CONSERVATION BIOLOGY OF THE CAVE BATS OF MEXICO

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The available information on use of caves by Mexican bats was examined to determine the effectiveness of a conservation strategy based on diversity. Diversity was estimated by species richness, or the number of bat species present in a cave. Sixty of the 134 Mexican species of bats regularly roost in caves. Seventeen of these species tend to roost in caves with low species richness (segregationists), 14 tend to roost in caves with high species richness (integrationists), and 29 show no tendency in terms of the species richness of the caves (indifferent). Of the 215 caves included in this study, 80% support few (three or less) species, whereas only 10% harbor six or more species. In general, species that share caves with many species form small or medium-sized colonies, and there is no positive correlation between species richness and total number of individuals in the caves. Few of the fragile and vulnerable species of Mexican bats roost in caves with high species richness or with large populations. A conservation plan based solely on diversity is not adequate for the protection of cave bats in Mexico.

Key words: conservation biology, cave bats, Mexico

Caves are essential roosting sites for many species of bats (Dalquest and Walton, 1970; Kunz, 1982*a*; Tuttle, 1976). Of the 39 chiropteran species that occur in the United States, at least 18 depend heavily on caves for roosting sites, and many others use caverns as occasional refugia (Culver, 1986; Humphrey, 1975; McCracken, 1989). Information is less precise for other parts of the world, but several species are known to rely completely on caves for roosting sites. An extreme case is Kitti's hog-nosed bat (*Craseonycteris thonglongyai*), which is known from only six caves in Thailand (Humphrey and Bain, 1990). For such species, destruction of caves would mean inevitable extinction.

Mexico has a rich bat fauna of 134 species (Jones et al., 1988; Ramírez-P. et al., 1986), many of which are known to use caves as roosts (Tuttle, 1976; Villa-R., 1967). Here, I review the available literature on use of caves by Mexican bats, provide a list of species that require caves as roosting sites, and a catalogue of caves that would be important in a conservation plan for these bats.

A central objective of this review is to analyze the concept that the protection of sites with high diversity or high population levels assures the preservation of endangered and threatened species. I test such an idea for Mexican cave bats by evaluating the distribution of species of particular concern among caves with different diversity and abundance. If bats of special concern frequently occur in caves with rich and abundant communities, then the preservation of these sites also would protect the fragile species. Conversely, if few or none of the species of particular concern roost in rich caves, separate strategies would be necessary to protect the caves and the bats.

METHODS

From a survey of the literature on distribution, natural history, and taxonomy of Mexican bats

(Appendix I), I constructed a list of caves harboring populations of bats. For each cave, I compiled a list of bat species, including in some cases information on population size.

I identified the most important caves for the conservation of Mexican cave bats based on their diversity and abundance. Diversity was estimated by species richness, or the number of species reported from the cave. Abundance was quantified by the number of individuals of all species present at a given time in a cave. Caves of low abundance were defined as sites sheltering multispecies populations of <1,000 individuals. Caves with high and very high abundance were defined as supporting multispecies populations of >1,000 and >10,000 individuals, respectively. Important sites were defined as caves with a high species richness and high or very high abundance.

Mexican bats were classified in four categories of cave use. The first category included species for which caves are the main roost, whereas the second contained bats that regularly use caverns as refugia, but frequently rely on alternative roosts. The third category included species that use caves occasionally, but usually roost in other sites, and the last group comprised species not known to use caves as roosts. Species in the first two groups (caves as main or alternative roosts) are treated here as cave bats, whereas those in the last two categories are considered non-cave bats. I assigned species to these categories based on information from sources in Appendix I and from personal experience. For consistency in classifying species, I followed special criteria. For a few poorly known species, single or few reports of use of caves in Mexico were sufficient to consider them cave forms. For example, the trumpet-nosed bat (*Musonycteris harrisoni*) has been reported from a cave only once (Winkelmann, 1962), but so little is known about its roosting habits that it was grouped with species that use caves as alternative refugia. Similar cases are those of Allen's big-eared bat (*Idionycteris phyllotis*—Czaplewski, 1983) and free-tailed bats of the genus *Nyctinomops* (Carter and Davis, 1961; Jones et al., 1972). Conversely, species of the United States that use caves as hibernacula, but that use other sites for summer refugia, generally were not considered cave species in Mexico. For most of these species there are no reports of hibernacula in Mexico. Examples include several species of mouse-eared bats (*Myotis*—Humphrey, 1982; Schowalter, 1980).

I developed a list of cave species of special concern for conservation based on the list of fragile and vulnerable species of Mexican bats presented by Medellín and Arita (in press). Additionally, I included species that are endemic to Middle America (Mexico and Central America) and those that virtually are endemic to this area, barely entering the United States (California leaf-nosed bat, *Macrotus californicus*; Mexican long-nosed bat, *Leptonycteris nivalis*; Mexican long-tongued bat, *Choeronycteris mexicana*). I included endemics in the analysis because the Mexican government treats them as species of special concern, along with rare and endangered forms, in its ecological regulations.

The distribution of species among caves was analyzed using "incidence functions." These are graphs of the proportion of caves occupied by a given species among categories based on species richness of the sites. These graphs are analogous to the incidence functions first used by Diamond (1974, 1975) to study distribution of birds on archipelagoes in relation to their colonization ability. In caves, incidence functions can be used to analyze patterns of use by bats at different levels of species richness.

I classified Mexican species of cave bats in three categories of incidence (Fig. 1). Species such as *P. davyi,* which tend to occupy caves with high species richness, are "integrationists." Species that tend to be found in caves with few species, such as the Mexican big-eared bat (*Plecotus mexicanus*) are "segregationists." Finally, species with no apparent preference for rich or poor caves, such as the common vampire bat (*Desmodus rotundus*) are "indifferent." I assigned species to these categories based on the shape of their incidence curves.

RESULTS

The literature survey yielded a total of 215 Mexican caves with information on bats. In these caves, species richness ranges from one to 13 species. The frequency distribution shows a negative exponential curve, with several caves supporting few species and few caves harboring many species. Only 10% of the caves contain six or more species, whereas 80% shelter three or fewer species (Fig. 2).

Most caves have low abundance; caves with high and great abundance are com-

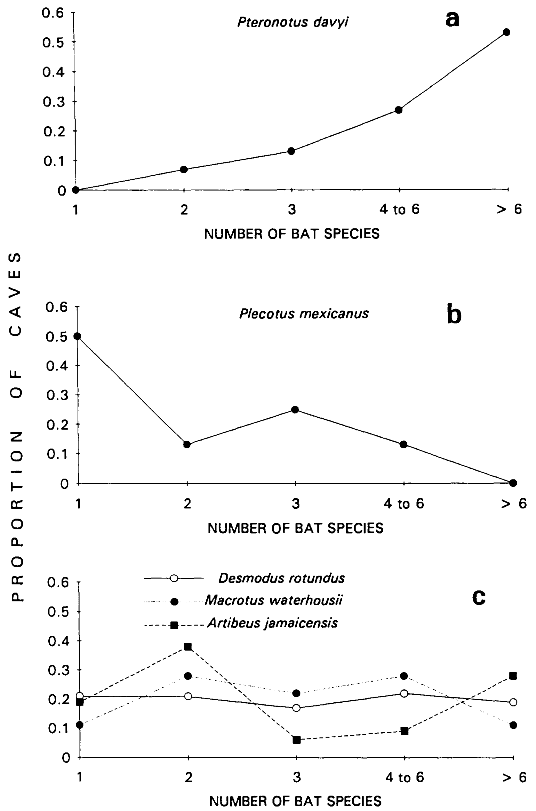

FIG. 1.—Incidence functions of cave bats in Mexico: a, *Pteronotus davyi* ($n = 15$), an integrationist species; b, *Plecotus mexicanus* ($n = 8$), a segregationist species; c, three indifferent species, *Desmodus rotundus* ($n = 63$), *Macrotus waterhousii* ($n = 18$), and *Artibeus jamaicensis* ($n = 32$).

paratively rare. Sites with the largest populations are refugia for the Mexican free-tailed bat (*Tadarida brasiliensis*), which in Mexico forms colonies ranging from a few thousand to $>1 \times 10^6$ individuals (Cockrum, 1969). Other species that frequently form large colonies (>1,000 individuals) in Mexican caves include some mormoopids (mustached bat, *Pteronotus parnellii*; naked-backed bat, *Pteronotus davyi*; the ghost-faced bat, *Mormoops megalophylla*—Bateman and Vaughan, 1974), some phyllostomids (Palla's long-tongued bat, *Glossophaga soricina*; little long-nosed bat, *Leptonycteris curasoae*—Villa-R., 1967; Wilson et al., 1985), the funnel-eared bat (*Natalus*

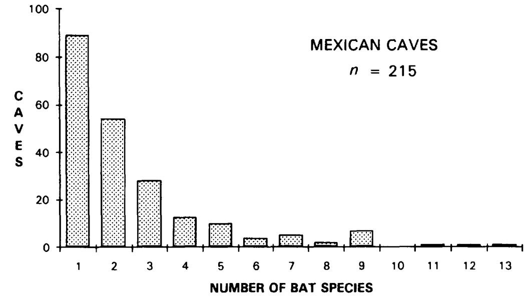

FIG. 2.—Species richness of cave bats in Mexico.

stramineus), and the cave myotis (*Myotis velifer* and *Myotis peninsularis*—Villa-R., 1967; Woloszin and Woloszin, 1982).

The list of important sites for the conservation of Mexican cave bats includes 12 caves (Table 1). All these sites shelter more than seven species of bats and support large multispecies populations.

Sixty (45%) of the 134 species of Mexican bats can be considered cave species. Of these, 27 primarily roost in caves, whereas 33 use caves as alternative refugia (Table 2). Of the remaining species, 18 use caves occasionally or rarely, and 56 do not use caves at all.

The distribution of cave and non-cave bats among taxa is not random. All mormoopids, desmodontines, and natalids are classified as cave species, as are the majority of glossophagines (10 of 12 species, binomial test with expected $P = 0.45$; $P < 0.01$). Conversely, fewer vespertilionids and molossids than expected by chance are considered cave dwellers (14 of 43 vespertilionids, four of 18 molossids; binomial test, $P < 0.05$ in both cases).

Fifteen fragile and four vulnerable species regularly use caves. There is no demonstrable association between use of caves and fragility or vulnerability; the distribution of species of concern among cave and non-cave categories does not deviate from expected by chance (contingency-table analysis, $\chi^2 = 0.36$, $P > 0.05$, $d.f. = 1$). Eleven of the Mexican cave bats are endemic to Middle America, and three others barely penetrate into the United States. There is

TABLE 1.—*Mexican caves with high species richness (more than seven bat species) and with high abundance (>1,000 individuals).*

Cave	Richness[a]	Abundance[b]	Fragile species[c]
Chiapas			
Cueva de la Trinitaria	8	very high	2
Guerrero			
Gruta de Juxtlahuaca	9	very high	1
Morelos			
Cueva del Cerro, Tequesquitengo	9	high	2
Cueva del Salitre, Tetecalita	12	high	0
Puebla			
Cueva de las Vegas	13	high	0
Sonora			
Mina del Tigre	9	very high	1
Tabasco			
La Murcielaguera	8	high	2
Cueva de Don Luis	9	high	1
Tamaulipas			
Cueva de Quintero	9	very high	1
Veracruz			
Cueva de la Laguna Encantada	9	high	1
Yucatan			
Gruta de Lol-Tún	11	high	2
Gruta Spukil	9	high	1

[a] Number of species of bats in the cave.
[b] Number of individuals of all species of bats in the cave: high (>1,000 individuals); very high (>10,000 individuals).
[c] Number of fragile, vulnerable, or endemic species of bats in the cave.

no association between cave dwelling and endemism among Mexican bats (contingency-table analysis, $\chi^2 = 0.06$, $P > 0.05$, $d.f. = 1$).

No definitive association exists between incidence and endangerment among Mexican cave bats. Five of the 17 integrationist species are fragile, vulnerable or endemic. The figures for segregationist and indifferent species are eight of 14 and 14 of 29, respectively. A contingency-table analysis shows no significant deviation from a random distribution of species among incidence types ($\chi^2 = 2.63$, $P > 0.05$, $d.f. = 2$).

Most species occur in caves in small colonies. Of the 60 cave species, 35 never form colonies of >100 individuals. Typical species of this class include the spear-nosed bat (*Mimon bennetti*), the wooly false vampire (*Chrotopterus auritus*), and *M. harrisoni*. Of the remaining 25 species, only seven form large populations of >10,000 individuals. Among these are *T. brasiliensis, P. parnellii, P. davyi, M. megalophylla,* and *N. stramineus.* There is no clear association between incidence and size of multispecies populations (contingency-table analysis, $\chi^2 = 3.21$, $P > 0.05$, $d.f. = 2$).

DISCUSSION

Many current conservation efforts concentrate on the protection of areas with high diversity (Soulé and Kohm, 1989; Wilson, 1988). The premise behind this approach is that sites with unusually high richness not only harbor more species, but also are preferred habitats for several endangered or threatened species. In some cases, the assumption seems reasonable. Tropical rain forests, for example, are ecosystems of high diversity that also feature a host of rare and endangered species. In other instances, the relationship between diversity and the presence of threatened species is not well established. The data presented here show the diversity approach to the conservation of Mexican cave bats to be inadequate.

I have presented evidence for a lack of correlation among the three variables used here to assess the suitability of a cave as a protected area: diversity, size of multispecies populations, and the presence of fragile, vulnerable, and endemic species. For instance, some caves with high or very high abundance were excluded from the list of important sites because they have low diversity. Several large colonies of the Mexican free-tailed bat in the states of Durango, Nuevo León, and Querétaro were excluded from the list because *T. brasiliensis* is the only species occupying these caves. Similarly, the caves in the Sierra de la Laguna in Baja California Sur that shelter large populations of the endemic *Myotis peninsularis* (Woloszin and Woloszin, 1982) were excluded because of their low species richness.

Similarly, some of the caves that provide shelter for fragile or vulnerable species have low abundance. This happens because threatened species usually exist at low population levels, but it also is due to the fact that species of concern usually are not associated with other species with higher populations. Species such as *M. bennetti,* the long-legged bat (*Macrophyllum macrophyllum*), and *M. harrisoni* always occur in small groups, but they seldom or never are found in association with other, more abundant species. The protection of caves with unusually high abundance would add little to the conservation of these endangered species.

The majority of fragile species are segregationist or indifferent to other species. Typical examples of fragile segregationist bats are the endemic *P. mexicanus* and the carnivorous phyllostomids like *M. bennetti* and the fringe-lipped bat (*Trachops cirrhosus*). These species almost always occur in caves by themselves or share the roost with few other species. Other bats of special concern, such as *T. brasiliensis* and *M. peninsularis,* are less segregationist, but seldom occupy caves with more than five species. In Mexican cave bats, diversity is a poor criterion if the intention is to protect bats of special concern.

Few of the fragile species regularly roost in caves with high diversity and high abundance (Table 3). Entries in the lower right cell of the table (integrationist bats that form colonies of >100 individuals) are the species that would benefit the most from protection of critical caves. However, only three species in this cell (the sac-winged bat, *Balantiopteryx io,* and the two species of *Leptonycteris*) are fragile, vulnerable, or endemic. Conversely, one-half of the species in the upper left cell of the table (segregationists that never form colonies of >100 individuals) are fragile or vulnerable (*M. macrophyllum, M. bennetti, T. cirrhosus, I. phyllotis,* and the fish-eating bat, *Myotis vivesi*). These species would benefit little from the protection of critical caves.

An effective plan for the conservation of Mexican cave bats would require a double strategy: the protection of caves with unusually high diversity and multispecies populations and the management of cave bats of special concern (fragile, vulnerable, and endemic species). Data presented here demonstrate that the implementation of a conservation plan for caves in Table 1 would not necessarily provide protection for fragile or vulnerable species. Despite this, caves listed in Table 1 are important because the great concentration of many species and individuals constitutes an unusual natural phenomenon that deserves protection. Richness and abundance by themselves are a sufficient reason for the conservation of caves in Table 1, despite their comparatively low contribution to the protection of endangered species.

Special conservation plans need to be de-

TABLE 2.—*Cave bats that occur in Mexico.*

Species	Cave use[a]	Incidence[b]	Size of population[c]	Status[d]
Emballonuridae				
Balantiopteryx io	Main	I	L, M	F, E
B. plicata	Main	S	L, M	E
Peropteryx kappleri	Alt.	I	L	F
P. macrotis	Main	I	L, M	F
Noctilionidae				
Noctilio leporinus	Alt.	S	L	
Mormoopidae				
Mormoops megalophylla	Main	I	M, H	
Pteronotus davyi	Main	I	M, H	
P. gymnonotus	Main	I	L	F
P. parnellii	Main	I	M, H	
P. personatus	Main	I	M	
Phyllostomidae				
Phyllostominae				
Macrotus californicus	Main	Ind.	M	E*
M. waterhousii	Main	Ind.	M	E
Micronycteris brachyotis	Alt.	Ind.	L	F
M. megalotis	Alt.	Ind.	L	
M. sylvestris	Alt.	Ind.	L	
Lonchorhina aurita	Main	I	L	F
Macrophyllum macrophyllum	Main	S	L	F
Mimon bennetti	Alt.	S	L	F
Trachops cirrhosus	Alt.	S	L	F
Chrotopterus auritus	Alt.	Ind.	L	F
Glossophaginae				
Glossophaga commissarisi	Alt.	Ind.	L	
G. leachii	Alt.	Ind.	L	
G. morenoi	Alt.	Ind.	L	E
G. soricina	Alt.	I	L, M, H	E
Hylonycteris underwoodi	Alt.	Ind.	L	
Anoura geoffroyi	Main	S	L	F, E
Leptonycteris curasoae	Main	I	L, M	F
L. nivalis	Main	I	L, M	V, E*
Choeronycteris mexicana	Main	Ind.	L	E*
Musonycteris harrisoni	Alt.	Ind.	L	V
Carolliinae				
Carollia brevicauda	Alt.	Ind.	L, M	
C. perspicillata	Alt.	Ind.	L, M	
C. subrufa	Alt.	Ind.	L, M	
Stenodermatinae				
Dermanura azteca	Main	S	L	E
Artibeus hirsutus	Main	Ind.	L, M	E
A. intermedius	Alt.	I	L	
A. jamaicensis	Alt.	Ind.	L, M	
A. lituratus	Alt.	I	L	
Desmodontinae				
Desmodus rotundus	Main	Ind.	L, M	
D. youngii	Main	Ind.	L	F
Diphylla ecaudata	Main	I	L	

TABLE 2.—*Continued.*

Species	Cave use[a]	Incidence[b]	Size of population[c]	Status[d]
Natalidae				
Natalus stramineus	Main	I	M, H	
Vespertilionidae				
Myotis californicus	Alt.	Ind.	L	
M. keaysi	Main	I	L, M	
M. lucifugus	Alt.	Ind.	L	
M. nigricans	Alt.	I	L	
M. peninsularis	Main	Ind.	M, H	F, E
M. thysanodes	Alt.	S	L	
M. velifer	Main	Ind.	M, H	
M. vivesi	Alt.	S	L	V, E
Pipistrellus subflavus	Alt.	Ind.	L	
Eptesicus fuscus	Alt.	I	L	
Plecotus mexicanus	Main	S	L, M	E
Plecotus townsendii	Main	S	L, M	
Idionycteris phyllotis	Main	S	L	
Antrozous pallidus	Alt.	S	L, M	
Molossidae				
Tadarida brasiliensis	Main	S	M, H	V
Nyctinomops aurispinosus	Alt.	Ind.	L	
Nyctinomops femorosaccus	Alt.	Ind.	L	
Nyctinomops laticaudatus	Alt.	Ind.	L	

[a] Cave use: Main, caves are the main roost for the species; Alt. (alternative), other types of roosts regularly are used.
[b] Incidence: I, integrationist; S, segregationist; Ind., indifferent.
[c] Size of population: L, low (usually <100 individuals); M, moderate (100–10,000 individuals); H, high (>10,000 individuals).
[d] Status: F, fragile; V, vulnerable; E, endemic to Middle America; E*, restricted to Middle America and a small portion of the southwestern United States.

veloped for fragile, vulnerable, and endemic species of cave bats. On-site research is required to verify that these species still occur in the caves where they have been recorded. More detailed studies, focused on the demography and ecology of some of the most vulnerable bats, would identify the key caves for each species. A complete conservation plan for Mexican cave bats should integrate the protection of caves in Table 1 with the preservation of caves that are needed by the species of special concern.

RESUMEN

Conservación de los murciélagos cavernícolas de México. En este trabajo se revisa la información que existe sobre los murciélagos cavernícolas de México. Se analiza la eficacia de una estrategia de conservación basada en la diversidad, que fue estimada usando la riqueza de especies, es decir el número de especies de murciélagos presentes en una cueva. Sesenta de las 134 especies de murciélagos mexicanos utilizan las cuevas regularmente. Diecisiete de estas especies son "segregacionistas" y comparten el refugio con pocas especies; 14 son "integracionistas" que están presentes en cuevas con varias otras especies y 29 son "indiferentes"

TABLE 3.—*Relationship between incidence and size of populations among cave bats of Mexico. Values in cells are the number of species in each category.*

Size	Incidence: Segregationist	Indifferent	Integrationist	Total
Low[a]	10	18	7	35
High[b]	4	11	10	25
Total	14	29	17	60

[a] Populations always are <100 individuals.
[b] Populations usually are >100 individuals.

que se encuentran tanto en cuevas con baja como con alta riqueza de especies. El 80% de las 215 cuevas incluidas en este trabajo tiene poblaciones de ≤3 especies, mientras que solamente el 10% sirve de refugio para ≥6 especies. En general, las especies integracionistas forman colonias pequeñas o medianas, de manera que hay poca correlación entre la riqueza de especies y el número total de individuos en las cuevas. De las especies frágiles y vulnerables, pocas se refugian en cuevas con alta riqueza de especies o alta abundancia. Los planes de conservación basados solamente en la diversidad resultan inadecuados para la protección de los murciélagos cavernícolas de México.

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APPENDIX I

Sources of information for the database on Mexican caves and for the classification of Mexican cave bats.—Alvarez, 1963; Alvarez and

González-Q., 1970; Alvarez and Ramírez-P., 1972; Anderson, 1972; Baker, 1956; Barbour and Davis, 1969; Birney et al., 1974; Carter and Davis, 1961; Cockrum, 1969; Cockrum and Bradshaw, 1963; Dalquest, 1953; Fenton and Barclay, 1980; Hall and Dalquest, 1963; Harrison, 1975; Hermanson and O'Shea, 1983; Jones and Arroyo-Cabrales, 1990; Jones et al., 1972, 1973; Kumirai and Jones, 1990; Kunz, 1982*b*; Lay, 1962; Manning and Jones, 1989; Medellín and López-Forment C., 1986; Medellín et al., 1983, 1985; O'Farrell and Studier, 1980; Pearse and Kellogg, 1938; Ramírez-P. and Alvarez, 1972; Ramírez-P. et al., 1977; Schaldach, 1965; Silva Taboada, 1979; Villa-R., 1967; Watkins, 1972, 1977; Watkins et al., 1972; Webster and Jones, 1984, 1985; Wilson et al., 1985; Winkelmann, 1962; Woloszin and Woloszin, 1982.