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SPATIAL SEGREGATION IN LONG-NOSED BATS, *LEPTONYCTERIS NIVALIS* AND *LEPTONYCTERIS CURASOAE*, IN MEXICO

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ABSTRACT.—Analysis of distributional patterns of bats of the genus *Leptonycteris* in Mexico showed a spatial segregation of the two species. Data on climate and vegetation were gathered for 43 localities of *L. nivalis* and 269 of *L. curasoae* reported in a recent taxonomic revision of the genus. A statistical analysis using a grid of quadrats of 1° of latitude and longitude showed no segregation of the two species at the macrogeographic scale. However, significant differences were found between the altitude and mean annual temperature of localities of the two species; *L. nivalis* occurs in higher and cooler places than *L. curasoae*. No significant differences exist in terms of mean annual precipitation; both species occur in drier zones of the country. *L. nivalis* occurs more frequently in areas with pine (*Pinus*)-oak (*Quercus*) and tropical deciduous forests than expected by chance, whereas *L. curasoae* is found mainly in areas with tropical deciduous and thorn forests. Bats of the genus *Leptonycteris* are the main pollinators of some species of maguey plants (*Agave*), and the ranges of the bats coincide with that of certain species of *Agave*, such as *A. angustifolia* (mezcal plant), *A. salmiana* (pulque plant), and *A. tequilana* (tequila plant).

Based on the competitive-exclusion principle, two species with identical or similar ecological requirements cannot occur in the same place at the same time. When two closely related species are sympatric, several mechanisms potentially can differentiate their niches and permit their distributional ranges to overlap. One such ecological mechanism is spatial segregation. Species can segregate within a given geographic area according to differences in habitat, vertical stratum, or altitude, or by presenting a checkerboard distribution in the case of archipelagoes (Diamond, 1975, 1986).

Jones (1965) and Findley (1969) found segregation of certain sympatric species of vespertilionid bats along altitudinal gradients in Arizona and New Mexico. Koopman (1978) and Graham (1983) presented several examples of altitudinal segregation of closely related species of the Andes of Peru. Start and Marshall (1976) observed segregation by habitat in two species of *Macroglossus* that occur sympatrically in Malaysia; *M. minimus* forages in coastal zones, feeding mainly on the flowers of *Sonneratia* sp., whereas *M. sobrinus* selects flowers of wild banana plants (*Musa* sp.) that grow inland. Handley (1967) and Bonaccorso (1979) documented several examples of segregation of sympatric bats by habitat and vertical stratum in Neotropical forests. Some other examples of segregation of bat species along gradients of altitude or habitat were discussed by Humphrey and Bonaccorso (1979).

Big (*Leptonycteris nivalis*) and little (*L. curasoae*) long-nosed bats are sympatric in central and northern Mexico (Arita and Humphrey, 1988). They are similar morphologically, and the difference in size is slight; the body-mass ratio *L. nivalis* : *L. curasoae* is 1.42:1 (from means of 43 *L. nivalis* and 13 *L. curasoae* males from Morelos and Distrito Federal). The existence of two species in North America was recognized when Davis and Carter (1962) reviewed the genus. The main food of both species is pollen and nectar of the flowers of some tropical and subtropical plants, especially cacti (Cactaceae) and certain species of *Agave* (Alvarez and González-Q., 1970; Gardner, 1977; Quiroz et al., 1986). Baker and Cockrum (1966) suggested geographic and ecologic separation of these two species in North America, *L. nivalis* occurring primarily in the highlands of eastern Mexico and *L. sanborni* (=*L. curasoae*) occupying lower elevations in western and central Mexico. Since then, many localities have been added to the known distribution of *Leptonycteris* in Mexico, allowing more rigorous analysis of Baker and Cockrum's (1966) idea. The objective of this paper is to use available information to test the hypothesis that spatial segregation allows coexistence of two species of nectar-feeding bats with similar ecological requirements.

Also examined herein is the association between bats of the genus *Leptonycteris* and certain species of maguey plants (*Agave*). Bats of the genus *Leptonycteris* are known to be the primary pollinators of magueyes (Eguiarte and Búrquez, 1987; Howell, 1979; Howell and Hartl, 1980; Howell and Roth, 1981; Martínez del Río and Eguiarte, 1987). If a close association exists between these plants and bats, matching distributional ranges are to be expected for both groups of organisms. Furthermore, if spatial segregation occurs between the two species of *Leptonycteris*, an association of each species of bat with a particular species of *Agave* might be predicted.

MATERIALS AND METHODS

Review of the literature pertaining to the distribution of the genus *Leptonycteris* has been hindered by nomenclatural problems. In a recent taxonomic review of the genus, Arita and Humphrey (1988) reported that many museum specimens labeled as *L. nivalis* were misidentified, and that this species has a more restricted distribution than formerly believed. To avoid problems with erroneous distributional records, I relied only on localities reported by Arita and Humphrey (1988), who examined specimens of *L. nivalis* from 43 localities and of *L. curasoae* from 269 localities (Fig. 1).

To test the hypothesis of geographic segregation of long-nosed bats, Mexico was divided into 218 quadrats of one degree of latitude and longitude. All localities of *Leptonycteris* in Mexico reported by Arita and Humphrey (1988) were located on a map and assigned to their respective quadrat. A two-by-two contingency-table analysis was employed to test the null hypothesis that the distributions of *L. nivalis* and *L. curasoae* in Mexico are independent.

For each locality, I compiled meteorological data from García (1981). These data included geographic coordinates, altitude, mean annual precipitation, and mean annual temperature. Most of the stations had records for both temperature and precipitation for ≥ 10 years of observations, but a few lacked information for one of these variables. I first performed a Shapiro-Wilk test for normality to analyze the frequency distribution of altitude, temperature, and precipitation of the localities of both species. All distributions were significantly different from a normal distribution ($P < 0.01$), and I used only nonparametric tests in subsequent comparisons.

Long-nosed bats are considered migratory species (Alvarez and González-Q., 1970; Easterla, 1973; Hayward and Cockrum, 1971; Quiroz et al., 1986), so seasonal movements in altitude or latitude of one or both species could obscure differences between the species. To analyze the extent of migration, I divided localities of each species into dry-season localities (records from November to May) and wet-season localities (records from June to October). Although this division could be considered arbitrary, it corresponds with the approximate duration of the two main seasons in most places in Mexico (García, 1981). Wilcoxon two-sample tests were performed to compare for each species the localities of the two seasons in terms of altitude, mean annual temperature, and mean annual precipitation. Subsequently, I used additional Wilcoxon two-sample tests comparing the localities of both species to test the hypothesis that differences in any of the three variables indicated spatial segregation of the two bat species.

I also compared the distributional range of the two bat species in terms of vegetation. I mapped localities of *Leptonycteris* on Rzedowski's (1978) vegetation map and tallied the number of localities of each species of bat in each of the eight major types of vegetation: tropical rain forest; semi-evergreen tropical forest; tropical deciduous forest; thorn forest; grassland or savanna; desert or chaparral; pine (*Pinus*)-oak (*Quercus*) forest; and cloud forest. I compared the frequency of each bat species in each vegetation type with a null distribution based on the proportion of Mexican territory covered by each of the eight types of vegetation. Deviation from the null distribution would suggest a nonrandom distribution of *Leptonycteris* species in terms of vegetation types, demonstrating a selection of some of the available environments. I also used a binomial test to compare the observed number of localities with the number of localities expected to fall in a given type of vegetation if the distributions were random.

Distributional data presented by Gentry (1982) for *Agave* species were used to compare the distributions of these agaves in Mexico with distributions of both species of long-nosed bats, looking for a geographic association supporting the hypothesis of an ecological relationship between the plants and one or both of the bat species. Special emphasis was given to three magueyes that are sources of traditional beverages in Mexico: *Agave angustifolia*, mezcal plant, *A. salmiana*, pulque plant, and *A. tequilana*, tequila plant. I tested the hypothesis of an association between *L. curasoae* and *A. angustifolia* by using a binomial distribution classifying localities of bats as inside or outside the range of the agave. I made a qualitative comparison of the distributions of *L. nivalis* and *A. salmiana*, but no quantitative test could be performed because of the small sample.

RESULTS

Of the 218 1° quadrats that include Mexican territory, 24 include localities of *L. nivalis* and 78 include *L. curasoae*. Sixteen quadrats include localities of both species. A two-by-two contingency-table analysis demonstrated a significant positive association between the two species of bats on a macrogeographic scale ($\chi^2 = 11.2$, *d.f.* = 1, $P < 0.001$, Fig. 1).

For *L. nivalis*, I found no significant seasonal variation in altitude (Wilcoxon two-sample test, $P = 0.56$), mean annual temperature ($P = 0.78$), or mean annual precipitation ($P = 0.16$). Similar results were obtained for *L. curasoae* ($P = 0.17$ for altitude, $P = 0.41$ for temperature, and $P = 0.32$ precipitation). These results indicate that no seasonal pattern can be detected at the macrogeographic level. Because no seasonal variation can be shown, I combined data for each species without regard to time of year.

Most localities at which *L. nivalis* has been collected are between 1,000 and 2,200 m elevation (Fig. 2a), but *L. nivalis* can reach higher elevations; Saussure (1860) described the type locality of this species at the snow line on the Pico de Orizaba, and Koestner (1941) reported a colony of *L. nivalis* in the Cerro Potosí, Nuevo León, at 3,780 m. In contrast, *L. curasoae*, occurs at lower elevations (Fig. 2a). Most locality records for this species are <1,800 m, and approximately one-third of them are <300 m. Unlike *L. nivalis*, *L. curasoae* frequently is caught at sea level. The altitude of the localities of *L. nivalis* is significantly higher than that of *L. curasoae* (Wilcoxon two-sample test, $P < 0.001$).

Correlated with differences in altitude, a significant difference in mean annual temperature exists between localities of the two species (Fig. 2b). The mode of the frequency distribution of localities of *L. nivalis* is 20°C, whereas that for localities of *L. curasoae* is 25°C. There is no significant difference in annual rainfall between localities of the two species of long-nosed bats (Fig. 2c). The frequency distributions of both species are almost the same, with a mode at about 750 mm.

Localities of *L. nivalis* show a nonrandom distribution among types of vegetation ($\chi^2 = 100.1$, *d.f.* = 7, $P < 0.001$, Fig. 3). Only four of the eight types of vegetation are represented among known localities of *L. nivalis*. The big long-nosed bat is positively associated with tropical deciduous and pine–oak forests (binomial tests, $P < 0.01$ and $P < 0.001$, respectively), and negatively associated with grassland ($P < 0.01$) and tropical rain forests ($P < 0.05$). Similarly, the distribution of *L. curasoae* among types of vegetation is not random ($\chi^2 = 624.7$, *d.f.* = 7, $P < 0.001$, Fig. 3). The little long-nosed bat occurs more frequently in dry forests (tropical deciduous, thorn, and semi-evergreen) than expected by chance ($P < 0.001$) and is negatively associated with deserts, grasslands, and tropical rain forests ($P < 0.001$).

The distribution of *L. curasoae* in Mexico coincides with the range of the mezcal plant, *A. angustifolia* ($P < 0.001$ in a binomial test classifying bat localities as inside or outside the range of the plant, Fig. 1b). The few localities of *L. curasoae* outside the range of the maguey are concentrated mainly on the Baja California peninsula and in northeastern Mexico. Also, some populations of *A. angustifolia* occur in the northern part of the Yucatán peninsula where the little long-nosed bat does not occur. *A. angustifolia* is mainly a form of the Mexican tropical lowlands, occurring chiefly in tropical savannas, thorn forests, and tropical deciduous forests, in areas with annual precipitation from 250 to 1,680 mm. Distributional records are from sea level to ca. 1,500 m (Gentry, 1982). The tequila plant (*A. tequilana*) is closely related to *A. angustifolia* and may only be a variety of the mezcal plant (Gentry, 1982). This plant grows wild in the vicinity of Tequila, Jalisco, where the little long-nosed bat has been collected (Arita and Humphrey, 1988).

The pulque plant (*A. salmiana*) and other species of the Salmianae group, as arranged by

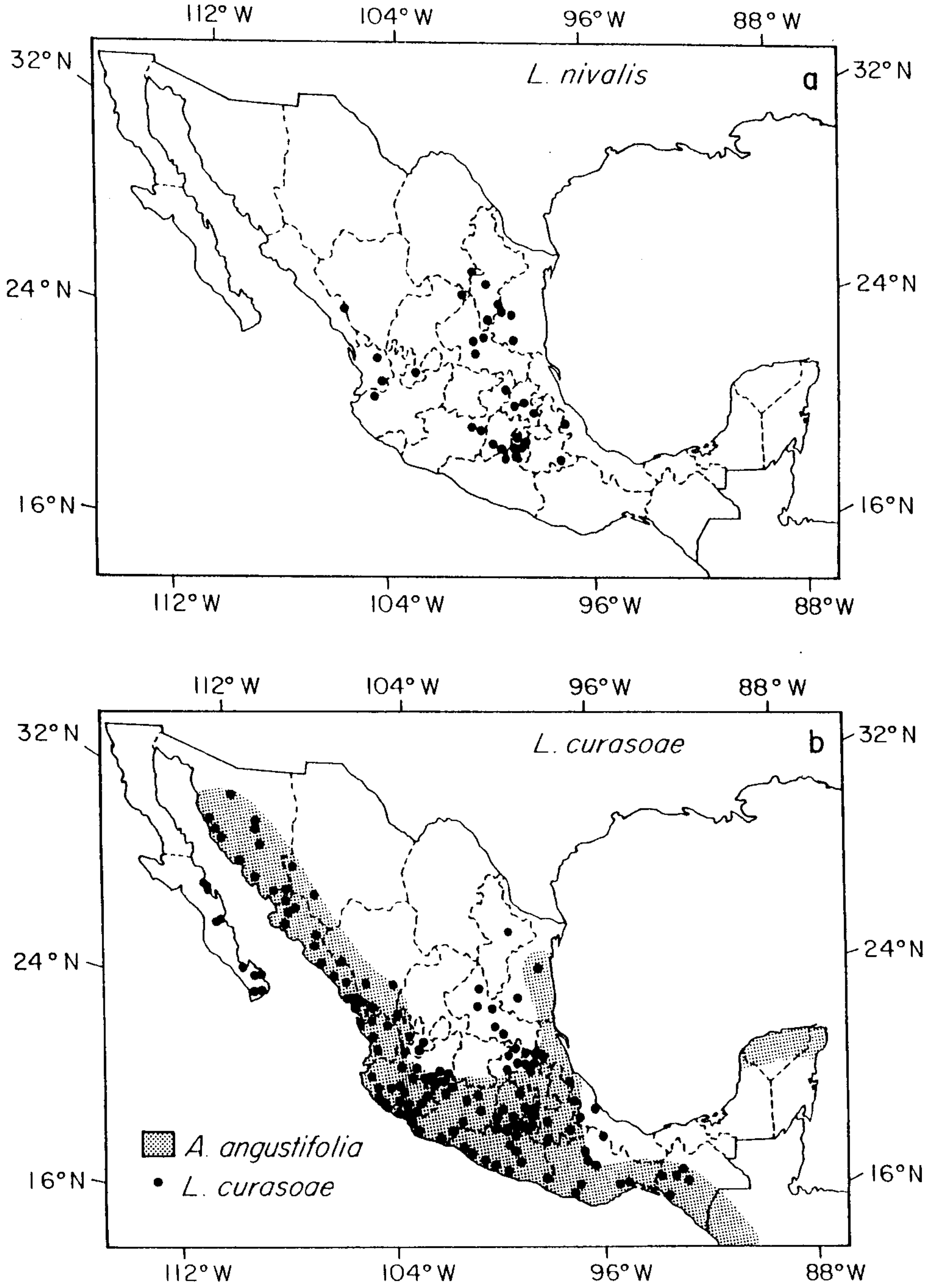

FIG. 1.—Distribution of: a, *Leptonycteris nivalis* and b, *L. curasoae* in Mexico, the latter superimposed on the distribution of *Agave angustifolia*. *L. nivalis* also occurs in a few localities in Texas and New Mexico; *L. curasoae* also occurs in Arizona, New Mexico, and some parts of Central and South America. Data on *Leptonycteris* from Arita and Humphery (1988); distribution of *A. angustifolia* adapted from Gentry (1982).

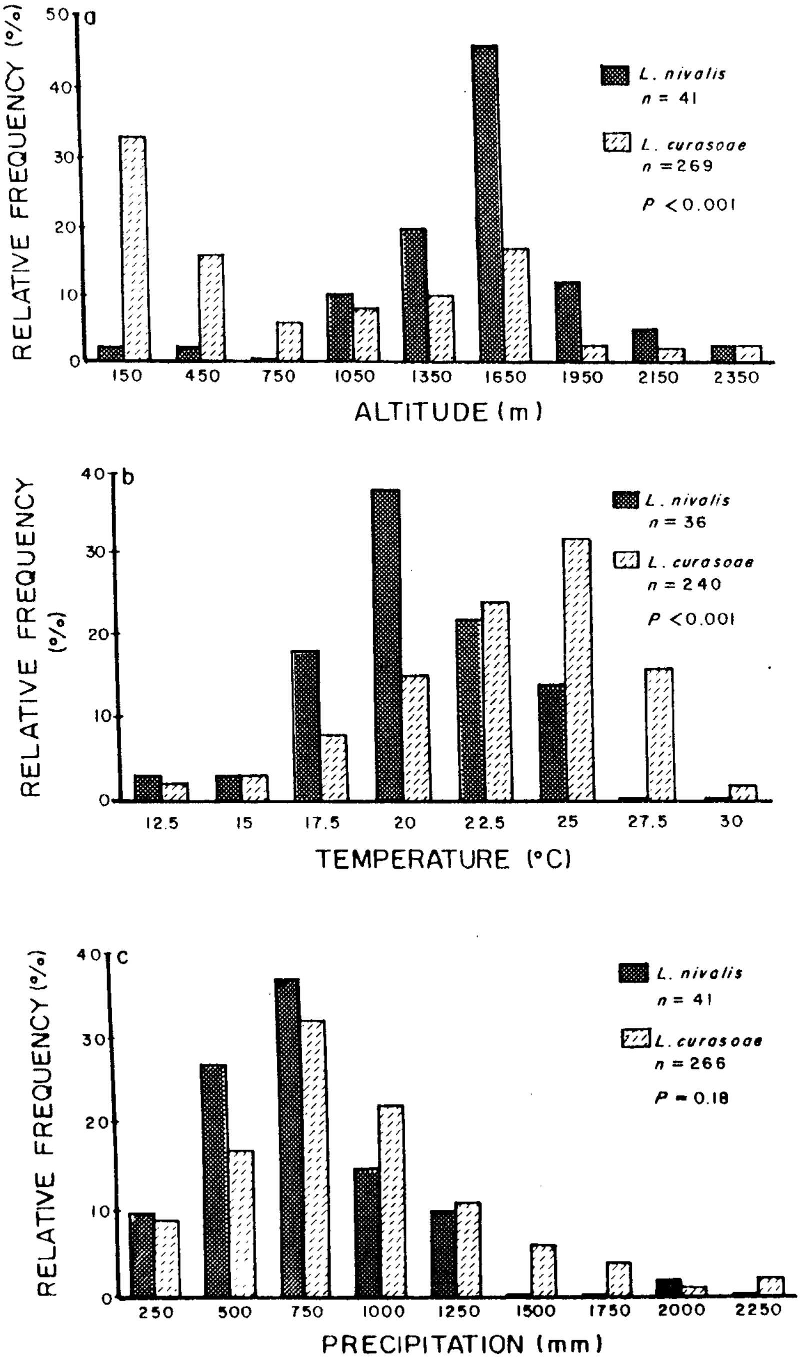

FIG. 2.—Relative frequency distributions of: a, elevation; b, mean annual temperature; and c, a rainfall at localities at which *Leptonycteris nivalis* and *L. curasoae* occur. Probability values in significance of differences in distribution of the species for variables (Wilcoxon two-sample test).

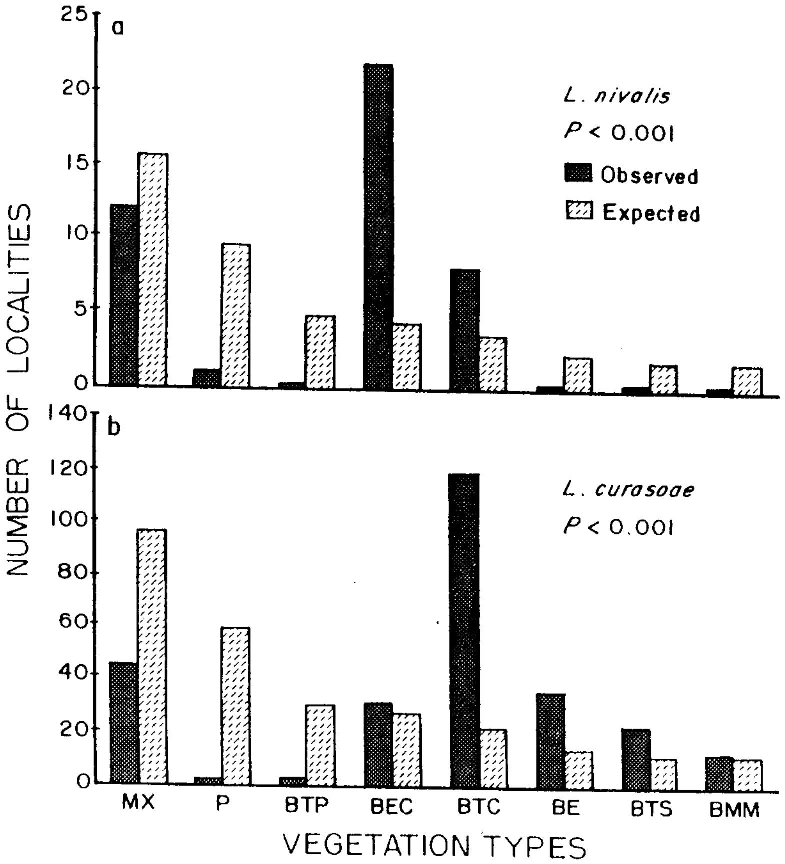

FIG. 3.—Number of localities in Mexico by vegetational type (Rzedowski, 1978) at which: a, *Leptonycteris nivalis* and b, *L. curasoae* were observed and were expected on the basis of the proportion of Mexican territory covered by each vegetation type. Probabilities are for chi-square tests comparing observed and expected distributions for each species. Abbreviations for vegetation types are: MX, desert or chaparral; P, grassland or savanna; BTP, tropical rain forest; BEC, pine-oak forest; BTC, tropical deciduous forest; BE, thorn forest; BTS semi-evergreen tropical forest; BMM, cloud forest.

Gentry (1982), grow in habitats where *L. nivalis* is abundant. These plants are native to the highlands of the Transverse Volcanic Belt and are found at elevations between 1,250 and 2,500 m, where annual rainfall ranges from 350 to 1,000 mm (Gentry, 1982).

DISCUSSION

Long-nosed bats are not geographically segregated. After Davis and Carter (1962) demonstrated the presence of two species of *Leptonycteris* in North America, it was believed that they were sympatric only in central Mexico. Most locality records reported by Baker and Cockrum (1966), Ramírez-P. and Alvarez (1972), and Hall (1981) showed that *L. nivalis* was found mainly in northeastern Mexico, whereas *L. curasoae* occurred chiefly in western and southern Mexico. However, the revision by Arita and Humphrey (1988) demonstrated that *L. curasoae* is more widespread in northeastern Mexico than formerly believed (Wilson et al., 1985), and that the idea of a geographic segregation between long-nosed bats was caused by misidentification of many specimens of *L. curasoae* as *L. nivalis*. In reality, the distributional range of *L. nivalis* is almost completely included in the range of *L. curasoae*. The only places outside the range of *L. curasoae* where *L. nivalis* is known to occur are the Big Bend National Park area in Texas

(Easterla, 1973) and some parts of Coahuila (Easterla, 1972; Wilson et al., 1985). My analysis confirms a positive association between the two *Leptonycteris* species at the macrogeographic scale.

As suggested by Baker and Cockrum (1966), long-nosed bats segregate in an altitudinal gradient, with *L. nivalis* occurring at higher and cooler localities than *L. curasoae* (Fig. 2). Both species are found more frequently in dry areas of the country, with annual rainfall <2,000 mm. Mexico generally is a dry country, although it includes regions with annual precipitation of >4,000 mm. Long-nosed bats do not occur in those parts of the country (Fig. 2), suggesting that bats of the genus *Leptonycteris* are adapted to arid conditions, as discussed by Koopman (1981). The two species of long-nosed bat occur at localities with different types of vegetation (Fig. 3). As observed by Baker and Cockrum (1966), the most common habitat for *L. nivalis* is the transition zone between tropical deciduous forest and pine–oak forest. Conversely, *L. curasoae* is more frequently found in places characterized by tropical and subtropical dry forests.

The mezcal plant and *L. curasoae* occur in almost identical areas; many of the localities of *A. angustifolia* listed by Gentry (1982) are close to collection sites of the little long-nosed bat. This geographic association, and the close plant–pollinator relationship demonstrated between *L. curasoae* and other species of Agavaceae (Eguiarte and Búrquez, 1987; Howell, 1979; Howell and Hartl, 1980; Howell and Roth, 1981) might suggest that *L. curasoae* could be a pollinator of wild mezcal plants. However, the possibility exists that the positive geographic association demonstrated herein may be only a consequence of both the bat and the agave occurring chiefly in arid parts of the country; only direct field observations could confirm an ecological association between these species. *A. salmiana* is a bat-pollinated plant (Martínez del Río and Eguiarte, 1987), but the identity of the species that pollinates this maguey remains unknown. On the basis of the habitats in which the plant grows, that pollinator could be *L. nivalis*, but this must be confirmed by field studies.

The two species of long-nosed bats seem to have similar feeding habits and foraging strategies. Alvarez and González-Q. (1970) found that both species of *Leptonycteris* depend heavily on plants of the genera *Agave*, *Myrtillocactus*, *Ceiba*, *Ipomoea*, and *Bombax*, and that the only dietary difference between the two species was the relative proportion of pollen of these plants in their diet. Given the altitudinal segregation of long-nosed bats, it is possible that even if the two species of *Leptonycteris* feed on nectar and pollen of the same genera of plants, as demonstrated by Alvarez and González-Q. (1970), they could specialize on different species; it seems that *L. curasoae* exploits lowland species of magueyes and *L. nivalis* feeds on highland species.

Diamond (1986) found spatial segregation to be the most frequent mechanism allowing pairs of bird species to exist sympatrically in New Guinea; among such pairs of species, he found little evidence of ecological segregation in feeding habits or body mass. Diamond (1986) found that pairs of bird species in New Guinea with body-mass ratios <1.7:1 are never truly syntopic, unless they have different diets or foraging behavior. Morphological and dietary similarities between the two species of *Leptonycteris* suggest that altitudinal segregation is the mechanism that allows them to be sympatric. This segregation, however, is incomplete; there is overlap in altitudes occupied by the two species (Fig. 2), and there are several reports of both species being caught in the same place at the same time (Villa-R., 1967; Wilson et al., 1985). Currently, no information is available to suggest an ecological mechanism that could explain these cases of syntopic occurrence of long-nosed bats.

RESUMEN

La existencia de una segregación espacial entre las dos especies de murciélagos magueyeros (género *Leptonycteris*) puede ser demostrada mediante el análisis de los patrones de distribución de estos animales. Se obtuvieron datos sobre el clima y la vegetación de 43 localidades de *L. nivalis* y 269 de *L. curasoae* en México usando como base los registros de una revisión taxonómica del género recientemente publicada. El análisis estadistico de la distribución de las especies utilizando cuadrantes de un grado por lado no pudo demostrar una segregación de las especies

a nivel macrogeográfico. Por el contrario, se encontraron diferencias significativas en cuanto a altitud y temperatura media anual entre las localidades de las dos especies. *L. nivalis* habita zonas más altas y frías que *L. curasoae*. No se encontraron diferencias entre la precipitación media anual de las localidades de las dos especies; ambas ocupan las partes más secas del país. *L. nivalis* se encuentra en áreas con bosque de encino y coníferas o con bosque tropical caducifolio con mayor frecuencia que la esperada al azar, mientras que *L. curasoae* se encuentra principalmente en los bosques tropical caducifolio y espinoso. Los murciélagos del género *Leptonycteris* son los principales polinizadores de algunos magueyes (género *Agave*), y sus patrones de distribución coinciden con los de algunas especies de magueyes de importancia comercial, como el maguey mezcalero (*A. angustifolia*), el maguey pulquero (*A. salmiana*) y el maguey tequilero (*A. tequilana*).

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