CONSERVATION BIOLOGY OF NECTAR-FEEDING BATS IN MEXICO

Héctor T. Arita and Karina Santos-del-Prado

Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 27–3 (Xangari), 58089 Morelia, Michoacán, Mexico

Nectar-feeding bats (tribe Glossophagini) are an important component of the rich chiropteran fauna of Mexico. Because of biological features associated with their specialized diet, nectar-feeding bats might be more vulnerable to extinction than other bats. Twelve species of glossophagines occur in Mexico. Most have restricted distributions, with two species endemic to the country and two species endemic to Middle America. Compared with other neotropical bats, nectar-feeding species are smaller in body mass and have smaller distributions but have similar local densities. In Mexico, most nectar-feeding bats are associated with tropical and subtropical dry areas (tropical deciduous forests and scrubland). Highest species richness occurs along the warm and dry Pacific versant, including the Balsas Basin. Caves are the main roosts of four of the Mexican nectar-feeding bats, and another six species use caves as alternate roosts. Critical faunas analyses performed using three criteria (species richness, presence of rare species, and phylogenetic value) indicated different sets of critical areas for conservation, nonetheless all criteria identified an area of the Pacific versant and lowlands of southeastern Mexico as priority areas for conservation efforts.

Key words: Glossophagini, bats, conservation, diversity, Mexico

Nectar-feeding bats of the New World (Phyllostomidae: Glossophagini) are a diverse group of 36 species that show morphological, physiological, and behavioral adaptations for feeding on pollen and nectar of flowers in tropical and subtropical habitats (Howell, 1974; Howell and Hodgkin, 1976; Koopman, 1981). Some species, such as the long-tongued bats of the genera *Glossophaga* and *Anoura,* feed regularly on pollen and nectar but also consume many insects. In contrast, more specialized species, such as long-nosed bats (*Leptonycteris curasoae* and *Leptonycteris nivalis*) and the hog-nosed bat (*Choeronycteris mexicana*), depend almost exclusively on nectar, pollen, and fruit (Alvarez and González-Q., 1970; Gardner, 1977).

Ecological attributes of glossophagines suggest that species in this tribe might be more susceptible to extinction than other neotropical bats. Specialists tend to be more vulnerable to extinction than generalists. Consequently, some nectar-feeding bats should be particularly sensitive to habitat loss and the concomitant disappearance of the plants from which they obtain food. Most species in the tribe roost in caves (Dalquest and Walton, 1970; Tuttle, 1976), confronting threats that are particular to cave-dwelling bats (Arita, 1993*a*; Kunz, 1982). Some nectar-feeding bats are migratory and encounter a number of different threats along their migratory routes (Nabhan and Fleming, 1993). Finally, some glossophagines are vulnerable to extinction because they are rare, exist at low population levels, or have restricted distributional ranges (Arita, 1993*b*).

There is evidence that populations of some North American nectar-feeding species are declining. For example, the Mexican and the United States governments include both species of long-nosed bats (*Leptonycteris*) in official lists of threatened species (Koopman, 1993; SEDESOL, 1994). Although controversy surrounds these assessments, particularly in the case of the

lesser long-nosed bat (*L. curasoae*—Cock-rum and Petryszyn, 1991; Nabhan and Fleming, 1993), it is clear that at least in some parts of Mexico, long-nosed bats, par-ticularly *L. nivalis,* are less abundant now than in past years (Wilson et al., 1985).

We analyzed the idea that nectar-feeding bats were vulnerable to extinction because of their particular ecological traits by study-ing the glossophagine fauna of Mexico. We chose this country because it has a rich fau-na of nectar-feeding bats, including several endemic species and some that are migra-tory. Moreover, distribution of nectar-feed-ing bats in Mexico is relatively well known, as is the natural history of most species. We also identified those areas of Mexico that would be of critical importance for imple-menting initiatives aimed at conservation of these bats. Although large-scale diversity has been traditionally measured in terms of species richness, several alternative criteria have been proposed in the past few years, including phylogenetic data (Cousins, 1991; Erwin, 1991; Faith, 1992; Humphries et al., 1995; Pressey et al., 1993; Vane-Wright et al., 1991), presence of threatened or endangered species (Ceballos and Brown, 1995; Sisk et al., 1994), or some index of rarity (Arita et al., 1997; Kershaw et al., 1994, 1995). Herein, we used those and other criteria to identify priority areas for the conservation of nectar-feeding bats in Mexico.

MATERIALS AND METHODS

We compiled a list of species of nectar-feed-ing bats in Mexico from current checklists (Koopman, 1993; Ramírez-P. et al., 1996). We augmented the list with information on body mass, feeding and roosting habits, phylogenetic relationships, and governmental conservation status. Information on body mass and natural history came from general sources (Arita, 1993*b*; Dalquest and Walton, 1970; Eisenberg, 1981, 1989; Nowak, 1991; Tuttle, 1976), re-search on particular species (Alvarez et al., 1991; Hall and Dalquest, 1963; Hensley and Wilkins, 1988; Jones and Homan, 1974; Phillips and Jones, 1971; Webster and Jones, 1984,
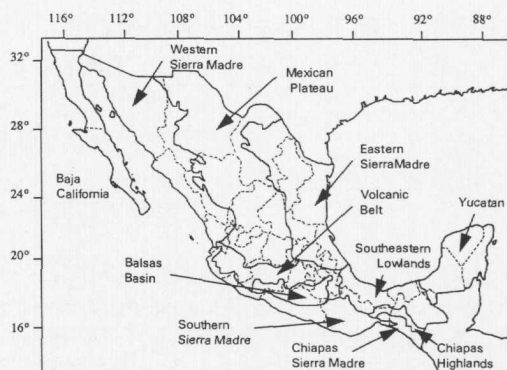

FIG. 1.—Physiographic areas of Mexico used as geographic units in the analysis of distribu-tions of nectar-feeding bats.

1985), or museum specimens in the mammal collection of the Institute of Biology, National University of Mexico (IBUNAM). We compared mean body size of a subsample of 16 glosso-phagines with 88 phyllostomids, including the 16 glossophagines, from several neotropical lo-calities (Arita, 1993*b*). We used log-transformed values to normalize data and a test designed to compare means of a subsample and a pool of species (Freund and Wallpole, 1987). Species were classified into four categories according to their use of caves: caves as main roosts, caves as alternate roosts, caves as occasional roosts, and no known use of caves (Arita, 1993*a*). We compared the percentage of nectar-feeding bats that used caves as roosts with the same percent-age for the whole Mexican bat fauna using a test based on the hypergeometric distribution, which is adequate when sampling without replacement from a finite population. We used the phyloge-netic and systematic arrangement of Baker et al., (1989) and treated Mexican nectar-feeding bats as members of the tribe Glossophagini. Conser-vation status of each species was extracted from the official list of rare, threatened, and endan-gered species in Mexico (SEDESOL, 1994).

Using maps in Hall (1981) as a starting point, we drew distributional maps that we updated with new records and taxonomic changes pub-lished in 1980–1993 (Ramírez-P. et al., 1996). We divided the country into 11 physiographic units based on the categories proposed by Ta-mayo (1980) and Rzedowski (1978) and noted the species that occur in each area (Fig. 1). Based on maps and published records, we as-

TABLE 1.—*Category of rarity (based on area of range and local abundance in Mexico), distribution, and conservation status for the nectar-feeding bats.*

Species	Range	Local abundance	Distribution[a]	Status[b]
Anoura geoffroyi	Widespread	Abundant		
Choeroniscus godmani	Restricted	Scarce		
Choeronycteris mexicana	Widespread	Scarce		T
Glossophaga commissarisi	Restricted	Abundant		
Glossophaga leachii	Restricted	Abundant	MA	
Glossophaga morenoi	Restricted	Abundant	MX	
Glossophaga soricina	Widespread	Abundant		
Hylonycteris underwoodi	Widespread	Scarce	MA	
Leptonycteris curasoae	Widespread	Abundant		T
Leptonycteris nivalis	Widespread	Scarce		T
Lichonycteris obscura	Restricted	Scarce		
Musonycteris harrisoni	Restricted	Scarce	MX	T

[a] MX, endemic to Mexico; MA, endemic to Middle America.
[b] According to the Mexican official list of rare, threatened, and endangered species (SEDESOL, 1994); T, threatened.

sessed occurrence of bat species in each of the vegetation types proposed by Rzedowski (1978) for Mexico. To analyze association of nectar-feeding bats with abiotic conditions, we compiled climatological data for 32 localities in Mexico with records of nectar-feeding bats (García, 1981; Rzedowski, 1978).

We classified species in dichotomous classes of rare species as proposed by Rabinowitz et al. (1986) and modified for bats by Arita (1993*b*). Species were assigned to one of four categories determined by their relative local abundance and area of distribution: locally rare and restricted, locally rare and widespread, locally abundant and restricted, and locally abundant and widespread. To estimate relative local abundance, we used the ranking of Middle American bats of Arita and Ortega (1998). Those authors augmented the database of Arita (1993*b*) for 150 bat species in 16 neotropical localities, with information for 19 additional localities in Middle America. Arita (1993*b*) and Arita and Ortega (1998) estimated the relative abundance of species using the following protocol: 1) for each locality, species were ranked by the number of individuals captured in mist-nets; 2) the rank for each species was divided by the total number of species in the locality to produce an index of relative abundance; and 3) for each species, the average of that index was calculated for all localities in which the species occurred. Because of the many uncertainties associated with that procedure, Arita (1993*b*) and Arita and Ortega (1998) used only two categories based on the ranks: locally rare (species below the median in

the rank series) and locally abundant (all other species). Herein, we used categories of Arita and Ortega (1998) for the 12 nectar-feeding bats of Mexico (Table 1). We measured area of the distribution of each species in Mexico using a digital planimeter. We ranked species according to those values and used the median to assign species to the two categories of size of distribution (widespread or restricted).

To identify sites that could be important for conservation of nectar-feeding bats, we used modified versions of the critical faunas analysis (Kershaw et al., 1994; Pressey et al., 1993; Vane-Wright et al., 1991). The purpose of that analysis was to find the most efficient set of areas that, if given sufficient protection, would contain the totality of a fauna. We used 11 physiographic units as areas for potential protection (Fig. 1). A potential problem with using those areas was their differences in size, which could have biased results, giving higher values to larger units that, simply because of their size, could have had higher species richness. However, clearly this was not the case for the nectar-feeding bats of Mexico, for which the richest areas were not necessarily the largest. Physiographic units were defined on the basis of natural patterns, and their use was less subjective than using arbitrary units. Finally, use of smaller units would have increased the risk of redundancy caused by spatial autocorrelation.

We performed priority-areas analysis using three criteria: species richness, presence of rare species, and phylogenetic value. First, in the species-richness approach, the first priority area

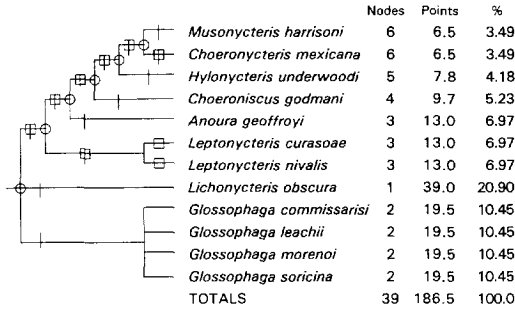|	Nodes	Points	%
Musonycteris harrisoni	6	6.5	3.49
Choeronycteris mexicana	6	6.5	3.49
Hylonycteris underwoodi	5	7.8	4.18
Choeroniscus godmani	4	9.7	5.23
Anoura geoffroyi	3	13.0	6.97
Leptonycteris curasoae	3	13.0	6.97
Leptonycteris nivalis	3	13.0	6.97
Lichonycteris obscura	1	39.0	20.90
Glossophaga commissarisi	2	19.5	10.45
Glossophaga leachii	2	19.5	10.45
Glossophaga morenoi	2	19.5	10.45
Glossophaga soricina	2	19.5	10.45
TOTALS	39	186.5	100.0

FIG. 2.—Phylogenetic relationships among nectar-feeding bats of Mexico, based on Haiduk and Baker (1982). Circles show nodes that define the position of *M. harrisoni* in the cladogram; vertical lines mark 13 branches associated with those nodes; squares show the nine branches needed to connect a set of species consisting of the two *Leptonycteris* species and *C. mexicana*; and columns show number of nodes, specific points, and percentage of the total phylogenetic value (Vane-Wright et al., 1991) corresponding to each species.

was selected as the physiographic unit with the highest number of species. The second area was the one with the highest species richness in the complementary fauna (species not found in the first priority area). The process continued until all species were included in selected areas.

A second analysis was performed using rarity as the criterion. Species were given a rank value according to their rarity: 1) species that were locally abundant and widespread; 2) species that were locally abundant and restricted or locally scarce and widespread; and 3) species that were locally rare and were restricted in distribution. The first priority area was selected as the site with the highest sum of those values, the second area as the one with the highest score using the complementary fauna, and so on.

Finally, in our analysis using phylogenetic information, species were assigned weights according to their positions on the cladogram depicted in Fig. 2. The relationships among genera in the cladogram were based on the phylogenetic hypotheses proposed by Haiduk and Baker (1982), who used their own data on G-banded chromosomes and data on morphology of the hyoid and lingual muscles gathered by Griffiths (1982). As discussed by Haiduk and Baker (1982), morphological data allowed better resolution close to the base of the cladogram, where-

as chromosomal data provided resolution in upper portions. Although phylogenetic relationships among glossophagine genera have been the subject of heated debate (Baker et al., 1989), we considered the hypotheses of Haiduk and Baker (1982) to be the best interpretation of extant data.

We performed two different analyses on phylogenetic data. First, we used the method of Vane-Wright et al. (1991) in which a phylogenetic score was calculated from the number of nodes of the cladogram that corresponded to each species. For example, six nodes were necessary to define the position of the trumpet-nosed bat (*Musonycteris harrisoni*) in the cladogram (Fig. 2). Because the sum of nodes across all species totaled 39, *M. harrisoni* was given $39/6 = 6.5$ points. Because the sum of those points across all species was 186.55, *M. harrisoni* had $(6.5/186.5)100 = 3.49\%$ of the total phylogenetic information in the cladogram. We repeated the analysis using May's (1990) criterion, in which the total number of branches that touched nodes that corresponded to each species was the basis for the calculations. For example, 13 branches touched nodes corresponding to *M. harrisoni* (Fig. 2). The principle in both methods was to give higher values to basal species, with the idea that they possessee more evolutionary information than terminal species (Vane-Wright et al., 1991).

We complemented those analyses by using a third index of phylogenetic diversity (Faith, 1992; Walker and Faith, 1995). In the original definition of the index, the phylogenetic diversity of a subset of species was calculated as the sum of the length of branches of the complete tree connecting all taxa in the subset (Faith, 1992). Because we lacked information on branch lengths, we arbitrarily assigned a length of one unit for all branches and simply tallied the number of such branches connecting all species of a given subset. For example, nine branches were necessary to connect *C. mexicana, L. curasoae,* and *L. nivalis* in the cladogram (Fig. 2). Therefore, a site in which those three species occurred had a phylogenetic value of 9 units using Faith's (1992) criterion.

RESULTS AND DISCUSSION

Mexican glossophagine fauna.—Twelve species of nectar-feeding bats in eight genera have been reported from Mexico

(Koopman, 1993; Ramírez-P. et al., 1996; Table 1). Most species have restricted distributions. Moreno's long-tongued bat (*Glossophaga morenoi*) and *M. harrisoni* are endemic to Mexico, and *Hylonycteris underwoodi* and *G. leachii* are endemic to Middle America (Arita and Ortega, 1998). Two additional species are restricted to Middle America, except for a few localities in the United States (*C. mexicana* and *L. nivalis*—Arita and Ortega, 1998). Four nectar-feeding bats are considered to be threatened on the Mexican official list of endangered species (SEDESOL, 1994).

Rarity.—On average, nectar-feeding bats are small phyllostomids. All glossophagine species have average body mass <30 g, whereas among Phyllostomidae as a whole, body mass ranges from 7 to 173 g. This difference is statistically significant ($\bar{X}$ = 16.97 g, n = 88 for all species: $\bar{X}$ = 10.21 g, n = 16 for Glossophagini, P < 0.01; test for a mean of a sample from a finite population—Freund and Wallpole, 1987). Small size of nectarivorous bats may be related to energetic constraints associated with their diet and foraging behavior. Most nectar-feeding phyllostomids can hover while feeding on pollen and nectar of flowers—a behavior that would be energetically too expensive for larger bats (Norberg, 1994; Norberg et al., 1993).

In mammals, body mass is correlated with two variables that measure rarity. Area of distribution is correlated positively with body mass, and local population density is correlated negatively with size (Gaston, 1994). Because nectar-feeding bats are relatively small, it would be reasonable to expect glossophagines to be locally abundant but geographically restricted. When compared with the entire neotropical bat fauna, nectar-feeding bats have smaller distributions than expected by chance, but they occur at local densities not significantly different from the average for the whole fauna (Arita, 1993*b*).

Nectar-feeding bats have restricted distributions because many of the species are associated with tropical dry areas (deciduous forests and scrublands, Koopman, 1981; see next section), and these areas are discontinuous in the Neotropics. Large continuous areas of tropical rain forest exist (or existed) in South and Middle America, and several bat species associated with humid forests have large distributions, occurring from southern Mexico to southern Brazil. In contrast, several species associated with dry forests are restricted to one or few of the isolated areas with this type of vegetation. For example, *Platalina genovensium* is restricted to a few dry areas of Perú (Koopman, 1981). In Mexico, *M. harrisoni* and *G. morenoi* are endemic to the tropical dry areas of the Pacific versant, and *C. mexicana* and *L. nivalis* are found only in dry areas of the central and northern parts of the country (Arita, 1991).

Some nectar-feeding bats are locally scarce, but others are abundant wherever they occur. In Mexico, species such as *Choeroniscus godmani* and *Lichonycteris obscura* are extremely rare, and bats such as *C. mexicana* and *L. nivalis* always occur at low to moderate population levels (Wilson et al., 1985). In contrast, species such as *Glossophaga soricina* are among the most abundant bats, especially in disturbed areas (Alvarez et al., 1991).

Mexican nectar-feeding bats are distributed equally among the four categories of rare species (Arita, 1993*b*). Species with restricted distributions and low local densities include *C. godmani, L. obscura,* and *M. harrisoni.* Species with restricted distributions but high population densities include *Glossophaga commissarisi, G. leachii,* and *G. morenoi.* Widespread species with low population levels are *C. mexicana, H. underwoodi,* and *L. nivalis.* Widespread species with high population levels include *Anoura geoffroyi, G. soricina,* and *L. curasoae.*

Association with vegetation types.—Neotropical nectar-feeding bats are found more frequently in dry areas (Koopman, 1981), and this rule holds for the Mexican fauna
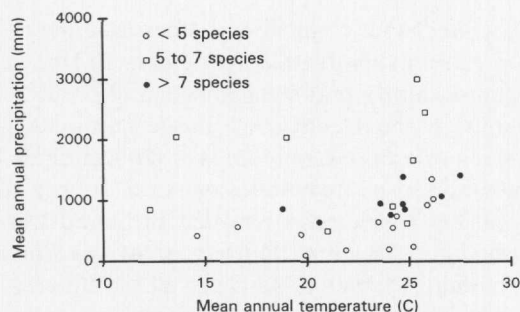
FIG. 3.—Species richness of nectar-feeding bats in 32 Mexican localities; data on mean annual rainfall and mean annual temperature from García (1981).
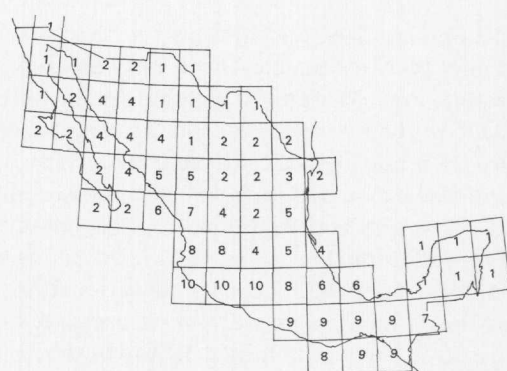

FIG. 4.—Number of species of nectar-feeding bats in 2- by 2-degree quadrats in Mexico.

(Valiente-B. et al., 1996). In a sample of 32 Mexican localities in which nectar-feeding bats have been recorded, sites with the highest species richness have relatively high mean annual temperature and low annual rainfall (Fig. 3). Vegetation that predominates in these sites are tropical deciduous and subdeciduous forests and semi-tropical scrubland.

Zones with the highest richness (10 species) are located mainly along the Pacific versant, including the basin of the Balsas River with tropical deciduous forests (Fig. 4). In contrast, fewer species of glossophagines occur in areas where tropical rainforest dominates. For example, eastern Chiapas (one of the richest areas for bats in general—Ceballos and Navarro, 1991; Fa and Morales, 1993) harbors only seven species of nectar-feeding bats. An exception to this rule is the northern part of the Yucatán Peninsula, an area originally covered with tropical dry forest that harbors only one nectar-feeding bat, *G. soricina.*

Species-by-species analyses confirm the association of nectar-feeding bats with tropical dry areas. All Mexican glossophagines but one (*L. obscura*) have been found in tropical deciduous forest, and seven have been observed in tropical subdeciduous forest. In contrast, only four species have been collected in tropical rain forest. Arita (1991) demonstrated that both species of

Leptonycteris are associated clearly with tropical dry forest, thorn forest, or desert vegetation in Mexico. Similarly, the two species endemic to Mexico (*G. morenoi* and *M. harrisoni*) occur only in the tropical dry forests of western Mexico.

Several species depend directly on plants in dry areas for food. Geographic ranges of Mexican nectar-feeding bats coincide with distributional and diversity patterns of some species of agaves (*Agave angustifolia*—Arita, 1991) and columnar cacti (Valiente-B. et al., 1996). Moreover, close ecological associations have been reported between glossophagines and plants that are typical of tropical dry areas in Mexico, such as *Ceiba acuminata* and *Pseudobombax ellipticum* (Baker et al., 1971; Eguiarte et al., 1987). Pollen of plants in tropical dry forests have been found in stomachs of bats caught outside tropical areas in highlands of central Mexico (Alvarez and González-Q., 1970), demonstrating elevational movements of nectar-feeding bats and suggesting a dependence of these bats on tropical dry areas. Additionally, carbon-stable-isotope analysis of several lesser long-nosed bats (*L. curasoae*) captured near Orizaba, Veracruz, at an elevation of 1,240 m, showed that individuals had fed mostly on CAM plants (presumably *Agave* and columnar cacti), demonstrating short-term elevational movements from the Tehuacán Valley (ca. 60 km

TABLE 2.—*Conservation value for 11 physiographic areas of Mexico based on distributions of nectar-feeding bats. Criteria include species richness (number of species), an index of rarity, and three phylogenetic values based on the position of species in Fig. 2. Phylogenetic values are percentages of the maximum values using each criterion.*

Physiographic area	Species richness	Rarity	Phylogenetic value		
			Vane-Wright et al. (1991)	May (1990)	Faith (1992)
Baja California	2	3	10.45	13.01	36.84
Western Sierra Madre	8	14	54.70	58.81	84.21
Mexican Plateau	3	5	17.42	21.47	42.10
Eastern Sierra Madre	5	7	34.84	38.39	63.16
Volcanic Belt	7	12	44.25	50.35	73.68
Balsas Basin	9	16	63.4	65.24	84.21
Southern Sierra Madre	9	17	61.66	63.36	84.21
Chiapas Sierra Madre	6	10	52.95	53.65	57.89
Chiapas Highlands	4	5	34.84	35.83	8
Southeastern lowlands	5	11	51.22	82.45	10
Yucatan	1	1	10.45	8.46	0

comparison, zones of lowest richness include Baja California (two species), the Mexican Plateau (three species), and the Yucatan Peninsula (one species). This pattern does not coincide with the one for other groups of vertebrates in Mexico. Areas in Mexico with the highest species richness of volant and non-volant mammals, reptiles, and birds are located in Chiapas or in the border between Chiapas and Oaxaca (Arita and Ortega, 1998; Ceballos and Navarro, 1991; Fa and Morales, 1993; Flores-V. and Gerez, 1994). Areas of high species richness of nectar-feeding bats such as the tropical dry forests do coincide with zones of high percentages of endemic species or species with restricted range (Arita et al., 1997; Ceballos and Rodríguez, 1993; Flores-V. and Gerez, 1994).

Priority-areas analysis yielded two possible combinations of zones that include all species of nectar-feeding bats. The first is the combination of the Balsas Basin (nine species) and the southeastern lowlands (three complementary species). The second is comprised of the southern Sierra Madre (nine species), western Sierra Madre (two complementary species), and the southeastern lowlands (one complementary species).

Results of analysis using weighted values

to account for rarity (area of distribution and density of local population) were similar to those using species richness. The southern Sierra Madre had the highest values (17 points; 70.8% of the highest possible value), followed by the Balsas Basin (16 points) and the western Sierra Madre (14 points). The priority-areas analysis yielded a set of three areas that encompassed the whole glossophagine fauna, taking into account rarity: southern Sierra Madre (17 points), southeastern lowlands (5 points for the complementary fauna), and any of the two areas in which *L. nivalis* occured (2 points).

Priority-areas analyses yielded different results when using indices of Vane-Wright et al. (1991), May (1990), and Faith (1992). In the first case, a set of three areas would encompass all of the phylogenetic information for nectar-feeding bats: southern Sierra Madre (61.7% of the phylogenetic information), southeastern lowlands (20.9%, including only the complementary fauna), and the Balsas Basin (17.4%, including only the complementary fauna). Using May's (1990) index, the ideal set would be the southeastern lowlands (82.5% of the phylogenetic information) plus the Balsas Basin (the remaining 17.6% in the comple-

from Orizaba), the closest site harboring those plants (Herrera-Montalvo, 1997).

Use of caves.—Most Mexican nectar-feeding bats roost in caves. Caves are used as main roosts by four species and as alternate roost by six species. Only two species (*C. godmani* and *L. obscura*) do not use caves as roosts. Sixty of 134 Mexican bats use caves as main or alternative roost (Arita, 1993*a*). The percentage of nectar-feeding bats that use caves (83.3%, 10 of 12) is significantly greater than for the entire Mexican bat fauna (44.8%; hypergeometric test, *P* < 0.05).

Besides threats common to all bats, cave-dwelling bats face particular hazards associated with their roosting sites that do not affect species that use other types of roosts (Culver, 1986). Direct and indirect effects, such as the ones produced by vandalism, unintentional damage to caves by spelunkers, and changes in the environment of the exterior can have a profound effect on bat populations (McCracken, 1989; Tuttle, 1979). In the Neotropics, another serious threat is control of vampire bats (*Desmodus rotundus*) that sometimes is conducted by inexperienced persons. Populations of insectivorous, frugivorous, and nectar-feeding bats have been lost, presumably as consequence of misdirected campaigns aimed at vampires (Villa-R., 1967).

Migratory behavior.—At least two of the Mexican nectar-feeding bats are migratory. Long-distance latitudinal movements have been well documented for the two long-nosed bats (*Leptonycteris*) in northern Mexico and southwestern United States (Cockrum, 1991; Fleming et al., 1993; Wilkinson and Fleming, 1996). In central Mexico, migratory movements are assumed to occur because some species are present at particular localities for only part of the year (Alvarez and González-Q., 1970). However, patterns of migration remain largely unknown, and some populations, such as the one in Chamela, Jalisco, Mexico (Ceballos et al., 1997) do not migrate. More research is needed to document movements of nec-

tar-feeding bats in central Mexico, especially along elevational gradients (Herrera-Montalvo, 1997).

This migratory behavior makes long-nosed bats susceptible to environmental conditions. Because a continual supply of blooming plants (a "nectar trail") must occur along the migratory path to guarantee viability of bats (Fleming et al., 1993; Gentry, 1982), any local change in the environment that affects flowering of plants could disrupt the entire process. Additionally, migratory movements are related to reproductive activity in long-nosed bats. In lesser long-nosed bats (*L. curasoae*), pregnant females travel to give birth in caves in Sonora and Arizona (Cockrum, 1991), and big long-nosed bats (*L. nivalis*) perform similar movements to reproduce in the northern Mexican states of Coahuila and Chihuahua and southwestern Texas (Schmidly, 1991; Wilson et al., 1985). Easterla (1972), observed fluctuations in size of the colony of big long-nosed bats in Big Bend National Park, Texas, and speculated that bats reach Texas only in years of high population levels or low food supply in Mexico. As pointed out by Cockrum and Petryszyn (1991), however, Easterla's (1972) suggestion had no empirical basis, and apparent fluctuations could have been an artifact of a non-systematic sampling over the years.

Because of its complexity, the migration of long-nosed bats can be considered an "endangered phenomenon" as defined by Brower and Malcolm (1991) for migratory behavior of monarch butterflies (*Danaus plexippus*). Its conservation requires protection of bats, plants on which the animals depend, sites where the bats roost, and all environments of the migratory route (Nabhan and Fleming, 1993).

Priority areas for conservation.—Areas with the highest species richness of nectar-feeding bats are located along the west coast of Mexico (Fig. 4, Table 2). The southern Sierra Madre and the Balsas Basin harbor nine species each, and the western Sierra Madre supports eight species. In

mentary fauna). By Faith's (1992) criterion, the most efficient combination of sites would be the Balsas Basin (16 units; 84.2% of the highest possible value) and the southeastern Mexico lowlands, that contains the complementary glossophagine fauna of the Balsas Basin.

Four regions emerge as priority areas for conservation of glossophagines in Mexico: western Sierra Madre, Balsas Basin, southern Sierra Madre, and the southeastern lowlands. Because of the high species richness of the region, lowlands of southeastern Mexico are relatively well represented in the Mexican system of protected areas (Gómez-Pompa and Dirzo, 1995). For example, 19.2% of the territory in Chiapas lies within protected areas (Flores-V. and Gerez, 1994). In contrast, tropical dry areas of western and southern Sierra Madre and Balsas Basin are represented poorly in the national system of protected areas (Flores-V. and Gerez, 1994; Gómez-Pompa and Dirzo, 1995). In particular, the Balsas Basin, is of prime importance both for nectar-feeding bats and chiropterophilous plants (Valiente-B. et al., 1996) and is almost totally unprotected. To guarantee preservation of Mexico's rich fauna of nectar-feeding bats, actions should be taken to increase the number of protected areas in this zone.

LITERATURE CITED

ALVAREZ, J., M. R. WILLIG, J. K. JONES, JR., AND W. D. WEBSTER. 1991. Glossophaga soricina. Mammalian Species, 379:1–7.

ALVAREZ, T., AND L. GONZÁLEZ-Q. 1970. Análisis polínico del contenido gástrico de murciélagos Glossophaginae de México. Anales Escuela Nacional de Ciencias Biológicas, México, 18:137–165.

ARITA, H. T. 1991. Spatial segregation in long-nosed bats, *Leptonycteris nivalis* and *Leptonycteris curasoae*, in Mexico. Journal of Mammalogy, 72:706–714.

———. 1993a. Conservation biology of the cave bats of Mexico. Journal of Mammalogy, 74:693–702.

———. 1993b. Rarity in neotropical bats: correlations with phylogeny, diet, and body mass. Ecological Applications, 3:506–517.

ARITA, H. T., AND J. ORTEGA. 1998. The Middle American bat fauna: conservation in the neotropical-nearctic border. Pp. 295–308, *in* Bat biology and conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C.

ARITA, H. T., F. FIGUEROA, A. FRISCH, P. RODRÍGUEZ, AND K. SANTOS DEL PRADO. 1997. Geographical range size and the conservation of Mexican mammals. Conservation Biology, 11:92–100.

BAKER, H. G., R. W. CRUDEN, AND I. BAKER. 1971. Minor parasitism in pollination biology and its community function: the case of *Ceiba acuminata*. Bioscience, 21:1127–1129.

BAKER, R. J., C. S. HOOD, AND R. L. HONEYCUTT. 1989. Phylogenetic relationships and classification of the higher categories of the New World bat family Phyllostomidae. Systematic Zoology, 38:228–238.

BROWER, L. P., AND S. B. MALCOLM. 1991. Animal migrations: endangered phenomena. American Zoologist, 31:265–276.

CEBALLOS, G., AND J. H. BROWN. 1995. Global patterns of mammalian diversity, endemism, and endangerment. Conservation Biology, 9:559–568.

CEBALLOS, G., AND D. NAVARRO. 1991. Diversity and conservation of Mexican mammals. Pp. 167–198, *in* Topics in Latin American mammalogy: history, biodiversity and education (M. A. Mares and D. J. Schmidly, eds.). University of Oklahoma Press, Norman.

CEBALLOS, G., AND P. RODRÍGUEZ. 1993. Diversidad y conservación de los mamíferos de México. II. Patrones de endemicidad. Pp. 87–108, *in* Avances en el estudio de los mamíferos de México (R. A. Medellín and G. Ceballos, eds.). Asociación Mexicana de Mastozoología, Mexico City.

CEBALLOS, G., T. H. FLEMING, C. CHÁVEZ, AND J. NASSAR. 1997. Annual population cycle of *Leptonycteris curasoae* (Chiroptera, Phyllostomidae) at a roost near Chamela, Jalisco, Mexico. Journal of Mammalogy, 78:224–234.

COCKRUM, E. L. 1991. Seasonal distribution of northwestern populations of the long-nosed bat, *Leptonycteris sanborni*, family Phyllostomidae. Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Serie Zoología, 62:181–202.

COCKRUM, E. L., AND Y. PETRYSZYN. 1991. The long-nosed bat, Leptonycteris: an endangered species in the southwest? Occasional Papers, The Museum, Texas Tech University, 142:1–32.

COUSINS, S. H. 1991. Species diversity measurement: choosing the right index. Trends in Ecology and Evolution, 6:190–192.

CULVER, D. C. 1986. Cave faunas. Pp. 427–443, *in* Conservation biology, the science of scarcity and di-

versity (M. E. Soulé, ed.). Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

DALQUEST, W. W., AND D. W. WALTON. 1970. Diurnal retreats of bats. Pp. 162–187, *in* About bats (B. H. Slaughter and D. W. Walton, eds.). Southern Methodist University Press, Dallas, Texas.

EASTERLA, D. A. 1972. Status of *Leptonycteris nivalis* (Phyllostomatidae) in Big Bend National Park, Texas. The Southwestern Naturalist, 17:287–292.

EGUIARTE, L., C. MARTÍNEZ DEL RÍO, AND H. ARITA. 1987. El néctar y el polen como recursos: el papel ecológico de los visitantes a las flores de *Pseudobombax ellipticum* (H. B. K.) Dugand. Biotropica, 19:74–82.

EISENBERG, J. F. 1981. The mammalian radiations. The University of Chicago Press, Chicago, Illinois.

―――. 1989. Mammals of the Neotropics. I. The northern Neotropics. The University of Chicago Press, Chicago, Illinois.

ERWIN, T. L. 1991. An evolutionary basis for conservation strategies. Science, 253:750–752.

FA, J. E., AND L. M. MORALES. 1993. Patterns of mammalian diversity in Mexico. Pp. 253–280, *in* Biological diversity of Mexico: origins and distribution (T. P. Ramamoorthy, R. Bye, A. Lot, and J. E. Fa, eds.). Oxford University Press, New York.

FAITH, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation, 61:1–10.

FLEMING, T. H., R. A. NÚÑEZ, AND L. S. L. DA SILVEIRA. 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. Oecologia, 94:72–75.

FLORES-V., O., AND P. GEREZ. 1994. Biodiversidad y conservación en México: vertebrados, vegetación y uso del suelo. Second ed. Universidad Nacional Autónoma de México, Mexico City, Mexico.

FREUND, J. E., AND R. E. WALLPOLE. 1987. Mathematical statistics. Fourth ed. Prentice Hall, Englewood Cliffs, New Jersey.

GARCÍA, E. 1981. Modificaciones al sistema de clasificación climática de Koppen (para adaptarlo a las condiciones de la República Mexicana), Third ed. Larios, México City, Mexico.

GARDNER, A. L. 1977. Feeding habits. Pp. 293–350, *in* Biology of bats of the New World family Phyllostomatidae. Part II (R. J. Baker, D. C. Carter, and J. K. Jones, Jr., eds.). Special Publications, The Museum, Texas Tech University, 13:1–364.

GASTON, K. J. 1994. Rarity. Chapman and Hall, London, United Kingdom.

GENTRY, H. S. 1982. Agaves of continental North America. University of Arizona Press, Tucson.

GÓMEZ-POMPA, A., AND R. DIRZO. 1995. Reservas de la biósfera y otras áreas naturales protegidas de México. Secretaría de Medio Ambiente, Recursos Naturales y Pesca, México City, México.

GRIFFITHS, T. A. 1982. Systematics of the New World nectar-feeding bats (Mammalia, Phyllostomidae), based on the morphology of the hyoid and lingual regions. American Museum Novitates, 2742:1–45.

HAIDUK, M. W., AND R. J. BAKER. 1982. Cladistical analysis of G-banded chromosomes of nectar-feeding bats (Glossophaginae: Phyllostomidae). Systematic Zoology, 31:252–265.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + 90.

HALL, E. R., AND W. W. DALQUEST. 1963. The mammals of Veracruz. University of Kansas Publications, Museum of Natural History, 14:165–362.

HENSLEY, A. P., AND K. T. WILKINS. 1988. *Leptonycteris nivalis*. Mammalian Species, 307:1–4.

HERRERA-MONTALVO, L. G. 1997. Evidence of altitudinal movements of *Leptonycteris curasoae* (Chiroptera: Phyllostomidae) in Central Mexico. Revista Mexicana de Mastozoología, 2:116–118.

HOWELL, D. J. 1974. Bats and pollen, physiological aspects of the syndrome of chiropterophyly. Comparative Biochemistry and Physiology, 48:263–276.

HOWELL, D. J., AND N. HODGKIN. 1976. Feeding adaptations in the hair and tongue of nectar-feeding bats. Journal of Morphology, 148:329–336.

HUMPHRIES, C. J., P. H. WILLIAMS, AND R. I. VANE-WRIGHT. 1995. Measuring biodiversity value for conservation. Annual Review of Ecology and Systematics, 26:93–111.

JONES, J. K., JR., AND J. A. HOMAN. 1974. *Hylonycteris underwoodi*. Mammalian Species, 32:1–2.

KERSHAW, M., P. H. WILLIAMS, AND G. M. MACE. 1994. Conservation of Afrotropical antelopes: consequences and efficiency of using different site selection methods and diversity criteria. Biodiversity and Conservation, 3:354–372.

KERSHAW, M., G. M. MACE, AND P. H. WILLIAMS. 1995. Threatened status, rarity and diversity as alternative selection measures for protected areas: a test using Afrotropical antelopes. Conservation Biology, 9:324–334.

KOOPMAN, K. F. 1981. The distributional patterns of New World nectar-feeding bats. Annals of Missouri Botanical Garden, 68:352–369.

―――. 1993. Order Chiroptera. Pp. 137–241, *in* Mammal species of the world, a taxonomic and geographic reference. Second ed. (D. E. Wilson and D. A. Reeder, eds.). Smithsonian Institution Press, Washington, D.C.

KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55, *in* Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York.

MAY, R. M. 1990. Taxonomy as destiny. Nature, 347:129–130.

MCCRACKEN, G. F. 1989. Cave conservation: special problems of bats. The National Speleological Society Bulletin, 51:47–51.

NABHAN, G. P., AND T. H. FLEMING. 1993. Endangered mutualisms. Conservation Biology, 7:457–459.

NORBERG, U. M. 1994. Wing design, flight performance, and habitat use in bats. Pp. 205–239, *in* Ecological morphology, integrative organismal biology (P. C. Wainwright and S. M. Reilly, eds.). The University of Chicago Press, Chicago, Illinois.

NORBERG, U. M., T. H. KUNZ, J. F. STEFFENSEN, Y. WINTER, AND O. VON HELVERSEN. 1993. The cost of hovering flight in a nectar-feeding bat, *Glossophaga soricina*, estimated from aerodynamic theory. Journal of Experimental Biology, 182:207–227.

NOWAK, R. M. 1991. Walker's mammals of the world. Fifth ed. The Johns Hopkins University Press, Baltimore, Maryland, 1:1–642.

PHILLIPS, C. J., AND J. K. JONES, JR. 1971. A new sub-species of the long-nosed bats, *Hylonycteris under-woodi,* from Mexico. Journal of Mammalogy, 52: 77–80.

PRESSEY, R., C. HUMPHRIES, C. MARGULES, R. VANE-WRIGHT, AND P. WILLIAMS. 1993. Beyond opportunism: key principles for systematic reserve selection. Trends in Ecology and Evolution, 8:124–128.

RABINOWITZ, D., S. CAIRNS, AND T. DILLON. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. Pp. 182–204, *in* Conservation biology: the science of scarcity and diversity (M. E. Soulé, ed.), Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

RAMÍREZ-P., J., A. CASTRO-C., J. ARROYO-C., AND F. A. CERVANTES. 1996. Lista taxonómica de los mamíferos terrestres de México. Occasional Papers, The Museum, Texas Tech University, 158:1–62.

RZEDOWSKI, J. 1978. Vegetación de México. Limusa, México City, Mexico.

SEDESOL (SECRETARÍA DE DESARROLLO SOCIAL). 1994. Norma oficial mexicana NOM-059-ECOL-1994, que determina las especies y subespecies de flora y fauna silvestres terrestres y acuáticas en peligro de extinción, amenazadas, raras y las sujetas a protección especial, y que establece especificaciones para su protección. Diario Oficial, 438:2–60.

SCHMIDLY, D. J. 1991. The bats of Texas. Texas A&M University Press, College Station.

SISK, T. D., A. E. LAUNER, K. R. SWITTKY, AND P. R. EHRLICH. 1994. Identifying extinction threats. Bioscience, 44:592–604.

TAMAYO, J. L. 1980. Geografía moderna de México, Ninth ed. Trillas, México City, Mexico.

TUTTLE, M. D. 1976. Collecting techniques. Pp. 71–88, *in* Biology of bats of the New World family Phyllostomatidae. Part I (R. J. Baker, D. C. Carter, and J. K. Jones, Jr., eds.). Special Publications, The Museum, Texas Tech University, 10:1–218 pp.

———. 1979. Status, cause of decline, and management of endangered gray bats. The Journal of Wildlife Management, 43:1–17.

VALIENTE-B., A., M. C. ARIZMENDI, A. ROJAS-M., AND L. DOMÍNGUEZ-C. 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. Journal of Tropical Ecology, 12:103–119.

VANE-WRIGHT, R. I., C. J. HUMPHRIES, AND P. H. WILLIAMS. 1991. What to protect?—Systematics and the agony of choice. Biological Conservation, 55:235–254.

VILLA-R., B. 1967. Los murciélagos de México. Universidad Nacional Autónoma de México, Mexico City, Mexico.

WALKER, P. A., AND D. P. FAITH. 1995. Diversity-PD: procedures for conservation evaluation based on phylogenetic diversity. Biodiversity Letters, 2:132–139.

WEBSTER, W. D., AND J. K. JONES, JR. 1984. Glossophaga leachii. Mammalian Species, 226:1–3.

———. 1985. Glossophaga mexicana. Mammalian Species, 245:1–2.

WILKINSON, G. S., AND T. H. FLEMING. 1996. Migration and evolution of lesser long-nosed bats, *Leptonycteris curasoae,* inferred from mitochondrial DNA. Molecular Ecology, 5:329–339.

WILSON, D. E., R. A. MEDELLÍN, D. V. LANNING, AND H. T. ARITA. 1985. Los murciélagos del noreste de México, con una lista de especies. Acta Zoológica Mexicana, nueva serie, 8:1–26.

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