliensis*), phyllostomids (e.g., *Leptonycteris nivalis, L. curasoae,* and *Macrotus californicus*), and one mormoopid (*Mormoops megalophylla*). Some species of *Myotis* were endemic to this biogeographic zone (e.g., *Myotis milleri, M. peninsularis, M. planiceps,* and *M. vivesi*).

The transitional zone started in the vicinity of Sierra El Encinal, a mountain range in the Mexican state of Sonora, and continued along the Pacific versant of the Western Sierra Madre. In eastern Mexico, the transitional zone began in the northern

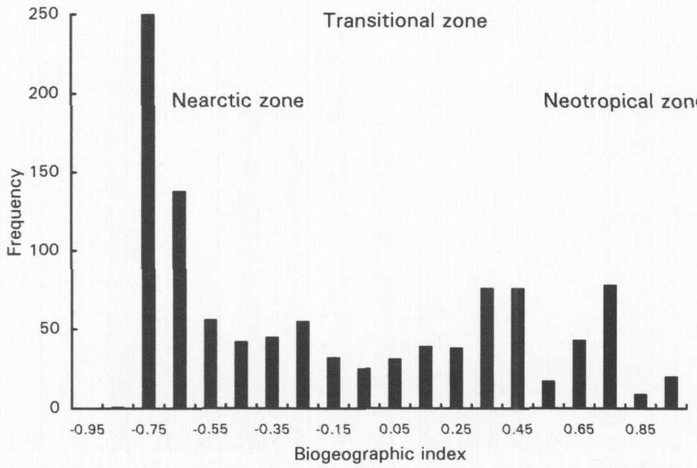

FIG. 2.—Frequency distribution of biogeographic indexes for 1,054 half-by-half-degree quadrats in Middle America. Because statistical limits vary with the sample size, limits between zones are not shown.

limit of the Eastern Sierra Madre and followed the Gulf of Mexico versant, including the Mexican Volcanic Belt and northern parts of the basin of the Balsas River and highlands of the Mexican states of Oaxaca and Chiapas. Vegetation types in this zone included tropical deciduous, cloud, oak, and pine forests (Rzedowski, 1978). Typical bats of the transitional zone included species shared with South and North America (e.g., *M. megalophylla, L. curasoae, Eptesicus fuscus, Lasi-*

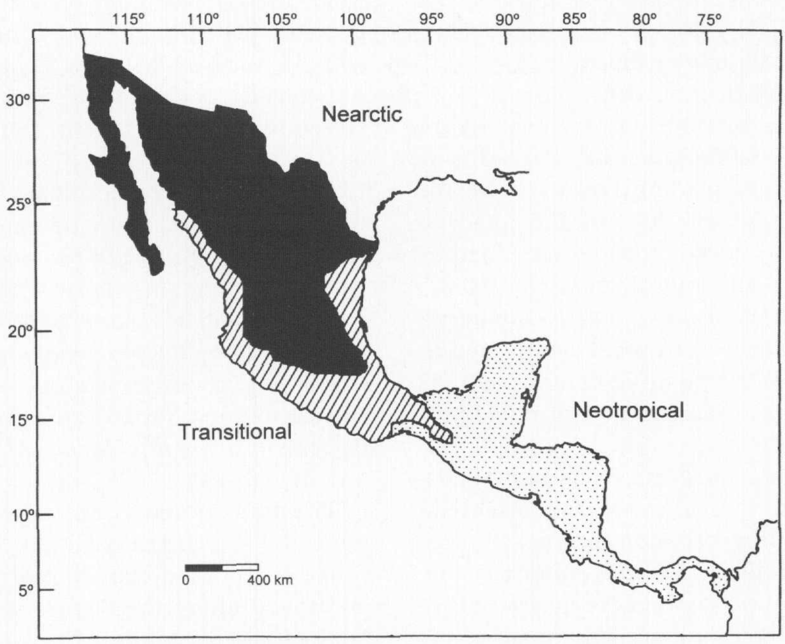

FIG. 3.—Biogeographic zones in Middle America determined by distributions of bats.

urus cinereus, Tadarida brasiliensis) and some Middle American endemics, such as *Corynorhinus mexicanus, Musonycteris harrisoni, Artibeus hirsutus,* two species of *Dermanura,* two species of *Glossophaga,* and six species of *Rhogeessa.*

Central America and parts of Mexico adjacent to Guatemala and Belize, including the lowlands of Tabasco, Chiapas, and all of the Yucatán Peninsula were considered as fully Neotropical. Typical vegetation in that zone was tropical rainforest but also included areas covered with tropical deciduous and cloud forests. Bat faunas in that zone were characterized by high species richness, presence of all Neotropical families, and a numerical dominance by phyllostomids. The zone had few Middle American endemics, the most representative being *Sturnira mordax, Artibeus inopinatus,* and *Rhogeessa aeneus.* Most species in the zone were shared with South America, and for some species, such as *Ectophylla alba, Ametrida centurio,* and *Mesophylla macconnelli,* Central America marked the northern limit of their distributions.

Discussion

Studies that have used distributional patterns of animals coincide in that major barriers of dispersal of organisms in North America are the Mexican Volcanic Belt and the Eastern and Western Sierras Madres (Goldman and Moore, 1946; Halffter, 1987; Moore, 1945; Smith, 1940; Udvardy, 1969). These mountain ranges traditionally are considered the limit between Neotropical and Nearctic regions. A different pattern was shown by Rzedowski (1978), who analyzed distributions of plants to propose that most parts of Mexico are of Neotropical affinity, with only northernmost regions being fully Nearctic.

Our definition of a Nearctic zone for bats corresponds, for the most part, with ones proposed for other vertebrates (Alvarez and de Lachica, 1974; Smith, 1940; Fig. 3). However, in the position of the Neotropical realm our results differed from previous studies. Other researchers have assigned lowlands of the Pacific and Gulf versants and most of Mexico south of the Volcanic Belt as part of the Neotropical region. According to those studies, there is a rather abrupt limit between the two regions along a narrow transitional area that extends along the Volcanic Belt and the Sierras Madres. We propose a broader transitional zone based on distributions of bats that corresponds better to the notion of a Mexican transitional zone, as defined by Halffter (1964), than to a clear-cut division between Neotropical and Nearctic regions (Fig. 3).

Nonsignificant values of our biogeographic index, corresponding to quadrats in the transitional zone, can arise from a numerical dominance of endemic or widespread species, a balance between number of Nearctic and Neotropical species, or a combination of those cases. Most quadrats in the transitional zone conform to the last case. For example, the quadrat corresponding to the state of Morelos, located in the basin of the Balsas River just south of the Volcanic Belt traditionally is considered Neotropical due to presence of several plant and animal species of tropical affinity (Alvarez and de Lachica, 1974; Smith, 1940). In the case of bats, 22 of 51 species with potential distribution in this area are phyllostomids, natalids, and mormoopids, groups of clear Neotropical origin (Koopman, 1976). However, 20 of the remaining species are vespertilionids, many of which also occur in North America north of Mexico (e.g., six species of temperate *Myotis, Corynorhinus townsendii, E. fuscus, Pipistrellus hesperus*), or are endemic to Middle America (e.g., *Corynorhinus mexicanus,* three species of *Rhogeessa*). This combination of species suggests that this zone is not fully Neotropical and it could be better described as a transitional area. Our biogeographic index corroborated this observation, allocating the whole Balsas Basin, including parts of the states of Michoacán, Guerrero, México, Morelos, Oaxaca, and Puebla, to the transitional zone.

A different case is the tip of the peninsula of Baja California. This area harbors some species of tropical origin (e.g., *Balantiopteryx plicata,* Emballonuridae; *Nyctinomops femorosaccus* and *N. macrotis,* Molossidae), but most species in the area are shared with North America (several vespertilionids of *Eptesicus, Myotis,* and *Pipistrellus*), and there is one Mexican endemic, *Myotis peninsularis.* Our index showed that, despite the partial tropical influence, this area can be described as fully Nearctic because of the dominance by species of North American affinity.

Highlands of the Mexican state of Chiapas were classified as transitional using our biogeographic index, but lowlands of the Pacific coast and the Selva Lacandona in the eastern part of the state were considered fully Neotropical. In mountain ranges of this state, species of Neotropical origin are present at low to intermediate elevations, but several Nearctic and endemic species occur from intermediate to high elevations. The combination of these two components produces transitional faunas recorded with our biogeographic index.

In Mexico, only lowlands of Chiapas, Tabasco, and the Yucatán Peninsula can be considered fully Neotropical on the basis of distributions of bats. Bat faunas in those areas consist of a large number of phyllostomids and other Neotropical bats and a smaller percentage of endemic bats and of species that occur in North America north of Mexico. Faunas in Central America are fully Neotropical, and species that occur there are almost the same that occur in northern South America.

Middle America is the area with the highest absolute number of endemic species of bats in the New World, although the Antilles and the dry Pacific coast of South America have higher percentages of endemics (Arita and Ortega, in press). Compared with the case of nonvolant mammals, however, the transitional zone harbors few endemic species. In Mexico, ca. 40% of all nonvolant mammals are endemic to the country (125 of 315—Ceballos and Rodríguez, 1993), but only 18% (31 of 169) of the chiropteran fauna of Middle America is endemic to the region, and only 10% (14 of 136 species) of Mexican bats are endemic to the country. Only three genera (*Bauerus, Hylonycteris,* and *Musonycteris*) are exclusive to Middle America.

Patterns that we detected with our biogeographic index are determined by the same factors that create the latitudinal gradient of species richness in Middle America. Quadrats in Central America, corresponding to the fully Neotropical zone (Fig. 3), include faunas of high species richness of bats (>50 species; Fig. 4), but quadrats in northern Mexico correspond to areas of Nearctic affinity and low species richness (<40 species; Fig. 4). The transitional zone includes quadrats with moderate to high species richness (>30 species; Fig. 4). As shown by Kaufman (1995), this pattern contributes greatly to the general latitudinal trend shown by all mammals, although it cannot explain it completely because nonvolant mammals show similar trends, albeit less pronounced than in the case of bats.

Differences between latitudinal patterns shown by bats and nonvolant mammals suggest that a biogeographic analysis using distributions of nonvolant mammals would not yield exactly the same limits that we propose. In particular, the high percentage of endemic species of nonvolant mammals in the Volcanic Belt would probably extend the transitional zone farther north than in the case of bats. Although speculative, this observation points to the fact that a full understanding of biogeographic patterns, and particularly of limits between zoogeographic regions, will come only through careful analyses of distributional patterns of different taxonomic groups.

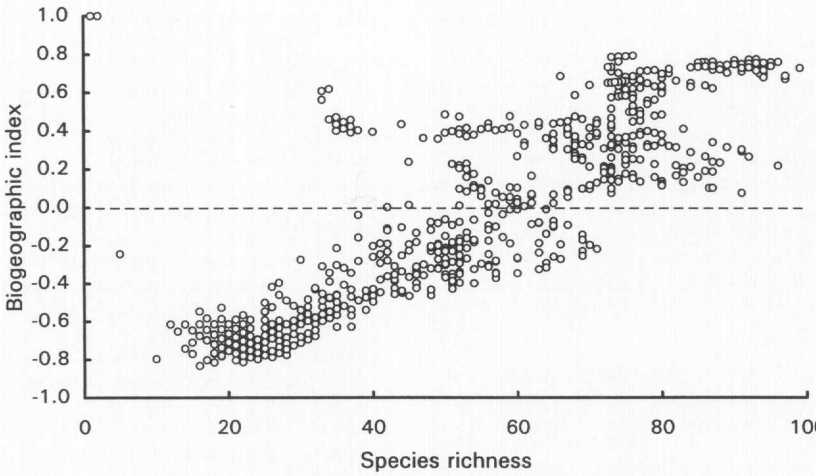

FIG. 4.—Relationships between the biogeographic index and total number of species for 1,054 quadrats in Middle America.

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