Geographical Range Size and the Conservation of Mexican Mammals

HÉCTOR T. ARITA, FERNANDA FIGUEROA, ASTRID FRISCH, PILAR RODRÍGUEZ, AND KARINA SANTOS-DEL-PRADO

Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510 México D. F., Mexico, email harita@miranda.ecologia.unam.mx

Abstract: Range was estimated for the 423 noninsular mammals of Mexico to identify those species with more restricted distributions and to detect priority areas for conservation based on the presence of such species. Thirty-eight percent of nonvolant mammals and 15.4% of bats are restricted in Mexico to areas of less than 114,000 km². Restricted species were defined as those occurring in ranges smaller than the median for bats and for nonvolant species. Following this criterion, most nonvolant species with restricted distribution in Mexico are either endemic to the country or are shared with the United States, whereas endemic chiropteran species are few, and most Mexican bats with restricted distribution also occur in South America. Nonvolant mammals with restricted distribution in Mexico tend to be of small body size, herbivore or granivore, and fossorial or semifossorial. Among bats, gleaners are significantly more restricted than aerial insectivores. Species with restricted distribution are inadequately represented in the current official list of endangered species with restricted distribution are not represented in the Mexican system of protected areas. Therefore, rarity, in this case measured by the area of distribution, should be included as an additional criterion for conservation of the Mexican mammal fauna.

Tamaño del Área de Distribución Geográfica y la Conservación de los Mamíferos de México

Resumen: Se estimó el tamaño de las áreas de distribución de las 423 especies de mamíferos mexicanos no insulares con el objeto de identificar a las especies más restringidas y de localizar las áreas prioritarias con el mayor número de especies raras. Treinta y ocho por ciento de los mamíferos no voladores y 15.4% de los murciélagos están restringidos en México a áreas de menos de 114,000 km². Se definió una especie como restringida si su área de distribución es menor que la media para murciélagos y para mamíferos no voladores. Siguiendo este criterio la mayoría de las especies restringidas de mamíferos no voladores son endémicas de México o son compartidas con los Estados Unidos, mientras que existen pocos murciélagos endémicos y la mayoría de las especies restringidas se comparten con América del Sur. Las especies no voladoras restringidas tienden a ser de tamaño pequeño, herbívoras o granívoras y excavadoras o semi-excavadoras. Entre los murciélagos, los animalívoros de substrato tienen áreas de distribución significativamente más pequeñas que los insectívoros aéreos. Las especies con distribución restringida están pobremente representadas en la lista oficial de especies en peligro, especialmente en el caso de los mamíferos no voladores. Asimismo, algunas áreas de México en las que existen poblaciones de varias especies restringidas no están representadas en el sistema nacional de áreas protegidas. Por lo tanto, la rareza, en este caso medida por medio del tamaño del área de distribución, debería ser considerada como un criterio adicional para la conservación de la mastofauna mexicana.

Paper submitted May 15, 1995; revised manuscript accepted February 16, 1996.

92

Conservation Biology, Pages 92-100 Volume 11, No. 1, February 1997

Introduction

______ne size, shape, and position of geographical ranges are the subject of study of areography (Rapoport 1975, 1982). In the past few years, a number of studies have closely examined the large-scale ranges of vertebrates, and a few general patterns have emerged (Lawton et al. 1994; Brown 1995). For example, it is well established that the frequency distribution of range sizes is always rightskewed, with many species having restricted distribution and few species having widespread distribution (Rapoport 1975, 1982; S. Anderson 1985; Pagel et al. 1991; Gaston 1994; Lechter & Harvey 1994; Smith et al. 1994).

Another well-known fact is that ranges tend to be smaller in lower latitudes, in a pattern that has come to be known as Rapoport's rule (Rapoport 1975, 1982; Stevens 1989), although some exceptions are known (e.g., the mammals of Australia; Smith et al. 1994). A third general pattern is that area of distribution and average local population density are positively correlated within sets of ecologically similar species (Hanski 1982; Brown 1984; Hanski et al. 1993; Lawton et al. 1994), but not among broader sets (e.g., Neotropical mammals; Arita et al. 1990). Finally, clear relationships between area of distribution and taxonomic position, body mass, phylogeny, and ecological traits have been shown for birds and mammals (Rapoport 1975, 1982; Brown & laurer 1987; Arita et al. 1990; Arita 1993; Fjeldså 1994; -Gaston 1994; Brown 1995).

For conservation purposes the distributional range of species has been used as a criterion of rarity (Rabinowitz et al. 1986; Arita et al. 1990; Arita 1993; Gaston 1994; Kershaw et al. 1994). In general species with small ranges are more prone to extinction than widespread forms (Terborgh 1974; Thomas 1991), so special conservation value has been given to taxa with restricted distribution, such as endemic species (Ceballos & Navarro 1991; Flores-V. & Navarro-S. 1993; Fjeldså 1994; Sisk et al. 1994).

For historical and practical reasons, large-scale diversity has been routinely measured in terms of species richness, the number of species found in a given region. In the last few years, however, alternative criteria have been proposed for the selection of sites for conservation purposes. Some authors have suggested the use of phylogenetic criteria (Cousins 1991; Erwin 1991; Vane-Wright et al. 1991; Pressey et al. 1993). Other researchers have used additional criteria, such as the presence of rare, endemic, or endangered species (Ceballos & Navarro 1991; Daniels et al. 1991; Kattan 1992; Sisk et al. 1994). Finally, the naturalness or the biological integrity of sites have also been proposed as criteria for conservation (Anderson 1991; Angermeier & Karr 1994).

We analyzed the distributional ranges of Mexican nammals. By using range size as a criterion of rarity, we identified species with potential conservation problems and we compared the results of our analysis with other studies that have used different criteria for conservation. We also studied the geographical pattern of distribution of restricted species to identify areas of Mexico that should be considered priorities for conservation.

Methods

Our study concentrates on the distribution of mammals in mainland Mexico. From a complete list of 503 Mexican mammals, we excluded introduced species, marine mammals, and those terrestrial forms known only from islands, which produced a database of 423 terrestrial, noninsular Mexican mammals. Insular species are relevant to any conservation strategy, but their particular distributional patterns make them incompatible with some of the analyses presented here, so they were not included in the study.

The use of Mexico as a study unit is based on conservation pragmatism. If it is true that species do not recognize political borders, it is also a fact that conservation decisions are made by countries, so the use of a political unit as a study site is justifiable. In any case, all studies on large-scale distributional patterns have necessarily relied on subjective political limits (Brown & Maurer 1987; Pagel et al. 1991; Lechter & Harvey 1994; Ceballos & Brown 1995; Smith et al. 1994).

We drew distributional maps for the 423 species. We used Hall's (1981) maps as a starting point but conducted an exhaustive review of the literature published after 1980 to update the information. Data analyzed include all major taxonomic changes and new distributional records up to the end of 1993. A complete list of references is available upon request from the first author.

To quantify the size of the distributional ranges, we used a grid of 0.5×0.5 degree quadrats. Because meridians converge toward the poles, quadrats at higher latitudes are smaller. In central Mexico, at a latitude of 23.5° , a 0.5×0.5 degree quadrat has an area of 2835.77 km². Maximum differences with respect to this average at the highest (32°) and lowest (15°) latitudes in Mexico are 7.45% and 4.98%, respectively. As discussed by Smith et al. (1994), this magnitude of error is not significant at the level of resolution attainable with maps of distribution.

We conducted separate analyses for bats and for nonvolant mammals. From early works on mammalian species diversity in North America, it is known that the temperate-tropical gradient in species richness is much more pronounced for bats than for nonvolant species (Fleming 1973; Wilson 1974; McCoy & Connor 1980). We also expected, and later confirmed, that bats should have larger distributional ranges than nonvolant species.

We estimated the size of the distributional range of each species by the number of quadrats included in its range. Using the method proposed by Arita (1993), we ordered species by the size of their ranges and assigned an inverse rank value to each, so species with smaller distributional ranges were assigned a higher value. In this way the rank value can be used as a measure of how restricted the distribution of a given species is. Also following Arita (1993), we arbitrarily used the median to define two classes: restricted and widespread species. As a consequence, half of the species were considered restricted and half were considered widespread. Because of the right-skewness of the frequency distribution curves for geographical ranges, traditional parameters such as the mean or the standard deviation have little value in assigning species to categories. The median or some percentile are better choices in this case (Rapoport 1975, 1982; Gaston 1994).

We used two variables to assess the conservation value of quadrats considering the presence of restricted species. The first variable was simply the number of restricted species (as defined above) for each quadrat. To assess the statistical significance of such numbers, we compared them to expected values calculated from a binomial distribution in which the probability of success was equal to the probability of getting a restricted species from a random draw from the pool of species. Probabilities were proportional to the number of quadrats in which a given species is present, so widespread species had higher probabilities of being drawn.

Our second variable took into account not only the number of restricted species present in a given quadrat, but also their degree of restrictedness. We used the index

$$\frac{\sum_{i=1}^{n_c} 1/A_i}{n_c},$$

where I_c is the value of the index for quadrat c, A_i is the area of distribution of species i, and n_c is the number of species in quadrat c. This second index is a modified version of the one proposed by Kershaw et al. (1994), which we found too sensitive to the total number of species in the quadrats.

Results and Discussion

Distributional Ranges of Mexican Mammals

The frequency distribution of range sizes is right-skewed for both volant and nonvolant mammals in Mexico (Ceballos & Navarro 1991; Ramírez-P. & Castro-C. 1993), but the pattern is more pronounced in the latter (Fig. 1). Of nonvolant species, 110 (38.5% of the total) occur in less than 114,000 km², whereas only 21 bats (15.4%) are so restricted. Half of the nonvolant species occur in areas smaller than 193,000 km²; in contrast, the median for bats is 493,500 km².





Figure 1. Frequency distribution of range area for bats and nonvolant mammals in Mexico.

Mexican mammals with restricted distribution can be classified in four categories according to their distributional pattern (Fig. 2): (1) endemic species such as Magdalena rat (*Xenomys nelsoni*) and trumpet-nosed bat (*Musonycteris harrisoni*); (2) species with wide distribution elsewhere in North America but with restricted distribution in Mexico, such as beaver (*Castor canadensis*) and silver-haired bat (*Lasionycteris noctivagans*); (3) species endemic to Middle America, such



Figure 2. Distributional ranges of some Mexican mammals with restricted distribution. The Mexican prairie dog (Cynomys mexicanus), the Magdalena rat (Xenomys nelsoni), and the volcano mouse (Neotomodon alstoni) are endemic to Mexico. The beaver (Castor canadensis) is a species widespread in United States and Canada but with restricted distribution in Mexico. Goodwin's short-eared shrew (Cryptotis goodwini) is endemic to Middle America. The naked-tailed arma dillo (Cabassous centralis) occurs in Central and South America but is known in only one site in Mexico. The distribution of restricted species among these categories is different for bats and nonvolant species. For nonvolant mammals, most restricted species are endemic to Mexico (87, or 61.8%) or to Middle America (15, or 6.2%), whereas a considerable percentage (29.9%, 37 species) are widespread in North America north of Mexico; only 2.1% (5 species) also occur in South America. In contrast, only 13 bat species (19.1%) are Mexican endemics and 6 (8.8%) are restricted to Middle America. Most bat species are shared with South America (44, or 64.7%), whereas only 5 species (7.4%) also occur in the United States.

Of the 103 mainland species of nonvolant mammals endemic to Mexico (Ceballos & Rodríguez 1993), we considered 89 to be restricted. The rest are species such as the Mexican agouti (*Dasyprocta mexicana*) that are endemic to the country but that have comparatively large distributional ranges. All noninsular bats that are endemic to Mexico, except the long-eared bat (*Corynorbinus mexicanus*), are considered here as restricted.

Different conservation strategies are needed for restricted volant and nonvolant mammals. Because most onvolant restricted species are endemic to the country or are shared with the United States, they tend to occur in dry areas of central and northern Mexico. As a consequence, areas with a high degree of endemism, such as the tropical dry forests of the Pacific coast and the highlands of the volcanic belt of central Mexico, do not coincide with areas of high species richness located in the tropical rain forests of southern Mexico (Ceballos & Navarro 1991; Ceballos & Rodríguez 1993). Therefore, the conservation of species-rich areas would contribute little to the protection of nonvolant mammals with restricted geographic ranges in Mexico.

For bats the situation is totally different. Most restricted Mexican bat species have large distributional ranges in South and Central America and are found in Mexico only in the tropical rain forests of the southern states. Because these areas are the richest in species (Ceballos & Navarro 1991; Fa & Morales 1993), a conservation strategy based on species richness would benefit the restricted bats of Mexico.

Undoubtedly, the protection of endemic species should be a priority for Mexico because at least onethird of all its mammals are exclusive to the country (Ceballos & Rodríguez 1993). The protection of species with restricted ranges in a country but widespread elsewhere is more controversial (Hunter & Hutchinson 1994; Dudley 1995). For example, the meadow vole (*Microtus pennsylvanicus*) is known in Mexico from only one population in Chihuahua that persists in an area of less than 0.5 km² (S. Anderson 1972), but the species has an enormous distributional range north of Mexico. Several arguments can be put forward to justify conservation efforts for this species in Mexico. First, the Mexican voles constitute a population genetically isolated to such a degree that it is considered a separate subspecies (M. p. chihuahuensis). Also this population is a relict that has been geographically isolated for at least 12,000 years; the closest population of the same species occurs at least 500 km away in New Mexico. The habitat of the Chihuahuan meadow vole is special too: the humid bank of an arroyo that flows in an otherwise dry area in the middle of the Chihuahuan desert. Finally, if Mexicans are interested in the preservation of their own fauna and natural environments, a conservation policy should definitively include taxa such as the meadow vole, regardless of whether or not the same species is common in other countries.

Ecological Correlates of Distributional Range

We found no significant correlation between the area of the distributional range of bats in Mexico and the body mass of the species (Spearman rank correlation, r =0.06, p > 0.05). This result coincides with the pattern for Neotropical bats found by Arita (1993), who attributed this lack of correlation to the comparatively small range in body size that exists among bats.

Using the taxonomic categories proposed by Arita (1993), we tested for a possible relationship between taxonomic position and the size of the distributional range. The taxonomic categories we used were the Emballonuridae, the Phyllostomidae and associated families (Mormoopidae, Noctilionidae), the Vespertilionidae and associated taxa (Natalidae and Thyropteridae), and the Molossidae, for a contingency table analysis with two categories of range size; restricted and wide (Table 1). Thus, we had a 2×4 table. We found no significant association between taxonomic position and range size ($\chi^2 = 4.56$, df = 3, p > 0.05).

In contrast, we demonstrated a significant relationship between range size and feeding habits using four feeding categories: aerial insectivores, gleaners, frugivores, and nectarivores ($\chi^2 = 14.39$, df = 3, p < 0.01). The two distinct patterns of feeding habits are that gleaners including carnivores and insectivores, have restricted distributions in Mexico and that aerial insectivores tend to have wide distributional ranges (Table 1).

Among nonvolant mammals we found significant relationships between range size and body mass, taxonomic position, diet, and substrate use (Table 2). A weak but significant correlation between area of distribution and body mass exists for nonvolant Mexican mammals (Spearman rank correlation, r = 0.24, p < 0.05). In general, smaller species such as rodents have the most restricted distributions, whereas large species such as the mountain lion (*Puma concolor*) are widespread.

Table 1. Classification of restricted and widespread Mexican bats by taxonomic and dietary criteria.*

	Rare species	Widespread species
Family		
Emballonuridae	6	3
Molossidae	6	12
Mormoopidae	1	4
Natalidae	0	1
Noctilionidae	1	1
Phyllostomidae	33	22
Vespertilionidae	20	25
Thyropteridae	1	0
Diet		-
Aerial insectivores	33	43
Animalivorous gleaners	15	6
Piscivores	1	1
Frugivores	12	10
Nectarivores	6	6
Vampires	1	2

*Some of the groups were combined or excluded for analytical purposes.

There was a clear relationship between taxonomic category and area of distributional range. We performed a contingency-table analysis using the orders for which expected values in the cells were greater than five (Artiodactyla, Carnivora, Insectivora, Lagomorpha, and Rodentia), thereby excluding orders with insufficient sample size (Didelphimorphia, Primates, and Xenarthra). The analysis showed a highly significant association ($\chi^2 = 40.22$, df = 4, p < 0.001), due to the fact that most rodents have restricted distribution, whereas artio-dactyls and carnivores tend to be widespread (Table 2).

A similar analysis using the major feeding categories (carnivore, frugivore, granivore, herbivore, and insectivore) showed a highly significant relationship between diet and area of distributional range ($\chi^2 = 77.9$, df = 4, p < 0.001). Piscivore and myrmecophage species were excluded from this analysis. In general, species that feed on plant material (herbivores and granivores) tend to have restricted ranges, whereas animalivorous mammals (insectivores and particularly carnivores) tend to be widespread (Table 2).

We also found a significant relationship between substrate use and area of distribution ($\chi^2 = 18.42$, df = 5, p < 0.01; Table 2). The most conspicuous pattern is that of fossorial and semifossorial species that tend to have restricted ranges, whereas terrestrial and scansorial mammals tend to be widespread.

In summary, a typical nonvolant mammal with restricted distribution in Mexico is small to medium sized, feeds mainly on plant material, and spends part or most of the time underground. Most species fitting this description are rodents such as spiny mice (*Perognathus* spp. and *Chaetodipus* spp.), kangaroo rats (*Dipodomys* spp.), and pocket gophers (*Geomyidae*).

Table 2. Classification of restricted and widespread Mexican nonvolant mammals by taxonomic, dietary, and ecological criteria.*

	Rare species	Widespread specie.
Order		
Artiodactyla	1	8
Carnivora	2	20
Didelphimorphia	3	5
Insectivora	15	7
Lagomorpha	3	8
Perissodactyla	0	1
Primates	1	2
Rodentia	118	80
Xenarthra	1	3
Diet		
Carnivore	1	15
Frugivores	32	40
Granivore	51	36
Herbivore	31	19
Insectivore	25	29
Myrmecophage	1	2
Piscivore	3	1
Substrate use		
Arboreal	10	9
Fossorial	18	4
Scansorial	16	26
Semifossorial	44	30
Semiaquatic	5	5
Terrestrial	51	68

*Some of the groups were combined for analytical purposes.

Distributional Range and Conservation Status

Bat species that we considered restricted are well represented in the official list of species of concern in Mexico. Twenty-nine of the bat species with geographical ranges smaller than the median are considered rare, threatened, or endangered by Mexican legislation (Secrertaría de Desarrollo Social [SEDESOL] 1994). Bats included in the official list that we did not consider restricted are species such as the long-nosed bats (Leptonycteris nivalis and L. curasoae) and the hog-nosed bat (Choeronycteris mexicana) that have comparatively large distributional ranges but that are locally rare or have shown population declines in recent years. Species not on the official list but that should probably be considered for incorporation based on the size of their distributional ranges include six bats endemic to Mexico (Glossophaga morenoi, Artibeus hirsutus, Rhogeessa aeneus, R. alleni, R. gracilis, and Myotis peninsularis) or Central America (Balantiopteryx io, Tonatia evotis, Bauerus dubiaquercus, and Myotis elegans).

Nonvolant mammals included in the official list are represented equally among restricted and widespread species. Seventy-four of the restricted species are on the official list, representing 46.8% of the total, whereas 84 widespread species constitute the remaining 53.2%. Some species with a very restricted distribution in Mex ico that are not included in the official list include the pocket gopher (*Cratogeomys zinseri*), the wood rat



Figure 3. Quadrats with the top 10% values of the index of restrictedness for bats (A) and nonvolant mammals (B). General priority areas for the conservation of nonvolant mammals are circled and marked with numbers that correspond to those in Table 3.

(*Neotoma nelsoni*), the small-cared shrew (*Cryptotis goodwini*), and several species of deer mice (*Peromyscus* spp. and *Habromys* spp.). Some widespread species are included on the official list because of their low local density or declining populations (e.g., the tropical felids, and the tapir [*Tapirus bairdii*], whereas other species are listed officially but are not included in the present study because they are insular species (e.g., the raccoons [*Procyon insularis* and *P. pygmaeus*] and several species of mice and rats of the genera *Neotoma*, *Peromyscus*, and *Dipodomys*).

Areas for Conservation

Regions with high values of the restricted-range index for bats coincide with the areas of high species richness.



Figure 4. Relationship between the number of species with restricted distribution and the total number of species in 0.5×0.5 degree quadrats for Mexican bats (A) and nonvolant mammals (B). The continuous line shows the number of restricted species that would be expected from a random draw of restricted and wide-spread species. The broken line shows the upper 95% confidence limit for the expected values.

Quadrats ranking within the top 10% in terms of range restriction are located in the states of Chiapas, Oaxaca, Veracruz, Tabasco, and southern Campeche and Quintana Roo, areas that have been identified as particularly rich in mammal species (Fig. 3; Simpson 1964; Ceballos & Navarro 1991; Fa & Morales 1993). This pattern is clear when the relationship between the number of restricted bats and the total number of species in the quadrats is analyzed (Fig. 4). Areas that harbor significantly more restricted bat species than expected by chance (points above the dashed line in Fig. 4) are those that support higher total species richness. In fact, all such quadrats contain 37 or more bat species.

Both the tally of restricted species and the index of restrictedness indicate that southestern Mexico is the key area for the conservation of chiropteran species. This is a direct consequence of the fact that most bats with restricted distribution in Mexico are species with large dis-

Table 3. Critical areas for the conservation of Mexican mammals with restricted distribution, with some examples of species found there.

Regions	a	Representative species
Bats		
	Southeastern Mexico	False vampire bat (Vampyrum spectrum)
		Round-eared bat (Tonatia bidens)
Nonvola	ant mammals	
1	Northern Baja California	Tule shrew (Sorex juncensis) ^b
	<i>,</i>	Broad-footed mole (Scapanus latimanus)
		California ground squirrel (Spermophilus beecheyi)
		San Quintin kangaroo rat (Dipodomys gravipes) ^b
2, 3, 4	Baja California Sur	White-tailed antelope squirrel (Ammospermophilus leucurus)
		Dalquest's pocket mouse (Chaetodipus dalquesti) ^b
5	Chihuahua	Chihuahuan mouse (Peromyscus polius) ^b
		Meadow vole (Microtus pennsylvanicus)
6	Tamaulipas Gulf versant	Tropical pocket gopher (Geomys tropicalis) ^b
		Texas pocket gopher (Geomys personatus)
		Marsh rice rat (Oryzomys palustris)
		Eastern hog-nosed skunk (Conepatus leuconotus)
7	Nayarit and Jalisco Pacific versant	Mexican giant shrew (Megasorex gigas) ^c
		Banderas bay mouse (Osgoodomys banderanus) ^c
		Magdalena rat (Xenomys nelsoni) ^c
8, 9	Trans-Mexican Volcanic Belt	Michoacán pocket gopher (Zygogeomys trichopus) ^c
		Woodrat (<i>Nelsonia</i> spp.) ^c
		Volcano mouse (Neotomodon alstoni) ^c
		Volcano rabbit (<i>Romerolagus diazi</i>) ^c
10	Omiltemi, Guerrero	Brown deer mouse (Peromyscus megalops) ^b
		Omiltemi rabbit (<i>Sylvilagus insonus</i>) ^b
11	Sierra Madre de Oaxaca	Oaxacan vole (<i>Microtus oaxacensis</i>) ^b
		Oaxacan mouse (Habromys chinanteco)
12	Isthmus of Tehuantepec	Oaxacan pocket gopher (Orthogeomys cuniculus) ^b
		Tehuantepec jack rabbit (<i>Lepus flavigularis</i>) ^b
13	Eastern Chiapas	Brown four-eyed opossum (Metachirus nudicaudatus)
		Naked-tailed armadillo (<i>Cabassous centralis</i>)

^aNumbers of regions correspond to those in Fig. 3.

^bSpecies endemic to Mexico.

^cGenera endemic to Mexico.

tributional ranges in the Neotropics and that occur in Mexico only in the tropical rain forests of the south. Because of the high species richness of this region, a relatively high percentage of the area lies within existing or proposed protected zones. In the state of Chiapas, for example, 19.2% of the territory is within protected areas (Flores-V. & Gerez 1994). Most bat species with restricted distribution benefit from the existence of these reserves.

Exceptions are some endemic species, such as the trumpet-nosed bat (*Musonycteris barrisoni*), the hairy fruit bat (*Artibeus birsutus*), and the little yellow bat (*Rbogeessa mira*), that occur only in the tropical dry forests of western Mexico, outside the priority areas marked in Fig. 3. Similarly, the range of the extremely rare flat-headed bat (*Myotis planiceps*), known from only three localities in the northern part of the Mexican plateau, lies far from the quadrats marked in Fig. 3. Species like these would require special conservation initiatives concentrated on the protection of particular taxa, rather than strategies based on rarity of all species. Bats of the tropical dry forest, however, could benefit from conservation actions based on the protection of restricted nonvolant mammals.

The case of the nonvolant species contrasts with that of bats. Although the same areas of high species richness in Chiapas emerge as important for restricted nonvolant species, other zones in the northern part of the country stand out as significant areas (Fig. 3; Table 3). For nonvolant mammals there is no clear relationship between the number of restricted species and the total number of species (Fig. 4). Quadrats with numbers of restricted species higher than expected by chance are almost evenly distributed along the axis of species richness in Fig. 4, although some quadrats that harbor between 45 and 52 species seem to have particularly high numbers of restricted species.

A national conservation strategy for restricted nonvolant mammals is much more complicated than in the case of bats because priority areas are scattered all around the country (Fig. 3). Some of these quadrats, such as those in Chiapas and in the Pacific lowlands of Jalisco, are comparatively well represented in the national system of protected areas. Studies are needed, however, to assess the real contribution of protected areas in the conservation of the several rare species found in these regions. In other cases the situation is more critical. The lowlands of the Gulf of Mexico of Tamaulipas, for example,

pipport several species with restricted distribution, but the state has only 1.84% of its territory in protected areas, and less than 0.02% correspond to the areas marked in Fig. 3 (Flores-V. & Gerez 1994). Similarly, the regions near Omiltemi, state of Guerrero, and in the vicinity of Vista Hermosa, state of Oaxaca, lack protected areas, although a state park in Omiltemi and a biosphere reserve in Oaxaca have been proposed.

A region that deserves special attention is the trans-Mexican volcanic belt, which has been identified as a site with a high degree of endemism (Fa & Morales 1991; Flores-V. & Navarro-S. 1993). Included in the fauna of this area are the endemic genera *Zygogeomys*, *Nelsonia*, *Neotomodon*, and *Romerolagus* (Table 3). Several protected areas exist along the volcanic belt (Fa & Morales 1991), but most of them are small and do not guarantee the maintenance of viable populations of the majority of species present in the area. In particular, the western section of the state of Michoacán (Fig. 3; area 8) is not protected at all, and no short-term plans exist for establishing natural areas in this sector.

Conclusions

Data presented here show that rarity, as measured by the size of the distributional range, provides an alternative criterion for preserving biodiversity that can be independent of species richness. In the particular case of Mexico, restrictedness is adequate for establishing conservation priorities for nonvolant mammals, but its use for bats is redundant with species richness. Some areas of Mexico with populations of restricted nonvolant mammals are not rich in species and therefore have not been considered in previous conservation analyses. Notable gaps in the Mexican system of protected areas include the vicinity of Buenaventura and Flores Magón in Chihuahua, Eastern Tamaulipas, the southern extreme of Nayarit, western and southern Michoacán, and central and southeastern Oaxaca.

The official list of species of concern (SEDESOL 1994) would require a revision to include rarity, measured by the area of distributional range, as a criterion. Although the list seems to be quite complete, especially in the case of bats, there remain several species with critically small distributional ranges that are not currently included on the list.

Acknowledgments

Junding for this project was provided by the Mexican Commission on Biodiversity through grant 075 and by a scholarship to A. Frisch by the National Autonomous University of Mexico. We are thankful the comments of L. Bojórquez, G. Ceballos, J. Ortega, J. Uribe, and especially of J. H. Brown.

Literature Cited

- Anderson, J. E. 1991. A conceptual framework for evaluating and quantifying naturalness. Conservation Biology 5:347-352.
- Anderson, S. 1972. Mammals of Chihuahua. Taxonomy and distribution. Bulletin of the American Museum of Natural History 148:149–410.
- Anderson, S. 1985. The theory of range-size (RS) distributions. American Museum Novitates 2833:1-20.
- Angermeier, P. L. and J. R. Karr. 1994. Biological integrity versus biological diversity as policy directives. Bioscience 44:690-697.
- Arita, H. T. 1993. Rarity in Neotropical bats: correlations with phylogeny, diet, and body mass. Ecological Applications 3:506–517.
- Arita, H. T., J. G. Robinson, and K. H. Redford. 1990. Rarity in Neotropical forest mammals and its ecological correlates. Conservation Biology 4:181-192.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255–279.
- Brown, J. H. 1995. Macroecology. University of Chicago Press, Chicago.
- Brown, J. H., and B. A. Maurer. 1987. Evolution of species assemblages: effects of energetic constraints and species dynamics on the diversification of the North American avifauna. American Naturalist 130:1-17.
- 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. Pages 167-198 in M. A. Mares and D. J. Schmidly, editors. Topics in Latin American mammalogy: history, biodiversity. and education. University of Oklahoma Press, Norman.
- Ceballos, G., and P. Rodríguez. 1993. Diversidad y conservación de los mamíferos de México. II. Patrones de endemicidad. Pages 87-108 in R. A. Medellín and G. Ceballos, editors. Avances en el estudio de los mamíferos de México. Asociación Mexicana de Mastozoología, México City.
- Cousins, S. H. 1991. Species diversity measurement: choosing the right index. Trends in Ecology and Evolution 6:190–192.
- Daniels, R. J. R., M. Hedge, N. V. Joshi, and M. Gadgil. 1991. Assigning conservation value: a case study from India. Conservation Biology 5:464-475.
- Dudley, J. P. 1995. Bioregional parochialism and global activism. Conservation Biology 9:1332–1334.
- Erwin, T. L. 1991. An evolutionary basis for conservation strategies. Science 253:750-752.
- Fa, J. E., and L. M. Morales. 1991. Mammals and protected areas in the Trans-Mexican Volcanic Belt. Pages 199–226 in M. A. Mares and D. J. Schmidly, editors. Topics in Latin American mammalogy: history, biodiversity and education. University of Oklahoma Press, Norman.
- Fa, J. E., and L. M. Morales. 1993. Patterns of mammalian diversity in Mexico. Pages 253–280 in T. P. Ramamoorthy, R. Bye, A. Lot, and J. E. Fa, editors. Biological diversity of Mexico: origins and distribution. Oxford University Press, New York.
- Fjeldså, J. 1994. Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. Biodiversity and Conservation **3**:207–226.
- Fleming, T. H. 1973. Number of mammal species in North and Central American forest communities. Ecology 54:555–563.
- Flores-V., O., and P. Gerez. 1994. Biodiversidad y conservación en México: vertebrados, vegetación y uso del suelo. 2nd edition. Universidad Nacional Autónoma de México, Mexico City.

- Flores-V., O., and A. G. Navarro-S. 1993. Un análisis de los vertebrados terrestres endémicos de Mesoamérica en México. Pages 387-395 in R. Gío-A. and E. López-Ochoterena, editors. Diversidad biológica en México. Sociedad Mexicana de Historia Natural, México City.
- Gaston, K. J. 1994. Rarity. Chapman and Hall, London.
- Hall, E. R. 1981. The mammals of North America. 2nd edition. Wiley, New York.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. Oikos 38:210–221.
- Hanski, I., J. Kouiki, and A. Halkka. 1993. Three explanations of the positive relationship between distribution and abundance of species. Pages 108–116 in R. E. Ricklefs and D. Schluter, editors. Species diversity in ecological communities. University of Chicago Press, Chicago.
- Hunter, M. L., Jr., and A. Hutchinson. 1994. The virtues and shortcomings of parochialism: conserving species that are locally rare, but globally common. Conservation Biology 8:1163–1165.
- Kattan, G. H. 1992. Rarity and vulnerability: the birds of the Cordillera Central of Colombia. Conservation Biology 6:64-70.
- 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.
- Lawton, J. H., S. Nee, and A. J. Lechter. 1994. Animal distributions: patterns and processes. Pages 41–58 in P. J. Edwards, R. M. May, and N. R. Webb, editors. Large scale ecology and conservation biology. Blackwell Scientific Publications, London.
- Lechter, A., and P. H. Harvey. 1994. Variation in geographical range size among mammals of the Palearctic. American Naturalist 144:30-42.
- McCoy, E. D., and E. F. Connor. 1980. Latitudinal gradients in the species diversity of North American mammals. Evolution 34:193– 203.
- Pagel, M. D., R. M. May, and A. R. Collie. 1991. Ecological aspects of the geographical distribution and diversity of mammalian species. American Naturalist 137:791–815.
- Pressey, R., C. Humphries, C. Margules, R. Vane-Wright, and P. Will-

- Rabinowitz, D., S. Cairns, and T. Dillon. 1986. Seven forms of rarif and their frequency in the flora of the British Isles. Pages 182-20. in M. E. Soulé, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, Massachusetts.
- Ramírez-P., J., and A. A. Castro-C. 1993. Diversidad mastozoológica en México. Revista de la Sociedad Mexicana de Historia Natural 44: 413-427.
- Rapoport, E. H. 1975. Areografía, estategias geográficas de las especies. Fondo de Cultura Económica, Mexico City.
- Rapoport, E. H. 1982. Areography. Pergamon Press, Oxford, England.
- Secretaría de Desarrollo Social (SEDESOL). 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.
- Simpson, G. G. 1964. Species density of North American Recent mammals. Systematic Zoology 13:57–73.
- Sisk, T. D., A. E. Launer, K. R. Swittky, and P. R. Ehrlich. 1994. Identifying extinction threats. Bioscience 44:592-604.
- Smith, F. D. M., R. M. May, and P. H. Harvey. 1994. Geographical ranges of Australian mammals. Journal of Animal Ecology 63:441-450.
- Stevens, G. C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. American Naturalist 133:240-256.
- Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. BioScience 24:715-722.
- Thomas, C. D. 1991. Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. Biological Conservation **55:**269–281.
- 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.
- Wilson, J. W., III. 1974. Analytical zoogeography of North Americanmammals. Evolution 28:124-140.

