

ECOLOGY AND CONSERVATION OF CAVE BAT COMMUNITIES IN YUCATAN,  
MEXICO

By

HÉCTOR T. ARITA-WATANABE

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IN MEMORIAM  
LUIS K. ARITA (1919-1990)

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By

Héctor T. Arita-Watanabe

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Chairman: Stephen R. Humphrey

Major Department: Wildlife and Range Sciences, School of  
Forest Resources and Conservation

Caves are among the most endangered ecosystems but have  
received little attention from conservation biologists.

This dissertation presents new information on the ecology of  
the cave bats of Yucatán, México, and provides the basis for  
a management plan for the caves. Although the emphasis is  
on the conservation of bats, this project is based on the  
concept that caves need to be protected as whole systems,  
not as collections of separate parts.

I studied 36 Yucatán caves during 1989 and 1990. These  
caves ranged from a simple tunnel <10 m long to a large and  
complex cavern system of >1,500 m of tunnels. Most caves  
had simple horizontal and vertical development and had very  
hot and humid environments.

A review of the literature on cave bats of México showed that 60 (45%) of the 134 Mexican bat species are cave forms. Most these species occupy caves with low species richness and form small colonies. Nineteen of the species are fragile or vulnerable and require some protection. Most caves harbor few species and small colonies of bats.

The bat fauna of Yucatán is a subsample of the pool of species of southeastern México. A series of comparisons using null models showed that the composition of the Yucatán bat fauna does not differ from the one expected by random sampling from the pool, except that species in Yucatán tend to have greater dispersal ability than expected by chance. Morphological comparisons showed little deviation from randomness and suggested that competition has, at most, a negligible effect on the composition of the Yucatán fauna.

Seventeen of the 31 bat species of Yucatán are cave forms. There is an overall positive association among the species, creating a pattern in which most species tend to use the same set of caves. Species richness and population abundance are positively correlated. A classification of caves based on the presence of bat species correlates well with other geological and ecological variables that seem to determine the distribution of bats among the caves. This classification identifies the caves that are important for the conservation of the cave bats of Yucatán.

## INTRODUCTION

Caves are natural laboratories for the study of ecology and evolution (Culver, 1982). The special physical conditions of caves, found in no other terrestrial habitat, determine the evolution of bizarre variations of those animal groups with representatives in the underground world. Because they harbor simple communities with few species and uncomplicated food webs, caves can serve as model ecosystems for the study of species interactions and other ecological phenomena. Because they occur in exceptionally low densities, have a very restricted distributional range, and show a high degree of habitat specificity, most cave animals are likely candidates for extinction. Caves are among the most delicate environments in the world (Culver, 1986).

This dissertation attempts to contribute to the conservation of caves in Yucatán, México. Its main objectives are to generate new information on the biology of the cave bats of Yucatán and to provide relevant conservation and management recommendations for local planners.

Caves are frequently neglected in conservation plans because they harbor only inconspicuous faunas that are generally poor in terms of both diversity and abundance.

Besides, caves lack the kind of charismatic species that capture the public's imagination and that have been used in many successful conservation campaigns. Chapter 1 is a literature review that intends to show why the conservation of caves is important, what are the major threats to these sites, and how a protection plan can be proposed to integrate caves to the mainstream of conservation biology.

The state of Yucatán is ideal for a study of cave conservation. As discussed in Chapter 2, the geological and climatic characteristics of the Yucatán Peninsula favor the development of numerous caves. Some of the caves of Yucatán, with their combination of geological, biological, and archeological attractions, are obvious choices in the new plans by the state government for the development of ecotourism sites. These caves will constitute a test for the idea that economic development and biological conservation are compatible.

Caves show a great deal of morphological and geological variation. Consequently, it is impossible for a conservation and development plan to provide simple strategies that are applicable in all cases. A solid plan must take into account this difficulty and must be based on field studies that include caves that are representative of the whole gamut of sites. Chapter 3 describes the 36 caves included in the present study and introduces the classification of the sites that is used in subsequent chapters.

Many local conservation programs suffer from lack of perspective because they focus too much on small-scale patterns and neglect phenomena that become evident only at larger scales. To provide a point of reference for the analysis of the fauna of cave bats of Yucatán, I review in Chapter 4 the available information on cave use by Mexican bats. This review provides lists of species and sites of special concern for the conservation of Mexican cave bats, and introduces new terminology that is used later in the dissertation.

Chapter 5 discusses the possible origin, the affinities, and the composition of the Yucatán bat fauna. The search for patterns in natural communities, like the one attempted in Chapter 5, is not only a purely scientific endeavor but an important way to obtain valuable data for conservation purposes. The comparison of the Yucatán fauna with its source pool intends to provide new data for the debate on whether or not natural communities are organized by particular forces. It also intends to identify the ways (if any) in which the assemblage of bats of Yucatán differs from the faunas of other areas. This information would allow the identification of species or patterns that would deserve special consideration in a conservation plan.

Many conservation plans in the Neotropics are hindered by a lack of knowledge of the basic natural history of most of the species involved. This is true in the case of cave bats. The notes on the natural history of cave bats of

Yucatán that are presented in the first of Chapter 6 are intended to fill this gap. The chapter also analyzes the patterns of use of Yucatán caves as bat roosts. Chapter 7 is a recapitulation and synthesis of the information presented in the previous chapters. It presents a series of recommendations for the protection of the cave bats of Yucatán.

A comprehensive plan for the conservation of caves in any site is a major endeavor, certainly far beyond the scope of a single dissertation project. Such a project would require the participation of experts on different areas of the natural and the social sciences. The following pages constitute the contribution of a single scientist, a bat biologist. I am confident, however, that the information presented here will be useful in the near future to protect the unique environment of the caves of Yucatán.

CHAPTER 1  
CAVES AND CAVE CONSERVATION

The Cave Environment

Caves are unique ecosystems. The absence of light precludes photosynthesis, so the only endogenous primary production is carried out by chemosynthetic bacteria (Barr, 1968; Caumartin, 1963; Cubbon, 1976). The contribution of these bacteria to the food webs inside the cave is negligible, and it is fair to say that cave communities depend totally on exogenous sources of nutrients for their maintenance (Culver, 1982). Nutrients can be taken into a cave in the form of detritus and plant material carried by streams, as dissolved organic matter percolating through minute cracks or exuding from tree roots (Howarth, 1972, 1983), or they can be deposited inside caves as feces of troglodytes, such as cave crickets (Raphidophoridae, Hubbell and Norton, 1978), birds, bats (Harris, 1970; Poulson, 1972), and other vertebrates including porcupines (Calder and Bleakney, 1965).

Food is very scarce in most cave ecosystems. Poulson and White (1969) estimated that biomass density in a typical North American cave can be as low as 1 g/ha in ponds or 20 to 30 g/ha in terrestrial passages. Biomass density increases in sites near entrances and can reach values of

$10^6$  g/ha at the entrance (Poulson and White, 1969). In contrast, passages covered with bat guano present an overabundance of nutrients and support very different communities (Barr, 1968; Harris, 1970; Poulson, 1972).

Constancy is the rule in the deep sections of caves. Temperature approximates the mean annual surface temperature (MAST) of the region, and its variance decreases as one moves deeper into the cave (Culver, 1982; Tuttle and Stevenson, 1978; Wigley and Brown, 1976). The annual and daily variation in temperature near entrances is appreciable but generally lower than the variation outside the cave (Culver, 1982; Wigley and Brown, 1976). Similarly, relative humidity in caves is rather constant and seldom falls below 80% (Culver 1982). Howarth (1980) advanced the idea that adaptation to a nearly water-saturated environment, in the form of an efficient water excretory system, is a requisite for terrestrial arthropods to be able to survive in the deep sections of caves.

#### Conservation Biology of Cave Animals

In response to extreme physical conditions, some cave animals have developed extreme adaptations (Barr, 1968; Culver, 1982; Vandel, 1964). The conspicuous external morphological adaptations of some troglobites to the absence of light, such as reduction of eyes and of pigmentation and the elongation or multiplicity of other sense organs, are classical examples of evolution (Eigenmann, 1909; Poulson,

1963; reviewed by Barr, 1968; Culver, 1982; Holsinger, 1988). Other less obvious adaptations to the cave environment are changes in internal organs (e.g., developed sensory lobes of the brain; Poulson, 1963), reduced metabolic rates (Burbanck et al., 1948; Dickson and Franz, 1980; but see counterexamples of Culver and Poulson, 1971; Schlagel and Breder, 1947), improved systems for water excretion (Howarth, 1980), and K-selection life history strategies (low population levels, increased life expectancy, delayed reproduction, larger and fewer eggs; Culver, 1982).

These extreme adaptations make cave animals very susceptible to changes in their environment. Juberthie (1969, in Culver, 1982) found that variations as low as a few tenths of a °C precluded the occurrence of the beetle *Aphaenops cerberus bruneti* from microsites in one cave in France. Similarly, Howarth (1980) and Ahearn and Howarth (1982) demonstrated that terrestrial troglobites are extremely sensitive to minute changes in relative humidity. The addition of organic matter to caves can produce dramatic changes in communities that occur in sites with very low levels of nutrients (Humphreys, 1991). In a world where constancy is the rule, even minute environmental changes can have pronounced ecological consequences.

Caves constitute real habitat islands for many terrestrial troglobites (Culver, 1970; Christiansen and Culver, 1987). The low levels of genetic similarity that

Laing et al. (1976) found among populations of the same invertebrate species in different caves and the high endemism of cave species (Barr and Holsinger, 1985; Culver, 1986) suggest that movement between caves is limited for most terrestrial troglobites (although there are exceptions; for example the collembolan *Pseudosinella hirsuta* is a widespread species [Christiansen and Culver, 1968]). Endemism seems to be higher for terrestrial species than for aquatic forms because many apparently isolated caves are in fact interconnected by subterranean water passages (Culver, 1986).

The combination of low population density, restricted distribution, and extreme habitat specialization makes cave animals rare in the three dimensions proposed by Rabinowitz (1981; Rabinowitz et al., 1986). Species with low population density are more prone to extinction because they are more susceptible to the effects of demographic and genetic stochasticity (Arita et al., 1990; Arita, M.S.b). Similarly, species with restricted distributional ranges or high habitat specificity are more vulnerable than widespread forms (Terborgh, 1974; Thomas, 1991) because a single or a few local extinction events can wipe out the whole species. Rarity is only one of many possible predictors of extinction proneness, but it is clear that cave organisms possess particular biological features that make them specially vulnerable.

### Conservation Biology of Cave Bats

Many bat species use caves as day roost or as a temporary refuge at night (Dalquest and Walton, 1976; Kunz, 1982; Tuttle, 1976). Several of these species are endangered. In the United States, all five officially endangered species of bats use caves as roost sites at least part of the year (McCracken, 1989). In Thailand, the endangered Kitti's hog-nosed bat (*Craseonycteris thonglongyai*) is known from only six caves (Humphrey and Bain, 1990). Because cave-roosting species spend at least half their lives inside caves (Kunz, 1982), the protection of cave environments is necessary to assure their conservation.

In common with non-cave species, cave bats face several threats that occur outside caverns. Deforestation and other types of habitat destruction, direct and indirect effects of pesticides on insectivorous species, and the impact of the loss of certain plants on nectar-feeding and frugivorous species are only some of the factors that can lower the population level of bats. Besides these factors, cave bats face other threats that occur inside caves. Many cave species are particularly vulnerable because they form huge concentrations in a few caves. If for some reason one of these caves is substantially perturbed, a significant fraction of the total population of bats can be extirpated.

This is particularly true for species that use caves to hibernate or to form maternity colonies (McCracken, 1989).

In the Neotropics, cave bats face a particularly serious threat. In areas infested with vampire bats (*Desmodus rotundus*) local ranchers regularly visit caves to exterminate the vampires but they are not able to differentiate them from other species of bats. In some cases, even government officials employed in vampire-control campaigns are inadequately trained to distinguish between vampires and other bats. Numerous cave colonies of insectivorous, frugivorous, and nectarivorous bats have been extirpated by actions aimed at vampire aggregations (Belwood and Morton, 1991).

### Threats to Caves

Because of the fragility of cave communities, human impact on caves is normally very severe. Threats to caves by humans can be classified in two categories: those with indirect and those with direct effects.

#### Indirect Human Impact

Indirect effects on caves occur when humans disturb any link between the cave and the external world. The most common case is the pollution of water that enters a cave by a stream or by percolating through karst terrain. In one of the few adequately documented examples, Holsinger (1966, in Culver, 1986) showed that when one cave in Virginia was polluted by the overflow of a septic tank the diversity of

the aquatic fauna declined. As Culver (1986) pointed out, the absence of surface streams in some karst terrains creates the illusion that pollutants disappear. These pollutants, however, simply percolate to underground water systems, in some cases affecting caves.

Another possible indirect effect of human activity on caves is the change in flow patterns in karst terrains as a result of deforestation (Culver, 1986). This kind of effect is very difficult to document, but it would be expected that the loss of the buffering effect of the vegetation cover would lead to overflow of the underground water systems, leading to flooding of caves.

Pesticide residues can accumulate in insectivorous bats and in the guano piles that these bats form inside caves (Clark, 1981; Geluso et al., 1981). McCracken (1989) contends that although the use of pesticides evidently has an impact on bat populations, the extent of this impact has been overemphasized without supporting evidence. It is clear that more research is needed to quantify the direct and indirect effects of pesticide poisoning on cave communities.

#### Direct Human Impact

Humans can produce a very dramatic and permanent effect on caves in those cases where land transformation is involved. When landowners decide to close the entrance to a cave or the land is developed for mining or quarrying

operations the effects are obvious and in most cases irreversible.

Less drastic but equally lamentable changes occur when caves are used as dumping sites for trash or garbage. The sudden increase in organic matter triggers an invasion of exogenous species that outcompete the cave species adapted to low levels of nutrients (Culver, 1986). Of course, a more notorious effect is the degradation of the scenic value of the area.

Vandalism and other forms of direct perturbation are disturbingly common in some areas. People that leave graffiti or that take "souvenirs" (pieces of speleothems) not only deprive others of the pleasure of enjoying the unique sight of a pristine cave, but they also may recklessly modify the environment for sensitive troglobites. Fire from torches, campfires, or even from carbide lamps can produce changes in the ambient temperature and humidity that might be imperceptible for humans but that can be lethal for some troglobites. Similarly, burning of caves in misdirected vampire control campaigns is a major problem in Latin America.

Any human visitation can have a profound and negative effect on cave communities. From occasional spelunkers to dedicated speleologists to one-time tourists, all humans entering a cave modify in some way or another the environment of these sites. Of course, a total ban on cave visitation would be ridiculous and impossible to enforce.

The ideal situation would be to find a compromise to reconcile cave use with cave conservation.

### Cave Conservation

McCracken (1989) proposed the creation of lists of "green" and "red" caves. Based on the idea of other conservationists (Diamond, 1988), McCracken suggested that those caves that should not be visited by humans at any time could be called "red" caves, whereas "green" caves would be those that are safe to visit. Of course the only way to determine the "color" of the cave would be to carry out biological surveys that are likely to disturb the fragile communities that we are supposed to protect. As in other conservation dilemmas, only a high dose of common sense and compromising can provide the right answer to the problem of assigning conservation value to caves.

I suggest a third category to be added to McCracken's (1989) dichotomy. "Yellow" caves would constitute the intermediate category between red and green, that is those sites that can be visited only on a limited basis or only during certain seasons. Additionally, I suggest that the categories should be assigned to "sites" (which could be entire caves or parts of caves) rather than to caves. For example, a large cavern system could be constituted by green passages (with no restriction), yellow sections (with restricted access), and red sites (with no access to the

public). This approach would allow a multipurpose use for complex cave systems and would alleviate possible conflicts of interest between conservationists and developers.

Smaller caves could still be considered as a single unit and be assigned a color according to their conservation value.

For the benefit of planners, the color of caves should be assigned with a possible use in mind. The category of red should be used only for those sites that are indispensable for the preservation of a particular geological or biological phenomenon. These include passages with unique speleothems that are too fragile to support frequent visitation, chambers with huge colonies of bats, or sections that harbor populations of endemic or rare species. Yellow caves could be assigned two possible functions: tourist sites or caves for visitation by sport speleologists. In both cases the access should be partially controlled to avoid unnecessary negative impacts on the caves. Green caves, those not requiring any protection, could be open for visitation at any time. These sites would contain no important geological or biological feature and, in general, would be small and inconspicuous caves. Because of this, the sites would have a low rate of visitation even if no restriction is applied. Finally, multipurpose systems would accommodate sections with different colors designed for different uses. A typical example would be a large system consisting of a restricted red area for the conservation of animal species of special concern, yellow

passages for tourists, a yellow section open only to experienced speleologists, and a series of green tunnels with no special status.

As in other conservation cases, the classification should be used with caution. Lists of red and yellow caves could be misinterpreted by the layman as an indication that all the other caves are green. To avoid these unfortunate situations, planners should elaborate lists as completely as possible before attempting to assign colors to the caves.

Planners should also realize that caves are not closed systems. Although most people perceive caves as strange sites totally separated from the outside world, the reality is that caves are intrinsically interdependent with the external ecosystems. Energy and matter interchange occurs by means of physical forces (water currents and percolation, air movement, sedimentation) or by biological phenomena (movements of troglodites, nutrient exchange through trees that develop roots inside caves). An efficient conservation strategy for a cave should involve the protection of the habitat surrounding the area above the cavern.

### Recapitulation

Caves are unique ecosystems with particular conservation requirements. A compromise between cave conservation and cave use has to be reached as it is unlikely that humans will quit cave visitation. Cave surveys and biological studies have to be done in as many

caves as possible to create lists of caves that can be used for different purposes: conservation, informal visitation, sport and scientific exploration, and tourism. A complete conservation strategy should include both the underground and the exterior habitats associated with the caves.

## CHAPTER 2 THE STUDY SITE

### Physiography

The Yucatán Peninsula is a flat, low-lying limestone shelf that projects from southern México and Central America into the Caribbean Sea (Figure 2.1). The state of Yucatán occupies the northwestern third of the Mexican portion of the peninsula, extending over an area of 38,402 km<sup>2</sup> (García and Falcón, 1986). (In this dissertation I will refer to the state of Yucatán simply as "Yucatán", and to the physiographic region as "the Yucatán Peninsula" or just "the peninsula.")

The Yucatán Peninsula lacks any major topographic feature except for the mountain ranges of Guatemala and Belize. In the northern extreme, the terrain rises gradually from the northern coast to the south of Yucatán, from 0 to about 20 m. This pattern is broken by the Sierrita de Ticul or Cordón Puuc, a lesser mountain range that consists of two narrow ridges separated by a shallow valley (Reddell, 1977). Maximum altitude in the Sierrita is approximately 200 m (topographic maps of INEGI, Instituto Nacional de Estadística, Geografía e Informática).

Reddell (1977) described five physiographic regions for Yucatán: (1) the coastal beach and supra-tidal zone of the

northwestern and northern coasts, from Punta Arenas to El Cuyo; (2) the northwestern coastal plain; (3) the northeastern coastal plain; (4) the central hill district, including the Sierrita de Ticul and the Sierra de Bolonchén; and (5) the eastern block fault district.

### Geology

The whole peninsula can be considered as a single block of limestone material of various ages. Sapper (in Lee, 1980) established a Quaternary origin for the land north of the 21° parallel. The coastal plain extending to the Sierrita de Ticul is formed mostly by limestone of Pliocene origin, whereas the Sierrita itself is of Miocene age (Arroyo-Cabrales and Alvarez, 1990; Hatt et al., 1953). Most of the area of Yucatán, southward to the Sierrita de Ticul was submerged until late Pleistocene time (Hatt et al., 1953; Jones et al., 1973; Paynter, 1955), thus being unavailable for land vertebrates until very recently (Lee, 1980).

The landscape of Yucatán consists of a very flat and simple terrain punctuated only by such karst features as caves and sinkholes. Yucatán lacks any major body of surface water, and the state depends completely on underground sources for its water needs. A remarkable feature of Yucatán is the water-filled sinkholes (cenotes, from the Mayan *dzonot*) and other types of collapse dolines (Finch, 1973). Caves are very numerous and diverse in morphology (Chapter 3).

Soils in Yucatán, where developed, are very poor with a high content of calcareous material (Mollisols) and they alternate with immature soils (Entisols). In many areas the bedrock covers a substantial percentage of the surface.

### Climate

Except for the northwestern extreme, where the climate is hot and very dry, most of Yucatán is hot, subhumid with summer rains ( $Aw_0$ ; García, 1981; Figure 2.2). The mean annual temperatures for Mérida and Tekax are 25.9 and 26.7 °C, respectively. The difference between the minimum and maximum mean monthly temperatures is 5.0 °C for Mérida (23.1 °C in January to 28.1 °C in May) and 6.3 °C for Tekax (23.1 °C in December to 29.4 °C in May). Freezing temperatures are unrecorded in Yucatán.

There is a clearly marked cycle of dry (November to April) and rainy (May to October) seasons (García, 1981; Figure 2.2). There is a gentle but clear gradient of increasing rainfall as one moves from the northwestern coast to the south and to the east. Progreso, located in the northwestern extreme of the peninsula, receives only 444.0 mm of annual rainfall, whereas the average annual precipitation in Oxkutzcab, located in the Sierrita de Ticul, is 1227.3 mm. The percentage of rainfall occurring during the rainy season is 82.8% for Mérida and 80.3% for Tekax (Figure 2.2).

### Vegetation and Land Use

The original vegetation of most of the state was tropical deciduous and semideciduous forest (Miranda, 1959; Rzedowski, 1978), but a substantial part of the surface has been modified to accommodate human activities (Green et al., 1987). Agricultural fields occupy 24.5% of the surface of the state, while 15.7% is devoted to cattle ranches (García and Falcón, 1986). Present-day vegetation in most parts is a matrix of stands of secondary deciduous forest of different ages of succession. Dominant arboreal and shrubby species observed in areas close to the study sites included *Bursera simaruba*, *Ficus* spp., *Vitex gaumeri* and several Leguminosae (*Acacia* spp., *Caesalpinia gaumeri*, *Enterolobium cyclocarpum*, *Lysiloma latisiliqua*, and *Mimosa bahamensis*).

### Fauna

For a tropical area, the Yucatán Peninsula has a comparatively poor fauna of vertebrates. The Yucatán fauna has been cited as an example of depauperization of peninsular faunas by decreased colonization probabilities (the peninsula effect; MacArthur and Wilson, 1967; Simpson, 1964), but other studies have pointed to the effect of other factors besides isolation to explain the poor faunas of the peninsula (Lee, 1980). It is possible that both the peninsula effect and the north-south gradient of rainfall (and thus of primary productivity) contribute to the low species richness of Yucatán.

The herpetofauna of the Yucatán Peninsula consists of 164 species representing 25 families and 93 genera (Lee, 1980). In spite of its isolation, Yucatán has only a moderate percentage of endemic amphibians and reptiles (Flores-Villela, 1991). The avifauna includes approximately 430 species, of which about 290 are considered to breed in the area (Paynter, 1955). There are about 70 species and subspecies that are endemic to the peninsula (Paynter, 1955).

The mammal fauna of Yucatán includes 35 species of bats (Arroyo-Cabrales and Alvarez, 1990; Birney et al., 1974; Jones et al., 1973) and 51 species of non-volant mammals (Ramírez-P. et al., 1986). There is no mammalian species endemic to Yucatán, and only a few rodents (one squirrel, *Sciurus yucatanensis*, and four mice and rats, *Heteromys gaumeri*, *Otonyctomys hatti*, *Peromyscus yucatanicus*, and *Reithrodontomys spectabilis*) are endemic to the peninsula.

### Economy

The poor soil and dry climate of Yucatán hinder any sustainable use of natural resources. In the past, the economy of Yucatán depended on the export of the henequen fiber, and a large percentage of the land was devoted to monocultures of the henequen plant (*Agave furcroides*). Plummeting international prices for natural fibers have produced a change in this pattern, and now agricultural land use has diversified to accommodate corn, beans, sugar cane,

and fruit crops, especially citrus. Cattle ranching is an important activity in Yucatán, especially in the east.

Yucatán depends a great deal on external trade to maintain its economy. Because of the tremendous cultural and historical richness of the state, tourism is one of the main external sources of income for Yucatán. In recent years, the State Government has shown an interest in supporting ecotourism projects to be coupled with the pre-existing cultural tourism developments.

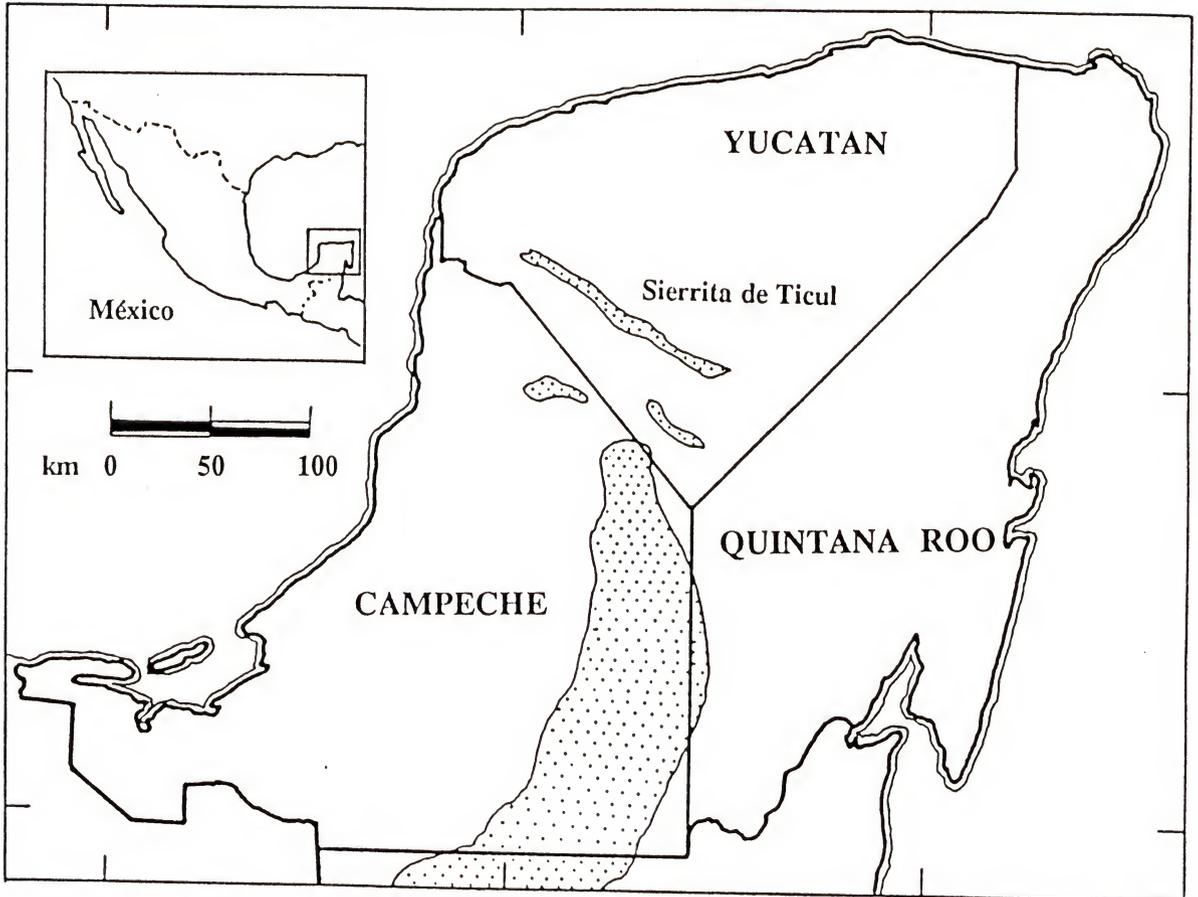


Figure 2.1--The State of Yucatán. Dotted pattern indicates areas with elevation >150 m.

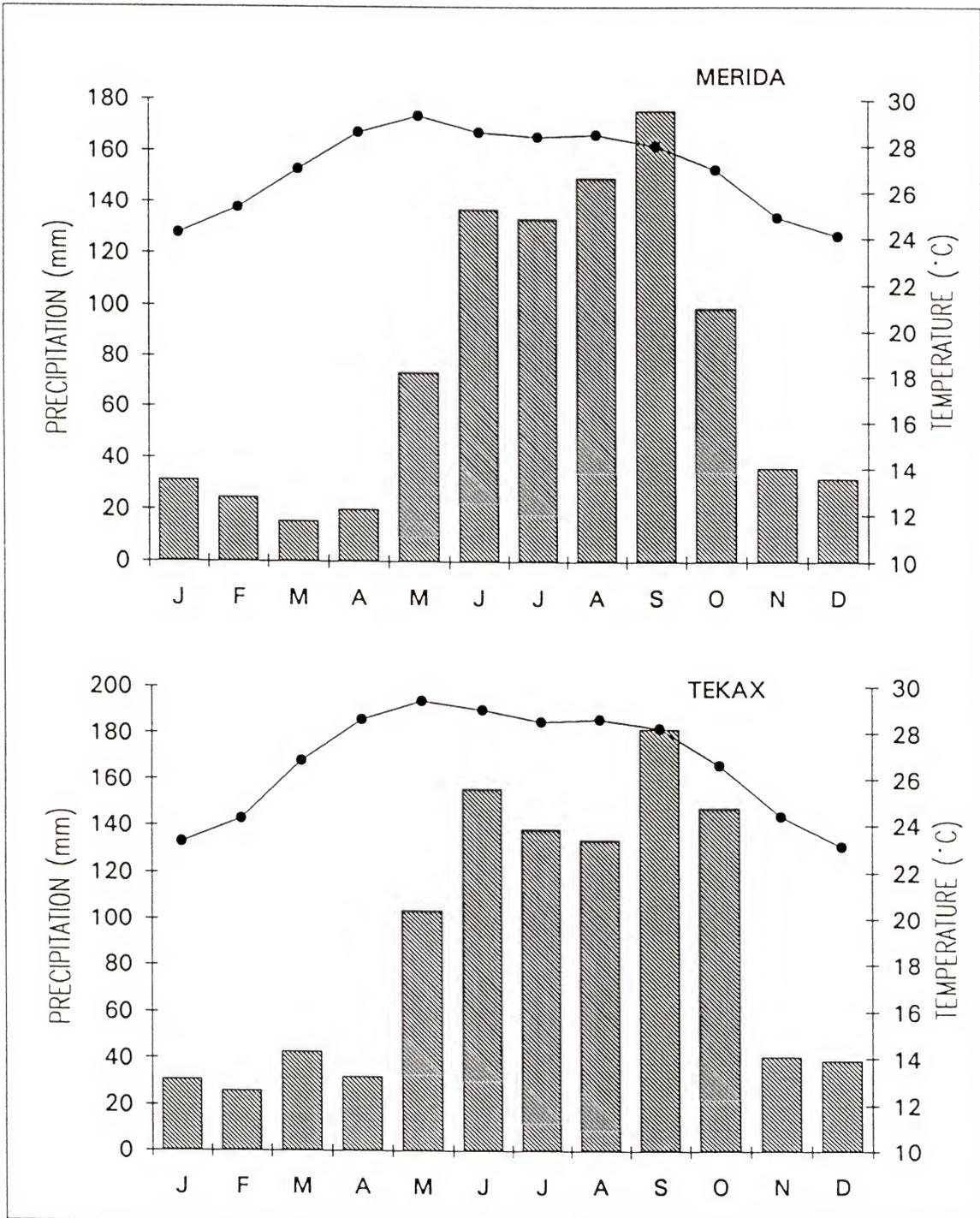


Figure 2.2--Climograms for two localities in Yucatán. Mérida is located in the northern part of the state (20°58'N 89°37'W, altitude 6 m). Tekax is located in the Sierrita de Ticul (20°12'N 89°11'W, altitude 20 m).

### CHAPTER 3 THE CAVES OF YUCATAN

In this chapter I describe the caves that were surveyed during this study. Contrary to standard usage in the scientific literature, in the description of the field methods in this chapter I use a plural grammatical construction to stress the fact that exploration of caves is not, and should not be, a single-person endeavor. In all visits to the caves I was accompanied by at least one other person, and in most cases my party consisted of three to six persons. In the description of the methods to analyze the data I use the standard singular construction.

#### The Caves

All caves surveyed are located in the state of Yucatán, México, and most are in or near the Sierrita de Ticul, the lesser mountain range that marks the southern border of the state. More details about the study site are presented in Chapter 2. The data presented in this chapter were gathered from July 1989 to August 1990. During 1989 we located and selected the caves that were suitable for this project, basing the search on previous reports (Reddell, 1977, 1981; also unpublished catalogue at Instituto Nacional de Antropología e Historia, Mérida Office), on tourist maps,

and on information from local guides. We conducted general surveys of the caves, noting such variables as location, size, number of entrances, ambient temperature, and humidity. We also collected specimens of bats and invertebrates to form reference collections that were deposited in biological collections of the National University of México (UNAM).

Beginning in January 1990, we made systematic visits to all caves included in the study. We scheduled at least two visits to each cave, one during the dry season (January to May) and one during the rainy season (after June). In each cave, we first located and censused the bat populations (Chapter 6). Then, we mapped the caves using standard cave survey procedures (Ellis, 1976), but we fixed the distance between survey points at 10 m. At each station ( $s_i$ ), we noted the time and measured the width of the passage at right angles to the survey line ( $w_i$ ), the height of the passage ( $h_i$ ), the ambient temperature and relative humidity, and the substrate temperature. Widths and heights were measured directly when the ceiling and walls were accessible or estimated using trigonometric calculations; ambient temperature and humidity were measured with a portable psychrometer, and substrate temperature was measured by inserting a long-stem thermometer in the soil or among the rocks on the floor. Using a pre-measured 10-meter cord we fixed the position of the next station ( $s_{i+1}$ ) and, with a magnetic compass, we measured the bearing ( $\theta_{i+1}$ ) and the

slope ( $\alpha_{i+1}$ ) from  $s_i$  to  $s_{i+1}$ . Because the distance between the stations was fixed ( $d_i = 10$  m), horizontal and vertical components were easily calculated (horizontal component,  $x_i = 10 * \cos \alpha_i$ ; vertical component,  $y_i = 10 * \sin \alpha_i$ ). The maps constructed using the network of stations (Figure 3.1) were not intended to be detailed topographic maps; rather, they were designed as graphical descriptions of the habitat for the studies detailed in Chapter 6. In the classification of Ellis (1976), our surveys are Grade 4 (horizontal and vertical angles accurate to  $1^\circ$ , distances accurate to 0.1 m, compass not calibrated), Class C (measurements of detail at survey stations only).

A list of the caves included in this study follows. For each cave I first report the approximate location of the entrance, geographic coordinates, INEGI (Instituto Nacional de Estadística, Geografía e Informática) coordinates, and elevation taken from INEGI maps. In each account I include general information on the morphology and geology of the cave, as well as on abiotic conditions during the visits. I also mention the vertebrates encountered during the visits. Because there was no systematic search for vertebrates other than bats, this information is to be taken as notes on natural history and not as part of a faunistic inventory. More information on the bat fauna of each cave is in Chapter 6. Finally, I conclude each account with notes on the use of each cave by humans, from ancient Mayans to present-day people.

## Definitions

Because the terms used to describe caves vary considerably from author to author, I provide a list of terms that I use in the accounts of the caves.

Cave. A cave is defined, quite anthropocentrically, as any underground space into which a human can fit (Jennings, 1985). In most cave surveys, a minimum length is set to define a cave; this lower limit is 150 m for the Alabama Cave Survey, but is as low as 6 m for other systems, such as the Virginia Cave Survey (White, 1988). Howarth (1983), considering the biology of cave invertebrates, provided a biological classification of subterranean voids in three categories: microcavernous (<0.1 cm), mesocavernous (0.1 to 20 cm), and macrocavernous (>20 cm). According to this criterion, all spaces >20 cm are equivalent from the point of view of an invertebrate. Since the emphasis of this project is on bats, I decided to adhere to the definition that uses 6 m as the minimum size.

Entrances. I classified the entrances of Yucatán caves in five broad categories according to their connection with the exterior:

Direct entrances. The cave connects directly to the exterior, with no external karst feature (e.g., dolines) damping the interchange of air.

Shallow doline. The cave is connected to the exterior through a shallow (<2 m deep) solution doline. This feature

buffers to some extent the effect of changes in the exterior conditions on the climate of the cave.

Chultún entrance. I named chultún entrance a small hole produced by the partial collapse of the ceiling (Figure 3.2). A chultún is an underground dome-shaped storage room used by the ancient Mayans that resembles a cave with a chultún entrance (Zapata-P., 1989).

Rock shelter entrance. A rock shelter is a space in the bedrock in which the extent is shorter than the width and shorter than the height. Shelters can be formed by continuing collapse of the ceiling in a chultún entrance (Figure 3.2).

Open doline (=sinkhole). Open dolines are defined here as more or less symmetric sinkholes, with walls uniformly vertical and with no rock shelters (Figure 3.2). These karst features are colloquially called "cenotes", but this usage is incorrect because the Mayan word *dzonot* means an underground water pool, and it is better applied to inundated sinkholes (Jennings, 1985) or to pools found inside the caves.

I also classified the entrances in ground entrances (connected to a horizontal surface, like the chultún entrance) and wall entrances (connected to a vertical surface). To enter a cave with a ground entrance, one has to move vertically; to enter through a wall entrance one has to move horizontally.

Passages. I use the word passage to describe any discrete section of a cave, limited by changes in width or height. For example, a tunnel ends and a room begins where the cave widens or heightens noticeably.

Narrow tunnel. Narrow tunnels were defined as those cave passages in which both the mean width and the mean height were  $<3$  m.

Constriction. Constrictions are very narrow passages in which one has to crawl or to walk laterally. I defined them as tunnels in which either the width or the height is  $<1.5$  m

Wide tunnel. Where average width is  $>3$  m and average height is  $<3$  m.

Room or chamber. The names room or chamber are defined loosely by speleologists as passages in which one can move comfortably. I defined these terms as passages with both mean width and mean height  $>3$  m. I classified chambers according to their connection to an entrance. First-order chambers connect directly to an entrance. To get from an entrance to a second-order chamber it is necessary to go through a first-order chamber and a narrow passage.

Canyon. A passage in which average height is much greater than average width. I restricted the definition to passages in which average width is  $<3$  m and average height is  $>3$  m.

Chimney. A narrow vertical pit. In Yucatán caves solution pits are very rare, and most of the vertical passages have been created by collapse of bedrock.

The names for solutional sculpturing features and for sediments (including speleothems) are more uniform in the literature than the terms defined above. Therefore, I do not provide explicit definitions here. As a standard terminology, I used the definitions provided by White (1988).

#### Roble Cave

Location.--2.5 km W Tekax, mun. Tekax. 20°12'N, 89°19'W, elev. 90 m. INEGI 16Q BT 583 358.

Located on a hill close to Tekax. Vegetation is second-growth thorn forest dominated by *Acacia* trees. The access to the cave is an open doline 13.2 m wide and 7 m deep. Inside the doline there is a circular *albarrada* (artificial rock barrier) made with big (>2 m) rocks. The cave is actually a deep chamber with a series of floors formed by accumulation of fallen rocks, without real passages.

Bedrock is fine-grained limestone that in most parts of the ceiling and walls is eroded and has traces of Fe<sup>++</sup> and Fe<sup>+++</sup> that give the rock a reddish color. There are practically no speleothems, and crystals are apparent only in localized areas in the deeper sections. Most of the floor is covered by collapsed rocks with fine sediment.

Guano is sparse and localized in areas below roosting sites of bats.

On January 1 temperature inside the cave was 26.5 °C at 1441 h. On 7 March temperature varied from 23.5 °C near the entrance at 1621 h to 24.0 °C at the deepest point at 1728 h. Relative humidity varied from 78% at the entrance to 83% at the deepest point. On 7 August temperature varied from 24.0 °C in the deepest part at 1015 h to 25.5 °C near the entrance at 0927 h. Relative humidity varied from 85% at the entrance to 92% in the deepest part.

The walls of the doline are roost sites for a group of 30 to 50 rough-winged swallows (*Stelgidopteryx ruficollis*). In some parts of the doline the floor is covered with pellets and feathers of the barn owls (*Tyto alba*). In the cracks near the entrance there was always a small (<20 individuals) group of sac-winged bats (*Peropteryx macrotis*). In April and August there was a small group (5 individuals) of fruit-eating bats (*Artibeus jamaicensis*) in one of the solution holes near the entrance and a colony of 12 big-eared bats (*Micronycteris megalotis*), and a group of long-tongued bats (*Glossophaga soricina*).

During explorations of the cave in January 1990 two nearly complete pieces of Mayan vats were recovered from this cave. These pieces are now in the Instituto de Antropología e Historia in Mérida. The Tekax City Council wanted to build a small museum near the cave, but as this writing no concrete plans have been announced. The cave is

very close to the road (< 10 m) but the deep sinkhole makes it inaccessible to most people.

Actun Sabak-ha

Location.--4 km S Tekax, mun. Tekax. Approx. 20°10'N, 89°16'W, elev. 55 m. INEGI 16Q BT 615 323.

The cave was explored and mapped in January 1990 by a team of the Brazilian Speleological Society. The expedition included a group of topographers, a team of biologists, and a group of archaeologists. I participated as coordinator of the team of biologists. The cave was divided in seven major zones for study. Section B0 included the external and well-lighted upper section of shallow dolines. B1 was a tunnel of about 50 m between two open collapse dolines. B2 was a zone of open dolines. B3 was a tunnel of 100 m that bifurcates into sections B4 (the N passage) and B5 (the SE passage). Section B6 was the end zone of the SE passage.

The upper zone (B0) is a series of shallow dolines that are illuminated, allowing plant growth. However, the humidity in these dolines is higher than in the external parts and the vegetation is different from the one covering the exterior. Cracks in the walls provide special microhabitats for arthropods and small vertebrates. The entrance to the cave is through a big open doline about 15 m wide and 10 m deep that communicates with wide passage B1. This chamber is 10-15 m wide and >5 m high and goes in a SW-NE direction to connect the entrance doline with a section

with a series of holes caused by the collapse of the roof (B2). From this section begins a short (<5 m) narrow tunnel (B3) that is appreciably warmer and more humid than the previous sections. Sections B4 to B6 are bigger chambers with many and spectacular speleothems (stalactites, stalagmites, columns, flowstone sheets, and rimstone dams). There are very few crystals on the walls and ceilings, however. Section B4 has an upward slope and acts as a heat trap, being very hot and humid in the end section.

Sections B0 to B2 are covered mostly by breakdown rocks produced by the collapse of the ceiling, with very little sediment. The interior sections (B3-B6) have much more sediment, and in some parts the floor is flooded with a combination of soft sediment, water, and bat guano.

On 15 March the interior sections (B3-B6) were hot and humid (temperature: 27.0 °C in B3 at 1453 h, 26.1 °C in B6 at 1348 h; relative humidity: 87% in B3, 91% in B6). The chamber B1 was cooler (22.0 to 24.0 °C at about 1510 h) and less humid (77 to 84%). In section B0 temperature and relative humidity were 23.5 °C and 80% at 1521 h. At about the same time the temperature and relative humidity of the area outside the cave system were 32.2 °C and 56%.

The small dolines in the upper section of the cave system provide special microhabitat for small vertebrates that cannot live outside. For example, the endemic salamander *Bolitoglossa yucatanica* is known only from this kind of habitat. One individual was found in one of the

dolines of Sabak-ha. Other small reptiles observed during a non-intensive search were a snake (*Masticophis mentovarius*), one gecko (*Thecadactylus rapicauda*), and one lizard (*Cnemidophorus angusticeps*). The dolines are used as roost by a group of swallows (*S. ruficollis*) and a pair of barn owls (*T. alba*), and perhaps by motmots (*Eumomota superciliosa*), as suggested by some feathers found in the site. The walls in the dolines and near the main entrance are used by several colonies of the sac-winged bat (*P. macrotis*) and little black bats (*Myotis keaysi*). Other bat species are found in the more humid parts of the system. for example, the fruit bat (*A. jamaicensis*) is found in all areas from B2 to B6, whereas other species such as the mustached bat (*Pteronotus parnellii*), the long-tongued bat (*Glossophaga soricina*), the hairy-legged vampire bat (*Diphylla ecaudata*), and the long-legged bat (*Natalus stramineus*) roost only in the deepest part of the cave. In B3 there was a large (>100 individuals) colony of the common vampire bat (*Desmodus rotundus*). A skull of the red bat (*Lasiurus blossevillii*) was found in a passage near the entrance. This skull might have come from an individual lost in the cave as described by Barbour and Davis (1969) for other *Lasiurus*, or it might have been deposited with other material in an owl (*T. alba*) pellet. There was evidence of use of the cave by mice (open seeds in dens, possibly of *Ototylomys phyllotis*) and porcupine (quills and feces of *Coendou mexicanus*).

Sabak-ha is a well-known cave system that has been visited by several researchers (Pearse, 1938; Reddell, 1977, 1982). It is an archeological site recognized by the Instituto Nacional de Antropología e Historia. Evidence of use by ancient Mayans (pottery, carvings, stone water-collecting systems) can be found at several sites in the cave. The purpose of the expedition of January 1990 was to assess the possibility of developing the cave as an ecotourism site. The team of speleologists concluded that Sabak-ha is more than adequate for such a purpose, but a project for development of the area as a tourism site has not been approved by the state and federal authorities.

#### Actun Chunkunab

Location.--1.5 km SW Ticum, mun. Tekax. 20°08'N 89°13'W, elev. 50 m. INEGI 16Q BT 683 291.

This small cave is located close to the archeological site of Chunkunab. The entrance is through a rock shelter that is covered with vegetation; the roots of a big *Ficus* tree partially conceal the only access. The cave extends for <35 m and descends to a maximum depth of 25 m from the ground level. The walls and ceiling are formed by fine-grained limestone with almost no crystals and no visible speleothems. The floor is covered with collapsed rocks and very little fine sediment, except in the deepest portion where sediment accumulates.

The cave is comparatively cool (23.3 to 23.9 °C at about 1130 h on 14 March) and with moderate humidity (from 78 to 82%). On January I observed a pair of mot-mots (*E. superciliosa*) at the entrance. The cave is inhabited by small colonies of *P. macrotis* and *A. jamaicensis*.

#### Actun Maas

Location: Very close to Actun Chunkunab. Same location and coordinates.

This cave is a small room (extent <50 m) with a single chultún entrance (Figure 3.3). The chamber has a gentle negative slope and ends at 35 m below ground level. The bedrock is fine-grained limestone and there are no crystals or speleothems except in the deepest part of the cave, where crystals can be seen in the fissures. The floor is covered with big collapse rocks and little fine sediment. On 14 March temperature varied from 26.5 °C in the deepest section at 1001 h to 27.8 °C in the entrance at 0922 h. Relative humidity varied from 80% at the entrance to 92% at the deepest part.

In March, a single mot-mot (*E. superciliosa*) emerged from the cave when my party approached. The cave is habited by a small colony of sac-winged bats (*P. macrotis*) and a few fruit-eating bats (*A. jamaicensis*).

### Bat Cave

Location.--0.5 km SW Ticum, mun. Tekax. 20°09'N, 89°13'W, elev. 70 m. INEGI 16Q BT 680 288.

The cave is located on the NE slope of the Sierrita de Ticul. The wall entrance is about 15 m wide and 1.5 high and is concealed by the secondary vegetation that grows in the exterior. Light penetrates most of the area of the first passage, which is about 10 m wide and 2 m high (Figure 3.4). A very narrow constriction separates this first-order passage from the main section of the cave, a chamber of about 30 by 20 m and three to four m high. There is a short tunnel at the S end of the chamber that ends in a shallow pit. Another tunnel at the NW end of the chamber goes up and narrows until it precludes access by humans.

The first-order passage and the main chamber have a bedrock of fine-grained limestone with numerous solution holes that are used as roosting sites by bats. The more interior sections present a spongework pattern (White, 1988) produced by differential erosion. These areas also have more stalactites. There are few collapse blocks, and the floor is covered mostly by fine sediment and bat guano.

On 8 March temperature and humidity were as follows. At the entrance at 1243 h: 25.0 °C and 79%; in the main room at 1217 h: 27.2 °C and 88%; in the interior passages at 1128 h: 30.0 °C and 92%. On 8 August conditions were: at the entrance at 1244 h: 27.0 °C and 93%; in the main chamber at

1135: 27.5 °C and 93%; in the interior passages at 1002 h: 30.0 °C and 93%.

Several swallows (*S. ruficollis*) and one mot-mot (*E. superciliosa*) were observed near the entrance. This cave has one of the biggest colonies of bats in the area. There are many large (>30 individuals) groups of *A. jamaicensis* and *G. soricina* and very big (>1,000 individuals) colonies of *P. parnellii*, the naked-backed bat (*Pteronotus davyi*) the ghost bat (*Mormoops megalophylla*), and *N. stramineus*. Additionally, one individual of the short-tailed bat (*Carollia perspicillata*) was captured on January. In one of the visits I saw an opossum (*Didelphis marsupialis*) trying to catch bats emerging from the cave at dusk.

I did not find any sign of human occupation or use in this cave. It could be important for the conservation of bats because it harbors large populations and has little potential for tourism.

#### Ramonal Cave

Location.--0.5 km NE Cepeda Peraza, mun. Tekax. 20°09'N, 89°15'W, elev. 50 m. INEGI 16Q BT 649 301.

The cave is located within the Ejido (communal land) of Cepeda Peraza. The entrance is a small (< 1.5 m in diameter) chultún entrance through which protrudes the dead trunk of a Ramón tree (*Brosimum alicastrum*) that gives the name to the cave. Beneath the entrance there is an accumulation of breakdown rocks and sediment. To the S,

there is a short passage (<20 m) and to the NW there is a bigger chamber that connects through a constriction with a wide tunnel that ends in a very shallow (<30 cm high) passage. There is an *albarrada* (artificial barrier) partially blocking the constriction.

The walls and ceiling of the main chamber are formed mainly by the bedrock, with almost no travertine. The area after the constriction presents more travertine and some stalactites, especially in the last tunnel. The floor of the main chamber is covered mostly by breakdown rocks with little sediment. The interior tunnels present some travertine, forming rimstone dams and "cave pearls" (concretions), and are covered by a layer of fine sediment and bat guano. On 5 January temperatures ranged from 26.0 to 28.0 °C. On 8 March, temperatures varied from 25.6 °C near the constriction at 1427 h to 27.2 °C at the end of the tunnel at 1442 h. Relative humidity ranged from 87 to 92%.

In March, one mot-mot (*E. superciliosa*) flew from the cave as my party approached. Cracks and holes in the ceiling are used for refuge by geckos (*T. rapicauda*) and by mice (*O. phyllotis*). In the area just N of the constriction a colony of about 50 common vampires (*D. rotundus*) roosted among straw stalactites. A small group of *G. soricina* was roosting in the S section. In the deepest part of the cave I found four *D. ecaudata* and six *N. stramineus*.

Apparently this cave has a low rate of visitation. Local people normally do not enter, and most spelunkers do

not know the existence of the cave. Some *haltunes* (stone water-collecting devices) and the *albarrada* are proof that the cave has been used in the past.

### Flor de Mayo Cave

Location.--Approx. 2.5 km SSW Tekax, mun. Tekax. 20°12'N, 89°18'W, elev. 35 m. INEGI 16Q BT 598 340

This cave is located on the shallow valley between the two lines of the Sierrita de Ticul. The name means May Flower and refers to the ornamental plant *Plumeria rubra* (Apocynaceae). There are two entrances to the cave. One is a very narrow (<1 m wide) tunnel that is on one of the walls of a deep (>15 m) open doline; the other is a small wall hole that appears almost at ground level on a shallow doline at the opposite side of the cave. The narrow tube connects to a big chamber with well-developed speleothems (stalactites, sheets, columns) and a deep accumulation of soft sediment. The apparent absence of stalagmites despite the abundance of stalactites and columns indicates that sediment has covered most of the original floor. The main room narrows gradually, turning into a single tunnel that ends in the second entrance. Horizontal distance between the two entrances is about 75 m. A concealed passage connects to an additional chamber with walls and floor covered with eroded substrate forming a spongework pattern. On 16 March temperature in the main chamber at about 1015 h

varied from 26.0 to 27.5 °C. Relative humidity ranged from 78% to 86%.

Holes in the walls of the sinkhole are used by swallows (*S. ruficollis*), fruit-eating bats (*A. jamaicensis*), and sac-winged bats (*P. macrotis*). On 8 January I saw a pair of barn owls (*T. alba*) flying from one of the walls. In the interior I found a small group of *N. stramineus* and saw guano of the common vampire bat (*D. rotundus*). During the exploration in January, a fossil mandible of a horse (*Equus conversidens*) was found in the main chamber of this cave.

The entrances to this cave are difficult to locate, so the site is not frequently visited. I found no evidence of previous visits, except in the external part of the sinkhole, where there was some trash.

#### Actun Kab

Location.--Approx. 2.5 km SSW Tekax, mun. Tekax. 20°12'N, 89°18'W, elev. 35 m. INEGI 16Q BT 598 340

Actun Kab (the cave of the bees) is a big (>30 m wide) rock shelter that descends with a steep slope (>30°). The floor is covered with big breakdown rocks and small amounts of fine sediment. A big (>100 individuals) group of swallows (*S. ruficollis*) roosts in the external part of the cave, and a colony of 15 *P. macrotis* roosts in the interior.

### Actun Kan-Lol

Location.--Approx. 2.5 km SSW Tekax, mun. Tekax. 20°12'N,  
89°18'W, elev. 35 m. INEGI 16Q BT 596 345

This is a series of short tunnels that connect several small sinkholes. The ceiling of the tunnels has several big stalactites, but the floor presents no stalagmites and is covered by a deep layer of sediment. This systems seems to be an old cave in which most of the walls and part of the ceiling have collapsed, leaving only the series of tunnels. I found some geckos (*T. rapicauda*) and a small colony of sac-winged bats (*P. macrotis*).

### Porcupine Cave

Location.--Approx. 2.5 km SSW Tekax, mun. Tekax. 20°12'N,  
89°18'W, elev. 35 m. INEGI 16Q BT 593 341

This cave consists of two chambers connected by a narrow and short tunnel. In the first chamber light penetrates through several holes produced by the collapse of the ceiling and provides a dim illumination to the chamber. The second chamber is a small oval room (12.7 m by 11.5 m) that is totally dark. The ceiling and walls present almost no feature, except some travertine. The floor is covered by fine sediment. On 16 March at 1130 h, temperature in the dark chamber was 25.5 °C and relative humidity was 87%.

On January 8, I saw a porcupine (*Coendou mexicanus*) that was using a niche in the wall of the illuminated chamber as a den. In subsequent visits the animal was not

present, but I found fresh feces in the den, along with quills. The dark room is used as refuge by many (>12) geckos (*T. rapicauda*), a small group of *A. jamaicensis*, and a small colony of *P. macrotis*. On 18 April, I also found another gecko (*Coleonyx elegans*). Both species of geckos found in this cave are considered rare and are difficult to find outside refuges. The fact that this small cave harbors so many individuals is remarkable.

#### Chocantes Cave

Location.--0.5 km SW Tekax, mun. Tekax. 20°12'N, 89°18'W, elev. 85 m. INEGI 16Q BT 599 351.

This large cave is located on the Sierrita de Ticul. The cave is a series of big chambers connected by narrower passages. The wall entrance is located in a shallow doline and has a steep slope (28°) and opens to the first big chamber. This room and the next one are wide and very high (>20 m). These rooms present few ornamentations (only a few stalactites) and their floor is covered mostly by breakdown rocks with little sediment. The next system of tunnels, which ceiling is covered with straw stalactites (most of them broken), connects with a series of very narrow tunnels (1.5 m wide, <1 m high) that extend for more than 150 m and appear to end by sediment choking. My guides discovered a very narrow passage that connects to a bigger chamber that is totally covered with crystalline formations (helictites and other calcite crystals on the walls, evaporation

crystals on the floor). The pristine condition of most crystals indicates that no one had been in that chamber before us.

On 6 May at 1015 h the temperature at the final chamber was 29.0 °C; relative humidity was 96%. Temperature in other parts of the cave, between 1100 to 1315 h, varied from 24.0 to 27.0 °C, and relative humidity ranged from 88 to 100%. This large cave has a remarkably poor fauna of vertebrates. I only found a colony of about 1,000 *P. parnellii* and a group of <50 common vampire bats (*D. rotundus*).

The cave is popular among spelunkers, and in some parts the walls are covered with graffiti and signs left by explorers. However, the existence of the last chamber has not been announced, and there are plans by the local authorities to implement a protection plan for the area.

### Actun Oxpehol

Location.--0.5 km N Canek, mun. Tekax. 20°12'N, 89°20',  
elev. 40 m. INEGI 16Q BT 565 355.

This cave is located close to the small town of Canek, on the SW slope of the Sierrita de Ticul. The first section of the cave is a chamber in which several parts of the ceiling and the walls have collapsed, allowing light to penetrate and fully illuminate the room. Several tunnels radiate from this chamber, the longest of which connects to other open dolines and a deep pit that was not explored. In

the middle of the first chamber there is a circular, artificial arrangement of rocks (*albarrada*). The ceiling present some ornamentation caused by differential erosion (mostly pendants and solution holes), but very little travertine and almost no stalactites. The floor is covered by soft sediment and in localized sites by guano of fruit bats (*A. jamaicensis*). Beneath the colonies of bats there are conspicuous aggregations of seeds and seedlings (apparently of *Ficus*). On 17 March at 0753 h, temperature in this chamber was 27.0 °C and relative humidity was 77%. This area provides roost for mot-mots (*E. superciliosa*), bats (*A. jamaicensis*), and one porcupine (*C. mexicanus*).

The main tunnel extends 100 m and ends in an elevated area that acts as a heat trap. On 17 March at 0925 h, near the entrance to this tunnel, temperature was 25.0 °C and relative humidity 87%. At the end of the tunnel at 0829 h, temperature was 27.0 °C and relative humidity was 89%. The tunnel is inhabited by small groups of three species of bats (*P. macrotis*, *A. jamaicensis*, and *D. rotundus*).

This cave is very close to the Ejido Canek, but apparently local people do not visit it frequently. There was a proposal for developing this cave as an educational site for local people, but no formal plans have been announced at the time of this writing.

Actun X-Maasit

Location.--0.3 km N Canek, mun. Tekax. 20°12'N, 89°20',  
elev. 40 m. INEGI 16Q BT 565 353.

Actun X-Maasit is a partially collapsed doline that continues in a short and narrow tunnel. It is located between Actun Oxpehol and the town of Canek. The collapsed wall forms a rock shelter with a steep slope (38°), at the end of which there is evidence of use by humans (an artificial barrier, *albarrada*) and *haltunes* (water collecting devices). In this area I found the skull of a paca (*Agouti paca*) and dry feces and quills of a porcupine (*C. mexicanus*). On 9 January I saw three individuals of *P. macrotis* hanging on one of the walls of the doline. On 17 April I did not see any bats.

At the deepest part of the rock shelter a short (45 m) and narrow (<2 m wide) tunnel begins. The entrance is partially blocked by rocks that seem to be artificially arranged. The ceiling of this tunnel is covered by minute straw stalactites that look complete (not broken). This suggests that this section is not visited frequently. On 17 March at about 1015 h temperature varied from 23.0 °C near the doline to 28.0 °C at the end of the tunnel. Relative humidity ranged from 82% to 92%. I did not see any bats in this tunnel, but I found localized accumulations of guano of an insectivorous bat (probably *P. macrotis*).

### Actun Dzonot

Location.--0.5 km S Canek, mun. Tekax. 20°11'N, 89°20'W,  
elev. 30 m. INEGI 16Q BT 565 342.

Actun Dzonot is a collapse doline about 12 m wide and 5 m deep with several short tunnels radiating from its walls. The interior of the doline is covered by second-growth vegetation in which bananas (*M. paradisiaca*) dominate. The longest tunnel descends steeply and extends for <40 m. The walls and ceiling present no conspicuous ornament and the floor is covered mostly by breakdown material, with an accumulation of soft sediment in the deepest part. On 9 January there was a single group of about 15 *P. macrotis* roosting on one of the walls of this passage. In the deepest part of the tunnel, the skull of a raccoon (*Procyon lotor*) was found.

### Iguana Cave

Location.--2.4 km W Tekax, mun. Tekax. 20°12'N, 89°18'W,  
elev. 90 m. INEGI 16Q BT 586 359.

This cave is located in the same hill as the Roble Cave, on the NE band of the Sierrita de Ticul. The wall entrance is on the end of a shallow doline (6 m long, 1.5 m deep) and is about 2 m high, allowing light to penetrate into the first chamber. Water drips from several parts of the ceiling, forming conspicuous speleothems (stalactites, stalagmites, columns, and rimstone dams). A particularly spectacular dam, with numerous "cave pearls" (concretions)

is located just at the beginning of the main passage. A steep tunnel (slope 32°) connects to the interior section of the cave, which is an oval chamber with fewer speleothems and a deep layer of soft sediment. I explored several small accessory passages, but none was >15 m long.

On 3 May at about 1500 h temperature near the entrance was 25 °C and relative humidity was 92%; in the interior chamber temperature was 24.0 °C and relative humidity was 92%. On 7 August between 1400 and 1500 h, temperature ranged from 28 °C near the entrance to 24.5 °C at the end of the chamber; relative humidity varied from 82% at the surface to 96% in the deepest section. This cave harbors a small colony of *A. jamaicensis* and a group of about 15 *P. macrotis*. Both groups roost on the walls of the exterior chamber, in the twilight zone.

The entrance to the cave is <20 m from a recently paved road, and the main passage actually passes under the road. I found trash in the entrance doline, but the interior of the cave is clean and no graffiti can be seen on the walls.

#### Doña Blanca Cave

Location.--2 km W Tekax, mun. Tekax. 20°12'N, 89°18'W,  
elev. 55 m. INEGI 16Q BT 591 360.

This is a small rock shelter with a pair of short (<15 m) tunnels in the walls. The exposed face of the shelter is partially covered by columns and stalactites. On 3 May at 1600 h, temperature in one of the tunnels was 25.5 °C and

relative humidity was 69%. The shelter provides roost for <10 *A. jamaicensis*, and one of the tunnels is occupied by a group of *P. macrotis*. The cave is <15 m from the road, but I found no evidence of frequent visitation by humans.

#### Cinco de Mayo Cave

Location.--2.5 km W Tekax, mun. Tekax. 20°13N, 89°18'W, elev. 60 m. INEGI 16QBT 585 366.

Cinco de Mayo Cave is located on the NE slope of the Sierrita de Ticul. The system consists of a big (30 m wide, >10 m high) rock shelter that connects to a series of short passages. The exterior part of the shelter is a steep slope covered by big rocks that ends on an flat area covered by deep soft sediment. The ceiling is formed by fine-grained limestone that forms several solution holes and big (>3 m) pendants. The entrance is partially hidden by columns. On 9 August at 0900 h, temperature and relative humidity at the shelter were 25 °C and 92%.

Several parts of the shelter are covered by owl (*T. alba*) pellets and bones of small mammals (shrews, bats, and mice). The area is used as roost by a group of about 50 swallows (*S. ruficollis*) and two mot-mots (*E. superciliosa*). I also found a small (5 individuals) group of *A. jamaicensis*, and a colony of about 6 *P. macrotis*. In several occasions I found tracks of a paca (*A. paca*).

An artificial barrier (*albarrada*) separates the rock shelter from a series of short tunnels. The longest of

these passages is only 70 m long. The walls and ceiling are formed by fine-grained limestone and there are many eroded speleothems. Only a few of these still present crystals. On 2 May between 0800 and 1126 h, temperature varied from 24.0 to 25.5 °C, and relative humidity ranged from 85 to 96%. On 9 August between 1003 and 1115 h, temperature ranged from 25.0 to 26.0 °C, and relative humidity varied from 89 to 96%.

In the interior passages I saw a group of <10 *G. soricina* roosting. At the deepest part I found a small accumulation of guano of the vampire bat (*D. rotundus*).

This cave is well-known among locals and tourists are frequently taken to visit it. The cave is mentioned in many papers on Yucatán caves (e.g., Pearse 1938, Reddell 1977, 1982). The walls and many speleothems are covered with graffiti of visitors. A message on one stalagmite recording a visit in the 1890s is fake, according to my local guides.

#### Cave "A" (no name)

Location.--The cave is <20 m from Cinco de Mayo Cave, same location.

This is a small rock shelter (10 by 3 m) that connects to a short tunnel (10 m long, 2 m wide, 2 m high). The bedrock is eroded limestone, and the walls and ceiling lack conspicuous ornaments. The floor is covered with big rocks and little fine sediment. On 2 May at 1250 h temperature and relative humidity in the shelter were 30.0 °C and 53%.

Inside the tunnel conditions were 28.0 °C and 66% relative humidity.

I found several owl (*T. alba*) pellets on the floor of the shelter, and on 2 May I observed a gecko (*C. elegans*). The tunnel is used by a colony of eight *P. macrotis*, and by several geckos (*T. rapicauda*).

This is a very small and inconspicuous cave. I found no indication of human visitation. The presence of the two species of geckos is interesting given the relative rarity of these species.

#### Ramonal y Naranja Cave

Location.--2.3 km W Tekax, mun. Tekax. 20°12'N, 89°19'W, elev. 60 m. INEGI 16Q BT 585 355.

This system consists of a central collapse doline from which three passages radiate (Figure 3.5). The sinkhole is about 20 m wide and about 8 m deep. It has a well-developed secondary vegetation in which a big *Ficus* tree dominates; this tree is visible from the exterior and helps in finding the cave. From the sinkhole, the N chamber extends for about 65 m with an ascending slope, and ends in a small wall entrance that connects to a shallow doline <2 m wide and 1 m deep. The S room also has a positive slope but terminates after 60 m by sediment choking, with no other entrance. The W chamber is completely covered with big rocks (apparently artificially arranged) and does not have another entrance.

This last room was explored but not mapped and not included in the biological study.

The walls of the collapse doline are the roosts for several mot-mots (*E. superciliosa*). I found a moderate number of owl (*T. alba*) pellets. In the solution holes on the ceiling at the entrance to the tunnels, I observed several groups of *A. jamaicensis*.

The bedrock in the N tunnel is coarse-grained coquina, with conspicuous shells. This passage presents areas with travertine and small speleothems (stalactites and draperies), but the ceiling and walls are formed mostly by exposed bedrock. The floor is covered mostly with breakdown rocks and little fine sediment. On 4 May temperature in this tunnel ranged from 24.0 °C near the doline at 1116 h to 27 °C near the second entrance at 1050 h. Relative humidity varied from 92% to 78%. On 11 August conditions near the doline at 0850 h were 24.5 °C and 96% R.H.; at 0810 near the second entrance were 26.0 °C and 85% R.H. Meanwhile, external temperature was 28.5 °C and relative humidity was 82%.

In one solution hole near the second entrance, I found a group of six geckos (*T. rapicauda*). The same number of animals was observed in the three visits to the cave (April, May, and August). Closer to the doline, I observed one gecko of another species (*C. elegans*). The N tunnel harbors a small group (10 to 15 individuals) of *A. jamaicensis* and a colony of 25 *P. macrotis*. I observed an accumulation of

guano with parts of big insects (Lepidoptera and Coleoptera) that indicates that the tunnel is used occasionally by an insectivorous bat (probably *M. megalotis*).

The S room is more diverse in ornaments. The ceiling and walls on most parts is covered with crystals or travertine. Stalactites, flowstone, and draperies are abundant. The floor is covered in many parts by travertine, in some cases forming rimstone dams. In the lower sections of the tunnel, a layer of fine sediment is also present. On 4 May at about 1145 h temperature in this tunnel was uniform at 25.0 °C, and relative humidity varied from 85 to 92%. On 11 August at 1000 h, temperature varied from 25.0 to 26.5 °C, and relative humidity ranged from 92 to 96%. The only vertebrates seen in this tunnel were bats, a group of 40 *P. macrotis* and two groups of *A. jamaicensis* roosting in the solution holes.

In the W chamber my local guides found several pieces of pottery and some bones. In other parts of the cave there are water-collecting devices and other proofs of past human use of this cave. I found no indication of any visitation by modern humans, despite the fact that the cave passes under a trail and that one of the entrances is practically beside the road.

Bejucos Cave

Location.--2 km W Tekax, mun. Tekax. 20°12'N, 89°19'W,  
 elev. 60 m. INEGI 16Q BT 590 351.

This is a small cave of <50 m located in a field cultivated with corn and squash. The wall entrance is 3 m wide and 1 m high and is partially concealed by the roots of shrubs and trees that grow above. The cave descends in a steep slope (from 8 to 18°) and ends in a small (<3 m wide) and flat room covered with sediment. In most of the cave the ceiling is <2 m high and is covered with travertine and speleothems (stalactites, straw stalactites, sheets, helictites). The floor is covered by rocks and soft sediment, and there are few stalagmites and columns. On 4 May at 1000 h temperature varied from 26.0 to 27.0 °C, and relative humidity ranged from 85% to 92%. Meanwhile, external conditions were 33 °C and 68% relative humidity. On 11 August at 1330, temperature ranged from 27.0 to 28.5 °C and relative humidity was constant at 93%.

On 19 April I observed one individual of each of the two cave geckos (*C. elegans* and *T. rapicauda*). The cave is used as a day roost by *A. jamaicensis* (about 20 individuals), *G. soricina* (<10 individuals), and *M. megalotis* (a colony of eight individuals).

This cave is readily visible from a rural road, and is very close to a well-known cave (X-Mahit). However, it is seldom visited because of its small size and (as I was told

by one local peasant) because of a swarm of wasps that nest at the entrance.

### Actun Tolok

Location.--2 km W Tekax, mun. Tekax. 20°12'N, 89°19'W,  
elev. 40 m. INEGI 16Q BT 588 348.

Actun Tolok is a small chamber (16 by 12 m, about 3 m high) located in the valley between the two lines of the Sierrita de Ticul (Figure 3.6). The entrance is 3 m wide and divided by several columns. Light penetrates to most of the chamber, and only the S extreme is completely dark. The walls and ceiling present little travertine and no conspicuous speleothems. There is an accumulation of breakdown rocks near the entrance, whereas the deepest section is covered with fine sediment. On 4 May at 0815 temperature was 26.0 °C and relative humidity was 86%.

On 19 April I observed two individuals (one male, one female) of *Basiliscus vittatus* that were roosting separately in the twilight zone. They were not present on 4 May. The cave is used by a small group (8 individuals) of *A. jamaicensis* and by a colony of about 15 *P. macrotis*.

### Guayaba y Aguacate Cave

Location.--2 km SW Tekax, mun. Tekax. 20°12'N, 89°18'W,  
elev. 40 m. INEGI 16Q BT 593 346.

This a big (about 30 m wide, 5 m deep) collapse doline with several short accessory tunnels. The center of the doline is formed by blocks of the collapsed ceiling and

covered by dense vegetation. On 19 April, one of the tunnels contained a colony of 20 *P. macrotis*. This tunnel has no visible speleothems and is covered by breakdown material and soft sediment.

Cave "B" (no name)

Location.--1 km SE Tekax, mun. Tekax. 20°11'N, 89°17'W,  
elev. 70 m. INEGI 16Q BT 610 346.

This cave is located in the NE slope of the Sierrita de Ticul, facing the town of Tekax. The entrance is a small (10 m wide, <1 m high) wall hole that connects to a series of narrow passages with a descending slope. The ceiling is never >2 high and is formed by fine-grained limestone with solution holes. Stalactites and crystals are present in low number. The floor is covered mostly by breakdown rocks with little sediment. On 5 May at 1530 h, temperature ranged from 27.0 to 29.0 °C, and relative humidity varied from 86 to 92%. On 10 August at 1000 h conditions were 27.0 to 28.0 °C and 93% relative humidity. This cave harbors a small group of *G. soricina* (<10 individuals) and a colony of 8 *P. macrotis*.

Actun Chac-Xix

Location.--1 km S Tekax, mun. Tekax. 20°11'N, 89°17'W,  
elev. 75 m. INEGI 16Q BT 606 348.

Actun Chac-Xix is a small cave with a very steep slope (from 14° to 67°). The access is through a very narrow (about 60 cm in diameter), short (<2 m), horizontal tunnel

that connects to a pit about 10 m deep. A rope is necessary to descend in this part. The whole system is actually a vertical hole, and there are no real tunnels, just trails determined by the location of breakdown material. The ceiling is mostly eroded limestone but presents a few formations (stalactites, sheets). The floor is covered breakdown material and in some parts fine sediment.

On 5 May at 1115 h, temperature and relative humidity inside the cave were uniform at 24.0 °C and 92%. On 10 August at 1330 h, temperature varied from 24.0 to 26.5 °C, and relative humidity ranged from 89 to 96%. The only vertebrates observed in the cave were a small group (from 3 to 5 individuals) of *P. macrotis*.

The cave is just a few meters from a local church and is well known among locals. However, most people do not enter the cave because it is necessary to go through the narrow tunnel and the deep pit. I found some trash near the entrance, but not in the deepest parts. This cave was included in the studies of Pearse (1938) and Reddell (1977).

#### Zorro Cave

Location.--1 km S Tekax, mun. Tekax. 20°11'N, 89°17'W,  
elev. 60 m. INEGI 16Q BT 603 348.

The cave of the zorro (opossum, *Didelphis marsupialis*) is a rock shelter with many small cracks and a few very short (<10 m) tunnels. I visited the site on 20 April and found a colony of *P. macrotis*.

### Aguacate Cave

Location.--1.5 km E Tekax, mun. Tekax. 20°12'N, 89°18'W,  
elev. 65 m. INEGI 16Q BT 596 356.

The site is also known as Actun On (the cave of the avocado), but here I use the Spanish name to avoid confusion with Actun On near Oxkutzcab. The cave is a collapse doline with a U-shaped room with a total extension of <20 m. The walls and ceiling are formed by fine-grained limestone and the floor is covered with soft sediment. On 5 May at 1320 h temperature in the room was 27.0 °C. Relative humidity was 71%.

On 20 April I saw no bats, but found many seeds (apparently of *Ficus*) and several seedlings growing in the dark section of the tunnel. On 5 May I observed a group of about 30 *A. jamaicensis* and five *P. macrotis*. These observations suggest that bats use this cave as alternate roost.

### Hoctún Cave

Location.--1 km S Hoctún, mun. Hoctún. 20°51'N, 89°12'W.  
INEGI 16 BU 710 080.

This cave is located in the south extreme of the town of Hoctún on a henequen (*Agave furcroides*) plantation. The entrance is a small ground hole of about 2 m in diameter that connects to a single conduit passage with a gentle downward slope (Figure 3.7). There is a medium-sized cenote (underground pool) at the end of the tunnel. Total length

of the cave is 160 m, and the maximum depth of the above-the-water section is 22 m.

The bedrock is fine-grained limestone with few speleothems (straw stalactites, almost no stalagmites). In some areas there is travertine with sculpturing (pendants). Most of the cave is covered by breakdown (large collapsed rocks) with little fine sediment. Human products (metal cans, wax candles, plastic bags, even shoes) are scattered everywhere along the tunnel.

On 2 March ambient conditions were as follows. In the twilight zone at about 1020 h: temperature 28.9 °C, relative humidity 84%; in the deepest section at about 1130 h: 27.5 °C and 96%. On 16 July at the twilight zone at 1044 h: 29.5 °C and 89%; at the deepest part at 1143 h: 27.5 °C and 96%.

The bat fauna of the Cueva de Hoctún was reported by Jones et al. (1973) and by Birney et al. (1974). I found the same species reported in these papers: *P. davyi*, *P. parnellii*, *M. megalophylla*, *D. rotundus*, *D. ecaudata*, and *N. stramineus*. Additionally, in all visits I observed a sizable (>500 individuals) colony of *M. keaysi*. I found the skeleton of an opossum (*D. marsupialis*). The aquatic fauna of the cave has been studied in some detail (Pearse 1938, Reddell 1977, 1981) and includes several troglobitic fish and crustaceans. On 16 July I observed a blind fish (*Ophisternon infernalis*); Hoctún is the type locality of this strange animal (Hubbs, 1938).

The cave is used by the local people as a recreational site. Many people go to the cave to bath in the cenote, especially during the dry season (December to May). Unfortunately, these visitors leave behind a considerable amount of trash. It is surprising that big colonies of bats and conspicuous populations of fish and crustaceans can occur in this cave despite these visitors. A well-designed educational campaign could contribute very much to the conservation of this ecosystem.

#### Cave of the Ruins of Kabah

Location.--Archeological zone of Kabah, mun. Santa Elena.

20°15'N, 89°39'W, elev. 60 m. INEGI 16 Q BT 234 408.

This small cave is probably an artificial hole carved by the inhabitants of the ancient city of Kabah to extract building material. It is located in front of the Palace, the main building of the archeological site. The external area has been adapted for tourism, so the only vegetation around is grass and thorny shrubs. The entrance is on a shallow doline (4 m diameter, <2 m depth) that continues in a tunnel <10 m long). The walls and ceiling are formed by compacted limestone particles with no outstanding features. On 27 April temperature and relative humidity at 1250 h were 27.0 °C and 89%. On 23 July conditions at 1205 h were 28.0 °C and 89% relative humidity. This hole contains a small group (about 22 individuals) of *P. macrotis*.

### Cave of the Ruins of Mayapán

Location.-- Ruins of Mayapán, 2 km S Telchaquillo, mun.

Tecoh. 20°38'N, 89°27'W, elev. 20 m. INEGI 16Q BT 436 829.

The cave is located within the archaeological zone of Mayapán, where the vegetation is second-growth dry forest dominated by thorny shrubs and trees (Leguminosae). Total length of the explored section is 160 m and total depth is 31.3 m (Figure 3.8). The entrance is a collapse doline of about 7 m in diameter and about four meters in depth. The first section of the cave is a linear to sinuous chamber of 35 m in length with a gentle downward slope. A short (5 m) and narrow passage connects to the main chamber that is divided into two short passages. Maximum height is about 4.5 m in the first passage and the minimum is <60 cm in the narrow tunnel. The main chamber has a diameter of about 20 m and is about 3.5 m in height.

Ceilings and walls are formed by exposed coquina with distinct shells. Speleothems are rare, except at the end of the passages where some straw stalactites cover the ceiling. Big (>2 m) rocks cover the floor in most sites. A shallow layer of guano is present at the end of the N and S passages. There is a small cenote at the end of the N passage.

On March 9 the temperature varied from 26.1 °C at the first tunnel to 28.3 °C at the main chamber. Relative

humidity varied from 76% at the entrance at 1224 h to 92% at the end of the N passage at 1414 h. On August 17 temperature varied from 26.0 °C near the entrance at 1201 h to 27.5 °C at the end of the N passage at 1000 h. Relative humidity varied from 92% close to the entrance to 100% at the north passage.

Birney et al. (1974) reported a colony of mustached bats (*P. parnellii*) from this cave. In all visits I found groups of these bats in the solution holes of the deepest section of the cave, where long-legged bats (*N. stramineus*) also roosted. Near the entrance and in the holes in open doline I routinely observed small groups of *A. jamaicensis*, and on 15 August 1989 I captured an immature male *P. macrotis* that was roosting singly in a small crack of the open doline.

The cave was visited by Stephens (1843) who found some human bones and pottery. Reddell (1977, 1982) reported the system as Chac Sikiin north and south. The access to the cave is limited because it is located within an archaeological zone, but I found evidence of repeated visits (pieces of metal cans, wax candles, and graffiti from a local group of Boy Scouts).

### Tzab-Nah Cave

Location.--1 km S Tecoh, mun. Tecoh. 20°44'N, 89°28'W.

INEGI 16Q BT 425 945.

This cave system is located in the vicinity of the town of Tecoh, <100 m from the local junior high school. The vegetation is very disturbed tropical dry forest with some isolated *Ficus* and *Ceiba* trees. The system is accessed through a small (10 m diameter, 1.5 m deep) doline that connects to the first room of the cave (Figure 3.9). In the center of the whole system there is a big collapse doline (about 20 by 25 m, and 10 m deep) from which several tunnels radiate. The bedrock is coarse coquina with conspicuous fossil valves of pelecypods. The system is a complex maze of short to medium-sized tunnels that anastomoses in three dimensions. I conducted my sampling in three of these tunnels.

The first section studied is the room that connects directly to the access doline. It is a rectangular chamber that receives dim light from several openings. The ceiling is eroded and presents a few straw stalactites and some solution holes that are used as roosting sites by bats. The floor is covered mostly by breakdown material with little soft sediment and almost no guano. On 12 March at about 1000 h, temperature varied from 25.0 to 26.1 °C and relative humidity varied from 79 to 87%. On 19 August at about 0830 h temperature was 27.0 °C and relative humidity was 92%.

In this section I routinely captured *P. macrotis*, *M. megalophylla*, and *D. ecaudata*. On 19 August I found a group of three woolly false vampire bats (*Chrotopterus auritus*) hanging from a shallow solution hole about 25 m from the entrance. They were a female with a male juvenile and other individual (presumably a male) that escaped.

The second section studied is a tunnel in the E part of the system. It is an angulate to sinuous passage (150 m long) that terminates by sediment choking. The walls and ceiling present diverse features including eroded coquina, solution holes, flowstones, pendants, and straw stalactites. The whole tunnel is covered with fine sediment, dry near the doline, more humid near the end section. On 20 July temperature varied from 24.5 °C near the central doline at 1222 h to 27.0 °C at the end of the tunnel at 1056 h. Relative humidity varied from 96% near the doline to 100% at the end. On 19 August conditions were: near the doline at 1122 h, 25.0 °C and 92% relative humidity; at the end of the tunnel at 0910 27.0 °C and 96% relative humidity.

The solution holes near the end of the tunnel are occupied by small (<20 individuals) groups of bats of the species *P. parnellii*, *A. jamaicensis*, and *D. ecaudata*. In one crack in the wall near the doline I found two individuals of *M. keaysi*.

The third section explored is a passage that goes N and continues as a flooded tunnel (not explored). The above-water section is 120 m long. The ceiling and walls present

little ornamentation and consist primarily of eroded coquina, in some places forming solution holes. The floor is exposed bedrock in most parts, with little soft sediment and only traces of bat guano. On 12 March temperature varied from 25.6 °C near the entrance at 1213 h to 27.8 °C in the middle of the tunnel at 1140 h. Relative humidity went from 84% near the entrance to 96% at the middle point. On 20 July temperature varied from 26.0 °C near the entrance at 1346 h to 28.0 °C at the end of the tunnel at 1305 h. Relative humidity varied from 92% to 100%. On 19 August conditions were identical as those of 20 July.

In the middle of this tunnel is a natural bridge (artificially reinforced) that crosses a wide (about 10 m) body of underground water. A colony of *A. jamaicensis* roosts beneath this bridge. In the more interior sections, I found small (< 100) groups of *P. parnellii*, *N. stramineus* and *G. soricina*. On 12 March I observed a blind fish (*Typhliasina pearsei*) in the pond at the end of the tunnel.

Grutas Tzab-Nah are well-known among natives, who used to visit the N tunnel aided by wax candles and nylon fishing line. The caves are advertised in tourist maps, but apparently there is little visitation by non-locals. I found some trash dumped in one of the flooded tunnels. This tunnel goes in the direction of a spring that locals use as a source of water, and it is very likely that the two systems are in fact connected.

Cave of Acanceh

Location.--600 m SE Acanceh, mun. Acanceh. 20°48'N,  
89°27'W. INEGI 16Q BU 450 030

This a small cave located in a private lot within the town of Acanceh. The area is mostly urbanized or covered with cultivated fields, but three big *Ficus* trees grow just above the cave. The entrance is through a shallow doline (2 m diameter, 1.15 m depth) that opens into a tunnel with a steep slope ( $>15^\circ$ ) that continues into a single, narrow passage. The ceiling and walls are formed mostly by bedrock with some solution holes, but no speleothems. The floor is covered with breakdown rocks and with guano and seeds dropped by a large ( $>100$  individuals) colony of *Artibeus jamaicensis*. On 12 March at about 1400 h, temperature varied from 26.7 to 27.8 °C and relative humidity ranged from 88 to 96%. The cave is inhabited by the colony of *A. jamaicensis* and a small group of *M. keaysi*. The entrance doline is used by neighbors to dump garbage, but apparently people do not enter the cave because they fear the colony of *A. jamaicensis* that is very close to the entrance.

Kabahchén Cave

Location.--200 m SW the Plaza at Maní, mun. Maní. 20°23'N,  
89°24'W, elev. 20 m. INEGI Q BT 500 559.

The cave is located within the town of Maní, and has been modified with artificial stairs and a protective wall. The cave is a system of several sinuous tunnels that connect

three collapse dolines, one of which is the entrance (Figure 3.10). Total length of the tunnels included in this study is 159 m. The W tunnel has a gentle upward slope and ends in what seems to be an artificial wall. My local guide informed me that archaeologists have made excavations to find out if this wall protects a hidden chamber, but have not been successful. The W passage is a sinuous tunnel that connects two of the sinkholes.

The ceiling and walls of the W tunnel are formed mainly by eroded limestone, in some areas forming a spongework pattern. Near the entrance are some flowstones. The floor is exposed bedrock and breakdown, with very little soft sediment. On 12 May temperature and relative humidity varied from 25.0 °C and 92% near the entrance at 1050 h to 27.0 °C and 96% at the end of the tunnel at 1153 h. On 25 July conditions were 26.0 °C and 89% relative humidity near the entrance at 1206 h and 27.5 °C and 96% R.H. at the end of the tunnel at 1135 h.

The W tunnel shows more diversity of formations. There is continuous flow of water on several parts of the ceiling and walls. The substrate forms a spongework pattern combined with incipient straw stalactites and travertine. The floor is covered by breakdown rocks with little soft sediment. Some sections are covered by travertine, forming rimstone dams. I observed some "cave pearls" (concretions) near one of those dams. On 12 May temperature ranged from 24.5 to 25.5 °C at about 1030 h; relative humidity varied

from 96 to 100%. On 25 July, I found identical conditions at about 1100 h.

The cave is inhabited by swallows (*S. ruficollis*). The bat fauna is poor and consists of a small group of *G. soricina* and occasionally some *A. jamaicensis*. The ponds at the bottom of two of the sinkholes contain an abundant fauna of cave crayfish (*Creaseria morleyi*).

The cave is located in the historical site where Diego de Landa burned all known documents on the Mayan culture in the XVI century. The wells inside the cave were for several centuries the main source of water for Maní. Today, many local people still gather in this area to chat or to remember past times. Despite the high level of visitation, the area is comparatively clean.

### Actun Sitz

Location.--1 km SW Oxkutzcab. 20°18'N, 89°25'W, elev. 60 m.

INEGI 16 Q BT 469 458.

Actun Sitz ("cool cave") is located near to a church locally known as La Ermita. The single entrance is a small (6 m diameter) ground hole located near private properties with cultivated fields. The explored section begins with a wide (>15 m) chamber with a steep slope (in some places >30°) that gradually narrows until forming a tunnel <2 m wide. This section has a total horizontal development of 130 m and a maximum depth of 27.8 m below ground level. The ceiling in the big chamber is mostly exposed bedrock but in

several places large stalactites and columns can be found, and the area is covered with travertine. In the narrow tunnel travertine covers most of the ceiling and walls and combines with straw stalactites, helictites, and other crystalline forms. The floor in the big room is mostly covered by big boulders with almost no fine sediment. In the tunnel, soft sediment accumulates over travertine formations (rimstone dams) and partially covers the small stalagmites.

On May 12 temperature varied from 27.0 °C near the entrance at 1422 h to 28.5 °C at the end of the tunnel at 1302 h. Relative humidity ranged from 92 to 100%. On 25 July at about 1330 h, conditions were 26.5 to 28.0 °C and 96 to 100% relative humidity. On 18 August at about 1030 h, conditions were 27.0 to 28.0 °C and 96 to 100% R.H. On the last date at 1140 h, the exterior was at 30.0 °C with 75% relative humidity.

The cave is used frequently by swallows (*S. ruficollis*). Bats are not abundant, and I observed only some individuals of *P. parnellii* and *G. soricina*. Additionally, I found a skull of *M. megalophylla*.

This fauna of this cave was investigated by Pearse (1938). Locals visit frequently the cave, as indicated by graffiti and numerous nylon and natural-fiber cords left as guiding lines. Most of the straw stalactites are broken, and crystals on the walls are clearly incomplete.

Actun On

Location.--1.5 km S Oxkutzcab, mun. Oxkutzcab. 20°17'N,  
89°25'W, elev. 50 m. INEGI 16 Q BT 472 452.

Actun On ("The cave of the avocado") is located on the outskirts of Oxkutzcab, on the NE slope of the Sierrita de Ticul. The system consists of a big (about 20 m in diameter) collapse doline with several small passages in its walls. I concentrated on a short tunnel on the NE wall of the sinkhole. This passage has an entrance 4 m wide and 2 m high that connects to a narrow (<2 m) linear passage of about 15 m. The bedrock is limestone with a reddish color (Fe<sup>+++</sup> ions), in some parts covered with calcite crystals and travertine. The floor is covered with breakdown material and bat guano. On 12 May at 1451 h temperature was 30.0 °C and relative humidity was 67%. On 27 July at 1125 and under cloudy conditions, temperature was 27.5 °C and relative humidity was 85%. The tunnel contains a small (about 25 individuals) colony of *P. macrotis*.

Actun Lol-Tun

Location.--7 km SW Oxkutzcab, mun. Oxkutzcab. 20°15'N,  
89°28'W, elev. 90 m. INEGI 16Q BT 433 414.

Actun Lol-Tun ("where rock turned into flower") is the most famous cave in the Sierrita de Ticul. It is a complex system of passages and spectacular sinkholes in an area of about 150,000 m<sup>2</sup>.

A tourist trail of a little more than 500 m is artificially illuminated. Understandably, the trail goes through the biggest chambers and tunnels where the spectacular formations are located. The entrance and the exit are located in big sinkholes located at opposite sides of the system. In all sites along the trail the passages are wide and high enough to allow easy walking. The walls and ceiling present a great diversity of forms. The bedrock is exposed in some areas and the walls and ceiling are patched by erosion and solution forms (holes, ripples, pendants). In other parts, the whole surface is covered with travertine and speleothems (stalactites, draperies, flow sheets). In most of the trail the floor is covered with fine sediment that has been compacted by the passage of people. Additionally, speleothems such as stalagmites, columns, and rimstone dams can be found in some areas. Near the entrances there are large accumulations of collapse material and albarradas (artificially arranged rocks).

Many other passages are not open to the public. These areas are generally narrower and with more running water than the tourist trail. To access many of them it is necessary to crawl through very narrow tunnels.

The sinkholes are used by groups of swallows (*S. ruficollis*), by mot-mots (*E. superciliosa*) and by barn owls (*T. alba*). During my visits to the area, I documented the presence of ten species of bats (*P. macrotis*, *P. davyi*, *P. parnellii*, *M. megalophylla*, *G. soricina*, *A. jamaicensis*, *D.*

*rotundus*, *D. ecaudata*, *N. stramineus*, and *M. keaysi*).

During night netting sessions in the doline at the main entrance, another five species have been collected (*Mimon cozumelae*, *Carollia perspicillata*, *Sturnira lilium*, *Dermanura phaeotis*, and *Lasiurus intermedius*; specimens of these species were collected during this study or by a party from the National University of México in 1982 (Arita, field notes). Lol-Tún is among the Mexican caves with highest species richness (Chapter 4), and if the five additional species are included, it would be the top cave in the list.

The fauna of Lol-Tún was examined by Pearse (1938), and subsequently other biological investigations have been carried out in the area (Reddell, 1977, 1981). Vertebrate remains accumulated in cave deposits in Actun Lol-Tún have been studied in some detail (Alvarez, 1982; Arroyo-Cabrales and Alvarez, 1990; Hatt et al., 1953)

Actun Lol-Tún has been in use by humans at least since the Preclassic Mayan era (1,200-600 B.C., González-L., 1986; INAH 1978). The archeological sequence of pottery styles spans without interruption from the Preclassic to the early years of the Spanish Viceroyalty (XVI Century). Lithic material found in association with fossil bones of extinct mammals suggest a much earlier occupation of the cave (about 5,500 B.C.). During the Caste War of the XIX Century, Lol-Tún was used as a refuge and probably as a garrison by rebel indians. Archeological exploration of the area goes back at least to the 1880s, when Teoberto Maler made some

explorations and Edward H. Thompson directed the Peabody Museum surveys of the cave.

Today, Lol-Tún is an important tourist site. Because of its unique geological and historical richness, and because of its nearness to the Uxmal site, Lol-Tún attracts thousands of tourists each year.

#### Actun Spukil (Cave of Calcehtok)

Location.--2 km S Calcehtok, mun. Opichén. 20°33'N, 89°55'W, elev. 80 m. INEGI 16Q AT 963 750.

Aktun Spukil (also spelled Xpukil, "cave of mice") is a large and complex system of passages that attracts many spelunkers and some tourists to the otherwise underdeveloped area of Calcehtok. The main entrance is through a collapse doline of about 15 m in diameter and about 10 m in depth. There is an artificial ladder to facilitate the access to tourists. During 1989 a swarm of africanized bees nested on one of the walls of the doline and inhibited access to the cave. Because of this difficulty, the cave was visited for this project only after the swarm was removed by personnel of the Mexican Ministry of Agriculture (July 1990).

The entrance doline is covered with second-growth vegetation dominated by Leguminosaeae (*Acacia* and *Caesalpinia*) and bananas (*Musa paradisiaca*). A short passage connects with a bigger doline (25 to 30 m deep). All these sections are fully illuminated by daylight. The bedrock is limestone with ferric (Fe<sup>+++</sup>) minerals. The

ceiling and walls present a spongework pattern left by differential erosion; in some parts there are big pendants (elongated hanging structures created by the dissolution of the surrounding bedrock). The floor is covered by large boulders covered by fine sediment and guano of swallows (*S. ruficollis*) and bats. The dolines are used by birds, especially by mot-mots (*E. superciliosa*).

Contrary to the majority of the caves in the area, Actun Spukil is a system with three-dimensional complexity, meaning that besides mazes of tunnels it has also complicated pits and vertical shafts. The walls and ceiling have a high diversity of forms (spongework pattern, pendants, stalactites, sheets, draperies, etc.). The floor is mostly formed by bedrock or breakdown rocks, but in some places there is soft sediment, mud, and bat guano. On 28 July I took readings of temperature and humidity at several locations in the interior of the cave. Temperature ranged from 26.0 to 29.5 °C and relative humidity varied from 92 to 96%.

This cave has been included in several biological surveys (Birney et al., 1984; Hatt, 1938; Hatt and Villa, 1950; Hatt et al., 1953; Pearse, 1938; Reddell, 1977, 1981; Villa-R., 1967). During the visit in July, I observed colonies of *P. parnellii*, *G. soricina*, *A. jamaicensis*, and *N. stramineus*. Night netting at the entrance revealed the presence of four additional species (*M. megalophylla*, *P. davyi*, *D. rotundus*, and *D. ecaudata*), and Villa-R. (1967)

reported also *P. macrotis* from this cave. The sinkholes provide a special habitat for some animals; particularly abundant are the mice (*Peromyscus yucatanensis* and *O. phyllotis*) that give the name to the cave.

The cave is an important archeological site. Evidence of use by ancient Mayans, such as pottery, water-collecting devices, and stone carvings, can be found even in the deepest parts of the cave. The area is visited by a moderate number of tourists, but the state government is considering several proposals to develop the zone to attract a larger number of visitors.

#### Classification of the Caves

In this section I provide criteria for classifying the caves of Yucatán. I chose these criteria with the idea of using them in the analysis of habitat for bats (Chapter 6) and for invertebrates (Chapter 7). The objective of this section is not to provide a single classification scheme for all caves. Rather, the idea is to identify those characteristics of the caves that might be key factors determining the spatial distribution of cave animals. Because of the heterogeneous character of the many criteria selected, a single classification system would lead to inevitably subjective decisions about the relative weight of the different factors.

### Topology of Yucatán Caves

Surfaces arranged in a three-dimensional space can be described using a branch of geometry called topology (Weeks, 1985). Topologists are interested only in the continuity and curvature of the surfaces, and completely ignore such parameters as size and shape of the objects. Because caves can be defined by describing their inner surfaces (the continuum of their ceiling, walls, and floor), topology can provide analytical tools to describe them.

In topology, surfaces are classified by their continuity and curvature, regardless of their size and shape. Objects of genus 0 are represented by the surface of a hollow sphere (Figure 3.11.A). Objects of genus 1 are represented by the torus (the surface of a doughnut-shaped object, Figure 3.11.B); genus 2 is represented by a two-holed doughnut (a "pretzel", Figure 3.11.C), and so on. The surface (ceiling, walls, and floor) of simple caves can be modeled as an object of genus 0 (imagine the cave as the interior surface of the hollow sphere in Figure 3.11.A). Caves with one loop (a tunnel with two connections to the same site) are objects of genus 1, caves with two loops belong to genus 2, and so on. Under this criterion, most Yucatán caves are of genus 0.

Discontinuities on a surface are called ends. Ends are equivalent to entrances in the topological cave analogy. For example, the sphere in Figure 3.11.D represents a cave

with a single entrance, Figure 3.11.E represents a cave with two entrances connected by a tunnel, and Figure 3.11.F represents a cave with one passage forming a loop around a single entrance. Because only a few of the caves under study belong to topological genera  $>0$ , the number of entrances (topological ends) constitutes a better initial criterion in the classification of Yucatán caves.

I relaxed the rules of topology in this adaptation for caves. In topology, both caves pictured in Figure 3.12 are identical (objects of genus 1 with one end) because by performing simple deformations (with no cutting and pasting) one could transform one into the other. To add more realism to the classification, I included information on the relative position of entrances and tunnels. I defined an arm of a cave as any passage or series of passages that is limited by an entrance or by the end (not in the topological sense) of a tunnel. I limited the definition to passages at least 10 m long. Arms are open if they have entrances at both extremes or blind if one extreme is closed. (A third case, a closed arm with no connection to the exterior, can be ignored for the purpose of this study.) Caves can be classified according to their number of entrances, open arms, and blind arms.

Different air circulation patterns occur in open and blind cave passages. Geiger (1966) considered blind passages as static caves, meaning that little air circulation occurs in this type of passage. He used the

term dynamic for caves or passages with more than one entrance, showing that air circulation is much more active in dynamic than in static caves. Wigley and Brown (1976) and Tuttle and Stevenson (1976) have shown that several physical phenomena can produce air circulation even in blind passages, but they acknowledged that the chimney effect that generates air movement in open tunnels is the dominant phenomenon determining the interchange of air between the cave and the exterior. Because this interchange is the ultimate determinant of ambient conditions in the interior of caves, it is reasonable to distinguish between blind and open arms in caves.

Seventy-five percent of the caves in the study area have only one entrance (27 of 36, Table 3.1). Six (17%) have two entrances, and only three (Kabahchén Cave, Actun Lol-Tún, and Actun Spukil) have >2. The frequency of cave entrances in several regions fits the Poisson statistical distribution (Curl, 1958; White, 1988). My sample size is too small for a statistical test, but apparently there is an excess of single-entrance caves to fit a Poisson distribution.

Twenty-nine (80%) of the caves have only one arm (Table 3.1). In only two cases this arm is an open tunnel (with two entrances) and in 27 caves the single arm is a blind passage. Two of the caves (Actun Oxpehol and Ramonal y Naranja Cave) have two arms, one open and one blind. Only five (14%) of the caves have >2 arms. Because the concept

of arm is new, a comparison of the caves of Yucatán with other sites in terms of their number of arms is not possible.

### Morphometrics

I used the data from the surveying procedure to calculate several morphometric parameters for the caves. Different morphometric and classification arrangements have been used by geologists (Dublyansky et al., 1987; Jennings, 1985; White, 1988). Most of these systems are designed to describe geological processes, however, and are not quite adequate for a description of caves from a biological point of view. I chose those parameters that best describe the caves as habitat for bats and invertebrates. A description of relevant parameters follows.

$s_i$ : survey and collecting stations (from  $s_0$  to  $s_n$ ).

$\alpha_i$ : slope angle between  $s_{i-1}$  and  $s_i$ .

$\theta_i$ : bearing from  $s_{i-1}$  to  $s_i$ .

$d_i$ : passage distance between  $s_{i-1}$  and  $s_i$ . In most cases  $d_i$  was standardized to 10 m.

$x_i$ : horizontal distance between  $s_{i-1}$  and  $s_i$ .  $x_i = d_i * \cos \alpha_i$ .

$y_i$ : vertical distance between  $s_{i-1}$  and  $s_i$ .  $y_i = d_i * \sin \alpha_i$ .

L: extent of a passage.  $L = \sum_{i=0}^n d_i$ . This is the real

distance that one has to travel to get from  $s_i$  to  $s_n$ .

$L'$ : projected extent.  $L' = \sum_{i=0}^n x_i$ . This is the distance from  $s_i$  to  $s_n$  as seen in a map.

$L_k$ : projected maximum horizontal distance between two points of the cave.

$w_i$ : width of the passage at  $s_i$ , measured at right angle to the survey line.

$w_0$ : width at the entrance of the cave.

$w_{\text{mean}}$ : Average width of a passage or cave.

$$w_{\text{mean}} = 1/(n+1) \sum_{i=0}^n w_i$$

$W_k$ : maximum projected width. Maximum horizontal distance between two points at right angle to  $L_k$ .

$h_i$ : height at  $s_i$ .

$h_0$ : height at the entrance.

$h_{\text{mean}}$ : average height of the passage.

$$h_{\text{mean}} = 1/(n+1) \sum_{i=0}^n h_i$$

$H$ : depth/height of the cave. Its magnitude is equal to the vertical distance between the entrance and the highest or lowest point of the cave.

$H_k$ : amplitude of the cave. It is equal to the vertical distance between the highest and the lowest points in the cave.

$C_v$ : coefficient of verticality.  $C_v = H_k/L_k$ . This parameter measures the vertical extent relative to the horizontal extent.

ID: index of development.  $ID = L'/L_k$ . This index is a measurement of complexity of passages. A simple linear passage would have an  $ID = 1.0$ , whereas a convoluted passage would have  $ID > 1.0$ .

Caves in Yucatán are comparatively small. Twenty-three (64%) of the caves in my sample have  $L' < 100$  m, and only Actun Lol-Tún has an extent  $> 1,000$  m. In contrast, the list compiled by Chabert (1977, in White, 1988) of the longest caves in the world includes 617 systems with extents  $> 3$  km, and the Mammoth Cave-Flint Ridge System in Kentucky extends for  $> 500$  km (White, 1988). The frequency distribution of cave extents is a variable determined by the karst characteristics of each area (Curl, 1966; White, 1988) and generally fits a lognormal distribution. A novel approach to the description of this distribution is Curl's (1986) formula:

$$N(l) = N(l_0) * (l/l_0)^{-v},$$

where  $N(l)$  is the proportion of caves with extent greater than  $l$ ,  $l_0$  is the shortest length for the distribution, and  $v$  is the fractal dimension as defined by Mandelbrot (1983). The caves of Yucatán fit Curl's (1986) formula, and the fractal dimension of the distribution of lengths, as estimated by the slope of  $\log N(l)$  as a function of  $\log (l/l_0)$ , is 0.66 (Figure 3.13). The fractal approach is a recent innovation and its interpretation and implications for the geomorphological and ecological study of caves are yet to be explored.

Most caves have simple development as indicated by the low values of the index of development (Table 3.1, Figure 3.14). The mean value for this parameter (1.40,  $s^2 = 0.25$ ,  $n = 34$ ) is close to the averages reported for karst regions in Europe (1.35 for France, 1.33 for Crimea, Dublyansky et al., 1987). Observed values for Yucatán varied from 1.00 or 1.01 for simple tunnels (Actun On, Doña Blanca Cave) to 3.12 for the complex system of tunnels of Actun Lol-Tún (Table 3.1).

The amplitude of the caves of Yucatán is in all cases <50 m (Table 3.1). In contrast, the Sistema Huautla in Oaxaca, México, has a depth of 1225 m (White, 1988). Most caves in Yucatán had a coefficient of verticality between 0.1 and 1.0 (mean = 0.32,  $s^2 = 0.11$ ,  $n = 34$ , Figure 3.15), indicating that in general the caves of Yucatán are more developed horizontally than vertically.

Both total extent and depth of explorable sections of Yucatán caves are limited by the closeness of the water table to the surface. It is possible that some of the many flooded caves in Yucatán extend for several kilometers. This speculation, however, is hardly relevant for the terrestrial animals under study.

### Ambient Conditions

Caves in Yucatán are in general very hot and humid (Figure 3.16). In all caves, temperature and relative humidity near entrances are variable and affected by

external weather, whereas conditions in the deep sections are more stable and independent of external climate (Culver, 1982; Howarth, 1980; Poulson and White, 1969; Tuttle and Stevenson, 1976; Wigley and Brown, 1976). In the caves of Yucatán, ambient conditions in the deepest part of the caves showed almost no seasonal variation. Differences in temperature between rainy- and dry-season measurements were always  $<1.5$  °C and in most cases of only a few decimals of °C. The average ambient temperature at the deepest part of the caves ( $26.9$  °C,  $s^2 = 2.4$  °C,  $n = 30$  caves) is very close to the mean annual surface temperature (MAST) in the area ( $27.0$  °C for Oxkutzcab,  $26.7$  °C for Tekax, García, 1981), as predicted by models of thermal equilibrium (Cropley, 1965; Culver, 1982; Tuttle and Stevenson, 1976).

Temperature at the deepest part varied according to the morphology of the caves. In caves with wide openings and predominantly negative slopes--with the entrance at a higher position relative to the end of the cave--mean ambient temperature was typically lower than the MAST (e.g.,  $24.0$  °C in Roble Cave,  $24.3$  °C in Iguana Cave,  $24.1$  °C in Actun Chac-Xix). In contrast, tunnels with a positive slope normally showed mean temperatures higher than the MAST (e.g.,  $30.0$  °C in Bat Cave). Caves with narrow entrances or with constrictions tended to have temperatures close to the MAST (e.g.,  $27.5$  °C in Hochtún Cave,  $27.9$  °C in the Cave of the Ruins of Mayapán,  $27.2$  °C in Ramonal Cave).

In most caves with an extent >30 m the relative humidity in the deepest section was always >85%. Exceptions were caves with wide openings (e.g., Roble Cave, 84%) or with more than one entrance (e.g., Ramonal y Naranja Cave, 81.5%). In small caves, relative humidity was more variable and considerably lower (e.g., Doña Blanca Cave, 69%; Cave "A", 66%). Constrictions produced noticeable changes in temperature and relative humidity. For example, in the Cave of the Ruins of Mayapán temperature varied from 25.6 to 27.2 °C and relative humidity from 83 to 92% in opposite sides of a 10-meter long constriction. (These sudden changes can be detected in phase diagrams as unusually long lines connecting two points, see for example the diagram for Mayapán in Figure 3.16). In many caves, natural constrictions have been made narrower by artificial barriers (*albarradas*), producing more isolated environments in the deeper parts of these caves. It would be interesting to investigate the possible use of *albarradas* as a management tool to create suitable environments for bats and other cave animals.

### Recapitulation

A useful characterization of the caves of Yucatán has to take into account the different classification criteria discussed in this section. Important geomorphological features are the number and type of entrances and the number and relative position of arms. The relative elevation of

entrances and passages, coupled with the position of internal constrictions, determine the pattern of air circulation in a cave; this pattern in turn fixes the temperature and relative humidity of the deepest passages. Several morphometric parameters can be used to describe the size and general shape of the caves of Yucatán, allowing a comparison with systems of caves in other karst regions.

Table 3.1.--General features and morphometric data for 36 Yucatán caves.

	Entrance s	Type of Entrance	Chamber s	Lk (m)	L' (m)	Hk (m)	I.D.	Cv
Roble Cave	1	open doline, inclined	2	30.2	62.4	18.8	2.07	0.58
Actun Sabak-ha	2	open doline, wall	4	240.3	410.0	30.0	1.71	0.12
Actun Chunkunab	1	rock shelter, wall	1	33.1	33.5	24.7	1.01	0.75
Actun Maas	1	chultún, ground	1	47.7	51.0	34.4	1.07	0.71
Bat Cave	1	direct, wall	3	100.8	160.2	20.0	1.58	0.20
Ramonal Cave	1	chultún, ground	3	83.3	103.2	6.0	1.24	0.07
Flor de Mayo Cave	2	open doline, shallow doline, wall	2	74.0	79.6	9.3	1.08	0.13
Actun Kan-Lol	multiple	wall	1	-	-	-	-	-
Porcupine Cave	1	open doline, wall	1	13.0	15.0	3.5	1.15	0.27

Table 3.1.--Continued.

	Entrance		Type of Entrance	Chamber s	Lk (m)	L' (m)	Hk (m)	I.D.	CV
	s								
Chocantes Cave	1		shallow doline, inclined	>6	183.4	261.6	49.9	1.43	0.27
Actun Oxpehol	2		shallow doline, wall	3	55.5	97.5	12.1	1.76	0.22
Actun X-Maasit	1		open doline, wall	1	40.0	44.1	9.4	1.1	0.24
Actun Dzonot	1		open doline, inclined	1	34.3	36.5	19.8	1.06	0.58
Iguana Cave	1		shallow doline, wall	2	27.5	47.5	15.2	1.73	0.55
Doña Blanca Cave	1		direct, wall	2	14.8	15.0	1.5	1.01	0.10
Actun Kab	1		rock shelter, inclined	1	37.4	42.3	22.1	1.13	0.59
Cinco de Mayo Cave	1		rock shelter, wall	2	55.9	76.7	2.5	1.37	0.04
Cave "A"	1		shallow doline, wall	1	9.9	9.9	3.04	1.00	0.31

Table 3.1.--Continued.

	Entrance		Type of Entrance	Chamber s	Lk (m)	L' (m)	Hk (m)	I.D.	CV
	s								
Ramonal y Naranja	2		open doline, shallow	3	120.6	155.7	11.9	1.29	0.10
Bejucos Cave	1		doline, wall direct, wall	1	32.9	41.2	10.8	1.25	0.33
Actun Tolok	1		shallow doline, wall	1	16.9	17.1	6.1	1.01	0.36
Guayaba y Aguacate	1		open doline, wall	1	21.1	22.5	6.8	1.07	0.32
Cave "B"	1		direct, wall	1	26.3	28.6	4.9	1.09	0.19
Actun Chac-Xix	1		shallow doline, wall	1	16.2	28.5	29.3	1.76	1.81
Aguacate Cave	1		rock shelter, wall	1	18.6	20.6	2.5	1.11	0.13
Zorro Cave	1		rock shelter, wall	1	7.1	8.6	1.5	1.21	0.21
Hoctún Cave	1		direct, ground	1	136.5	147.9	21.7	1.08	0.16

Table 3.1.--Continued

	Entrance s	Type of entrance	Chamber s	Lk (m)	L' (m)	Hk (m)	I.D.	Cv
Ruins of Kabah	1	shallow doline, wall	1	6.9	7.1	1.0	1.03	0.14
Ruins of Mayapán	1	open doline, wall	3	108.3	164.0	31.3	1.51	0.29
Tzab-Nah Cave	2	open doline, shallow dolines, wall	4	157.7	372.5	21.3	2.36	0.13
Acanceh Cave	1	shallow doline, wall	1	26.2	39.4	6.2	1.50	0.24
Kabahchén Cave	3	open doline, wall	4	59.9	158.7	6.9	2.65	0.12
Actun Sitz	1	direct, ground	2	94.1	114.6	27.5	1.22	0.29
Actun On	1	open doline, wall	1	10.0	10.0	1.2	1.00	0.12
Actun Lol-Tún	5	open doline, wall	>10	500	1560	45	3.12	0.09
Actun Spukil	2	open doline, wall	>10	-	-	-	-	-

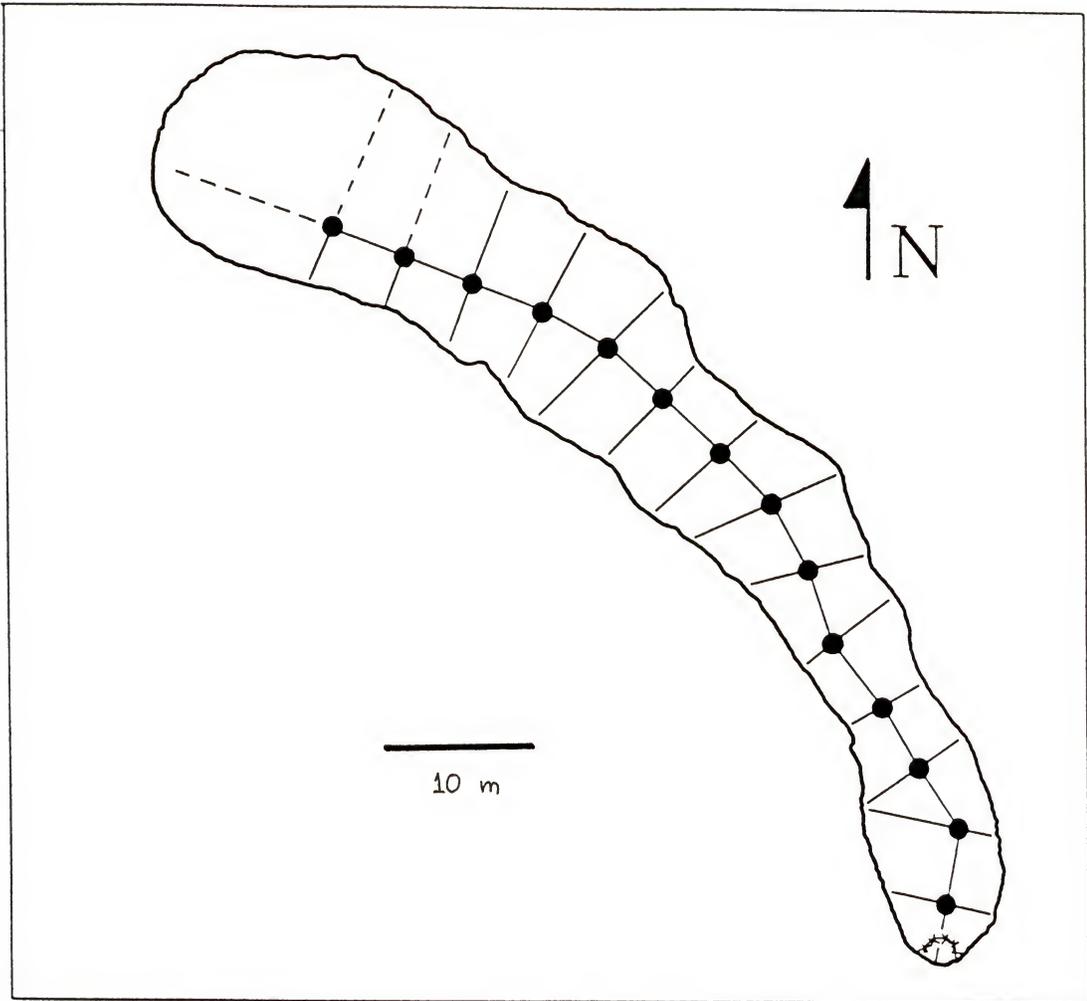


Figure 3.1-- Outline of Hochtún Cave, Hochtún, Yucatán, México, showing the network of stations used for surveying the cave and taking readings of ambient conditions.

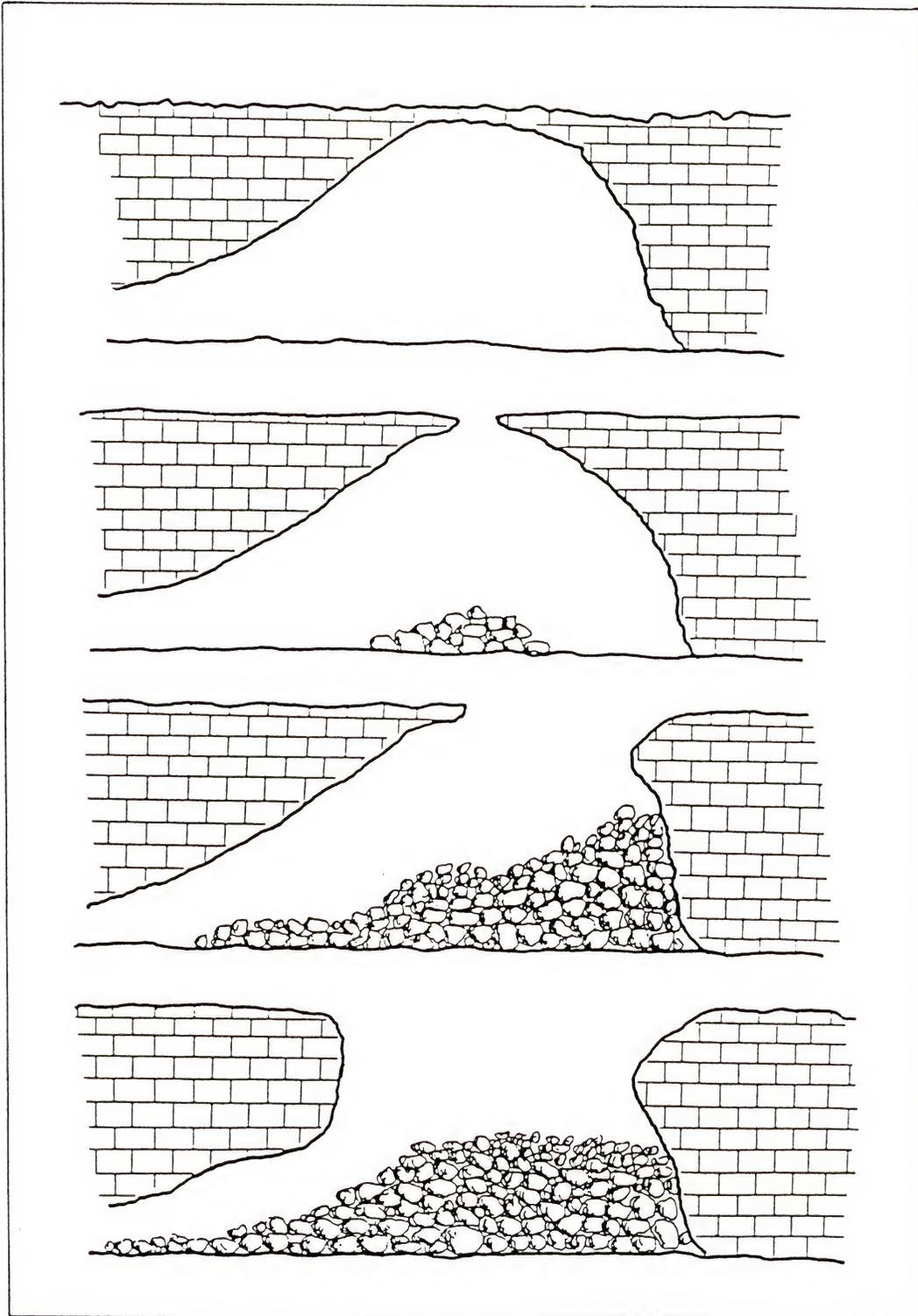


Figure 3.2--Hypothetical evolution of a cave entrance in Yucatán. A: a cavity with no entrance; B: partial collapse of the ceiling, forming a chultún entrance; C: continuing asymmetrical collapse of the ceiling, forming a rock shelter in the left; D: complete collapse of the ceiling, producing an open doline (sinkhole).

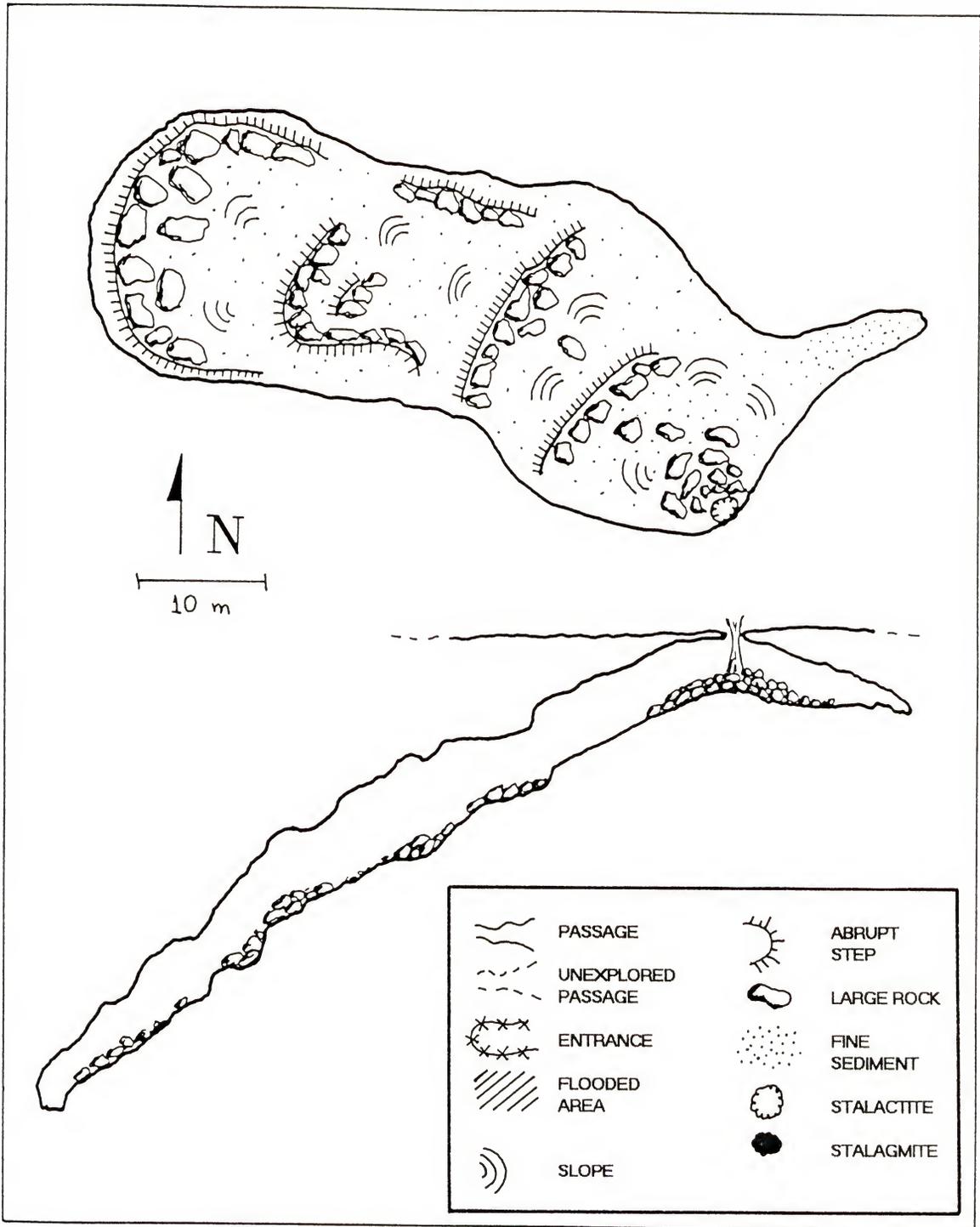


Figure 3.3--Actun Chunkunab, Tekax.

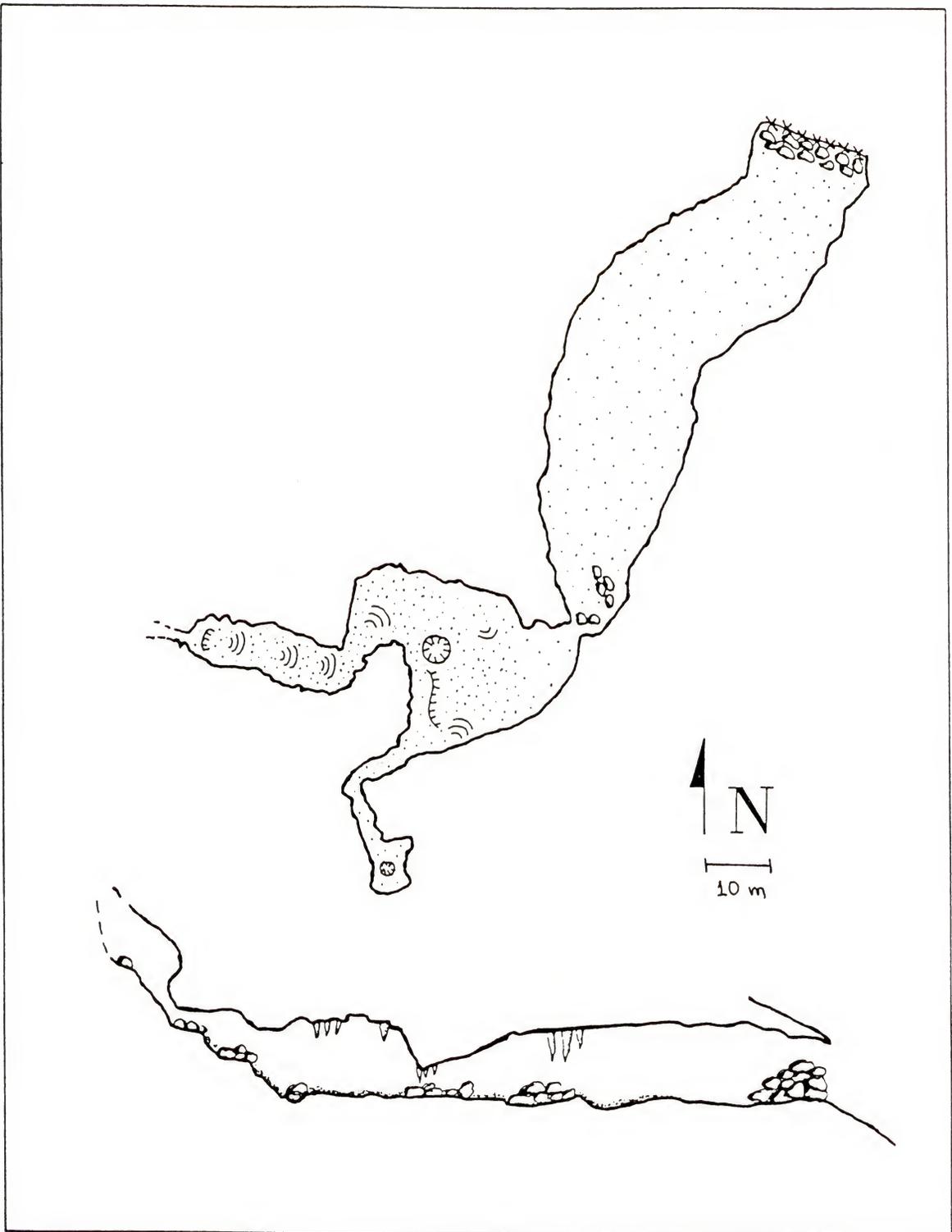


Figure 3.4--Bat Cave, Ticum.

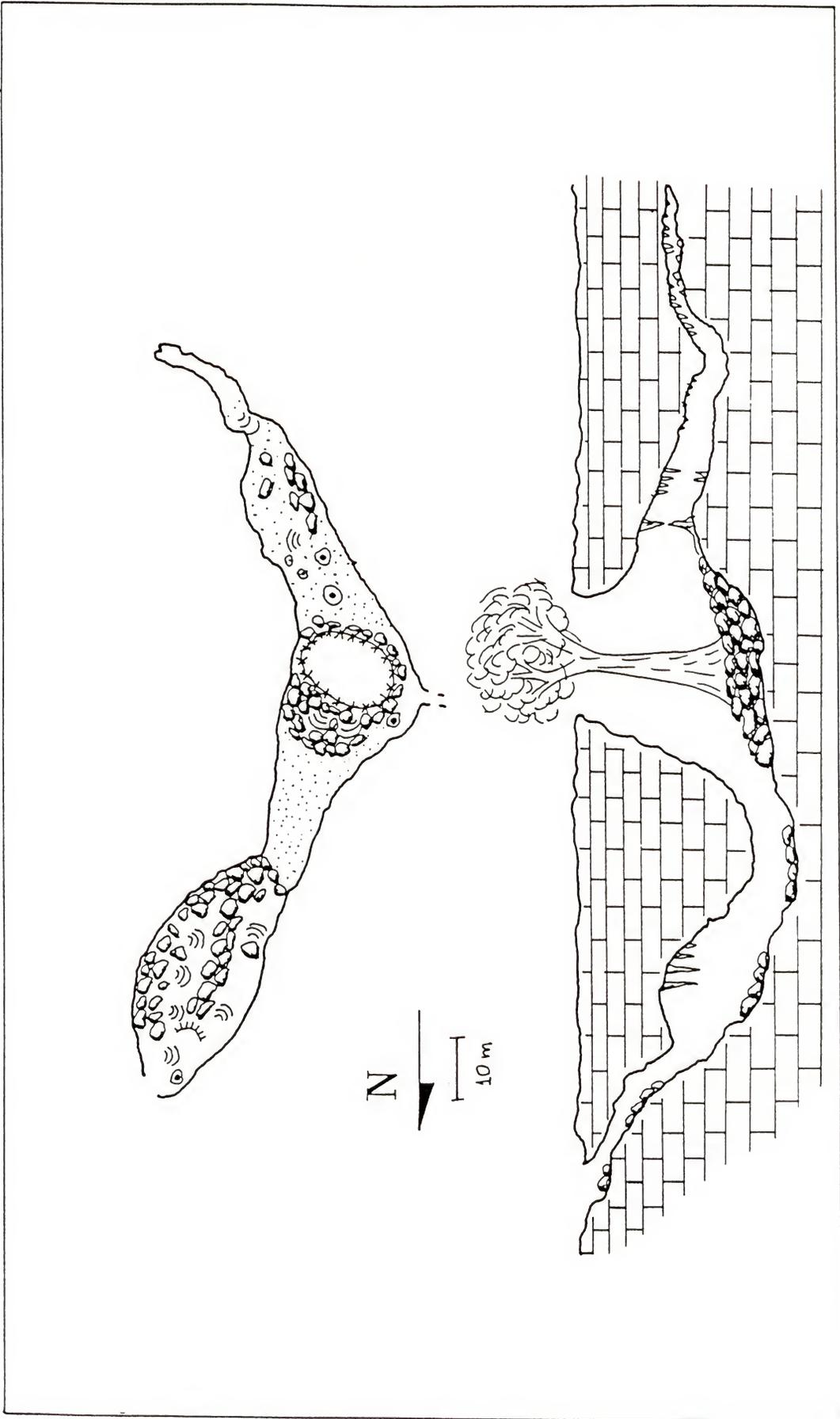


Figure 3.5--Ramonal y Naranja Cave, Tekax.

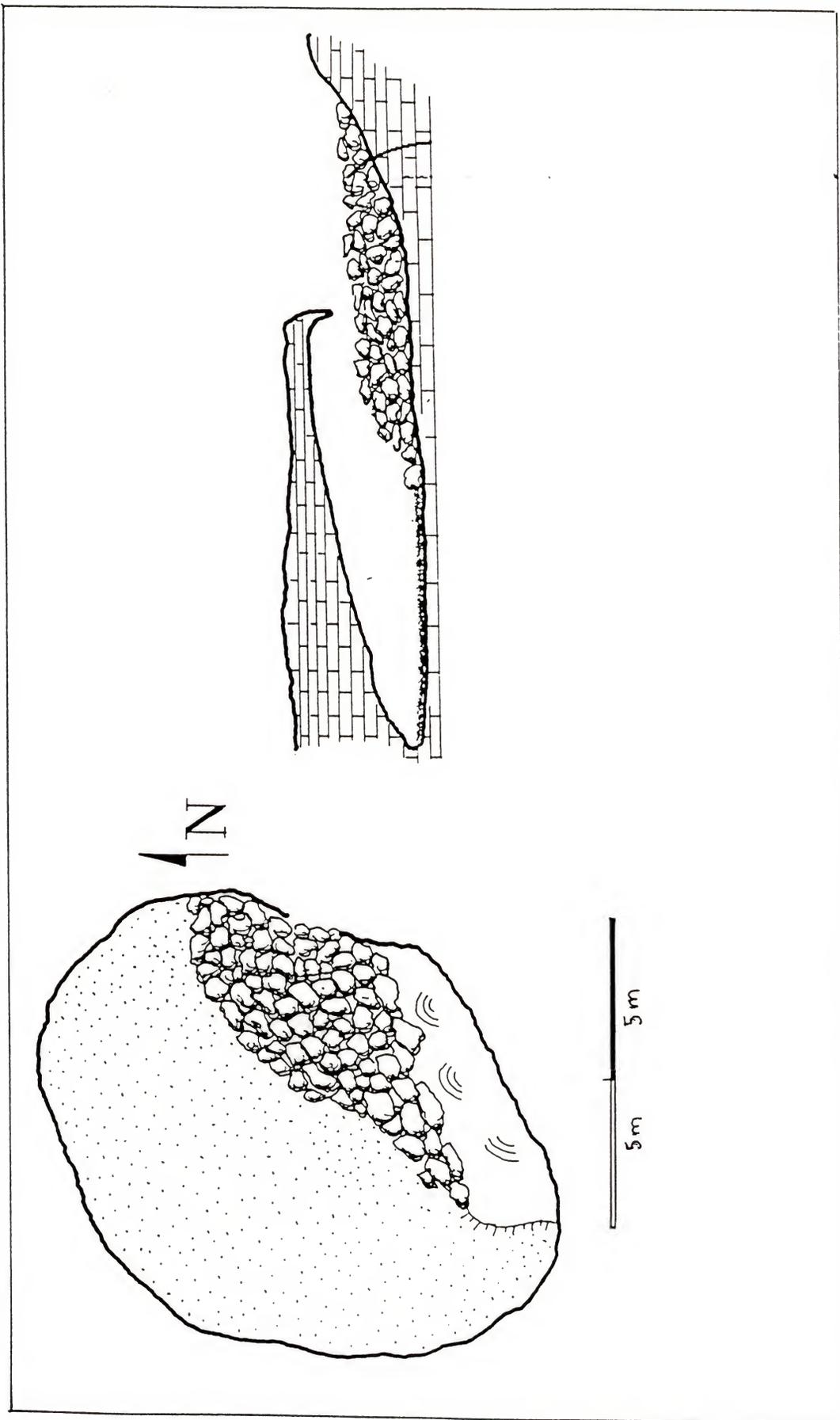


Figure 3.6--Actun Tolok, Tekax.

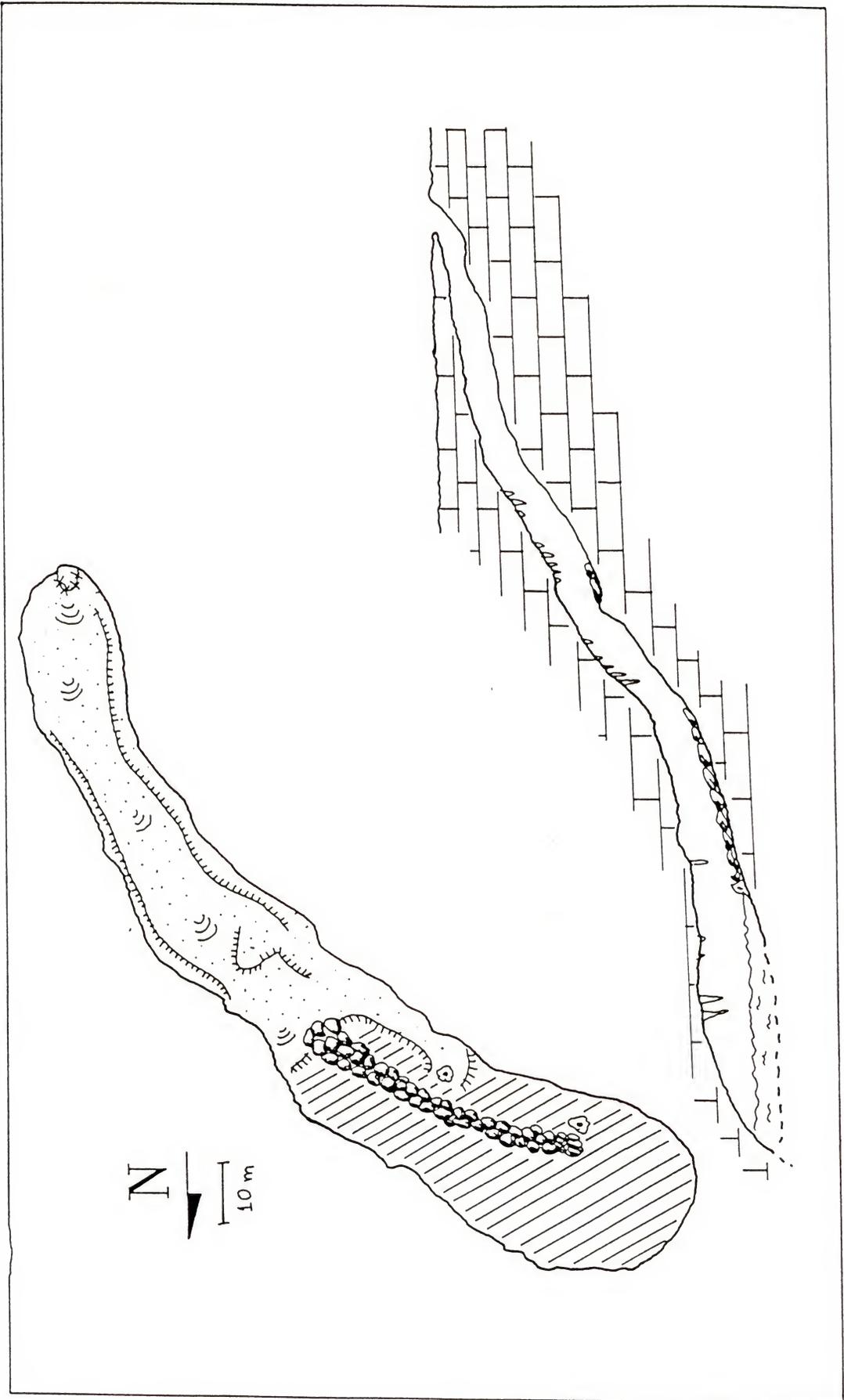


Figure 3.7--Hochtún Cave, Tekax.

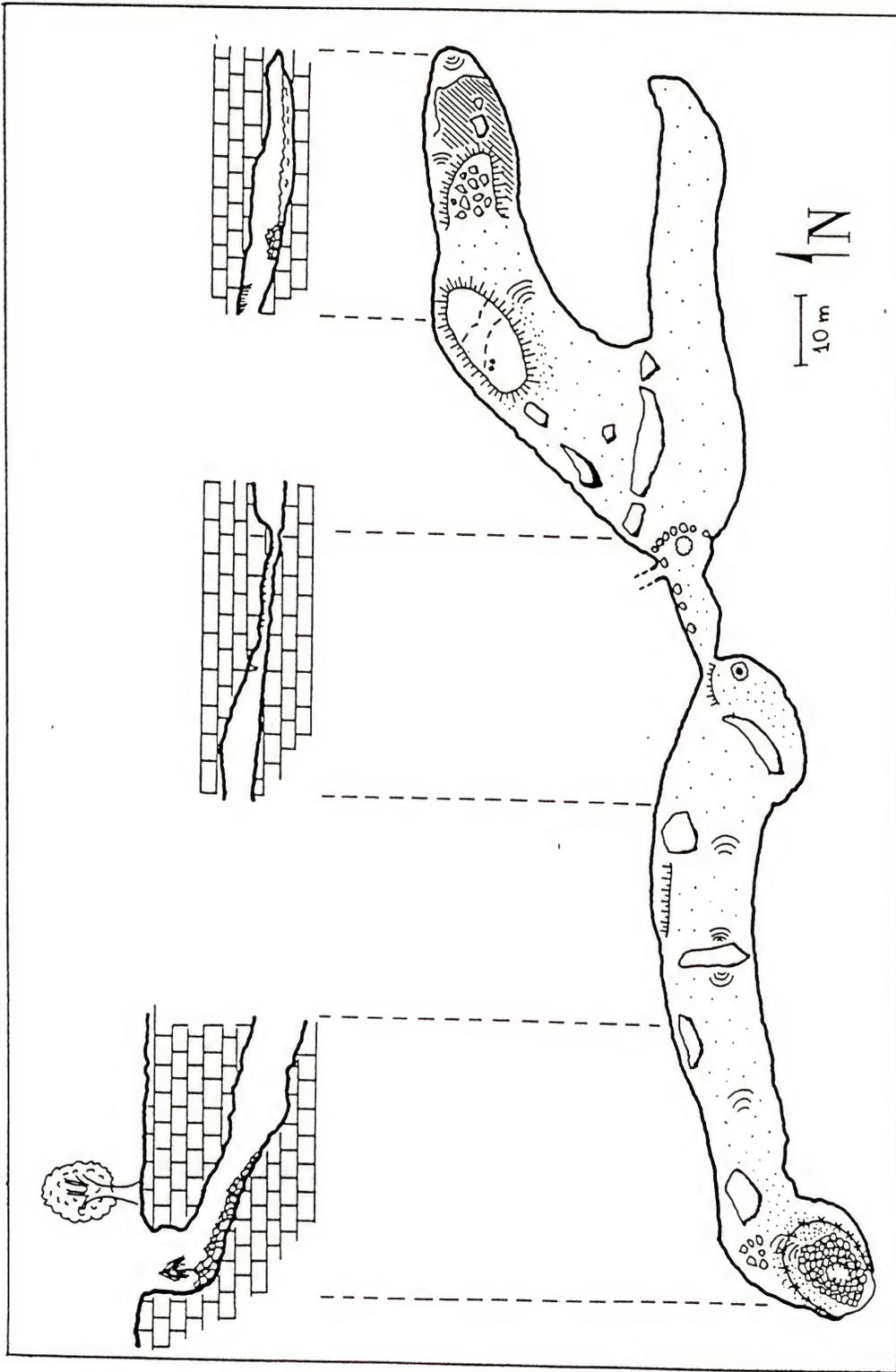


Figure 3.8--Cave of the Ruins of Mayapán, Telchaquillo

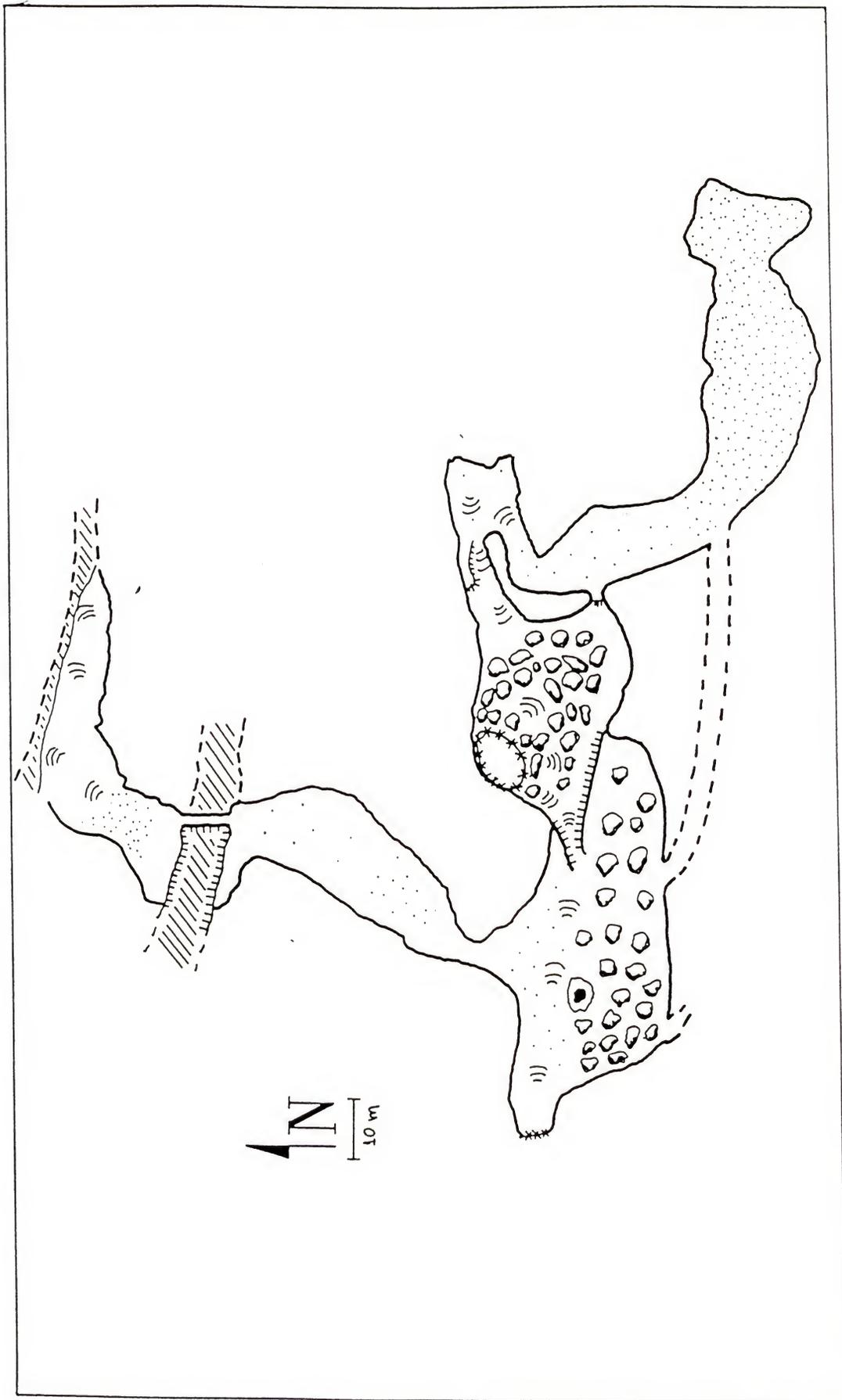


Figure 3.9--Tzab-Nah Cave, Tecoh.

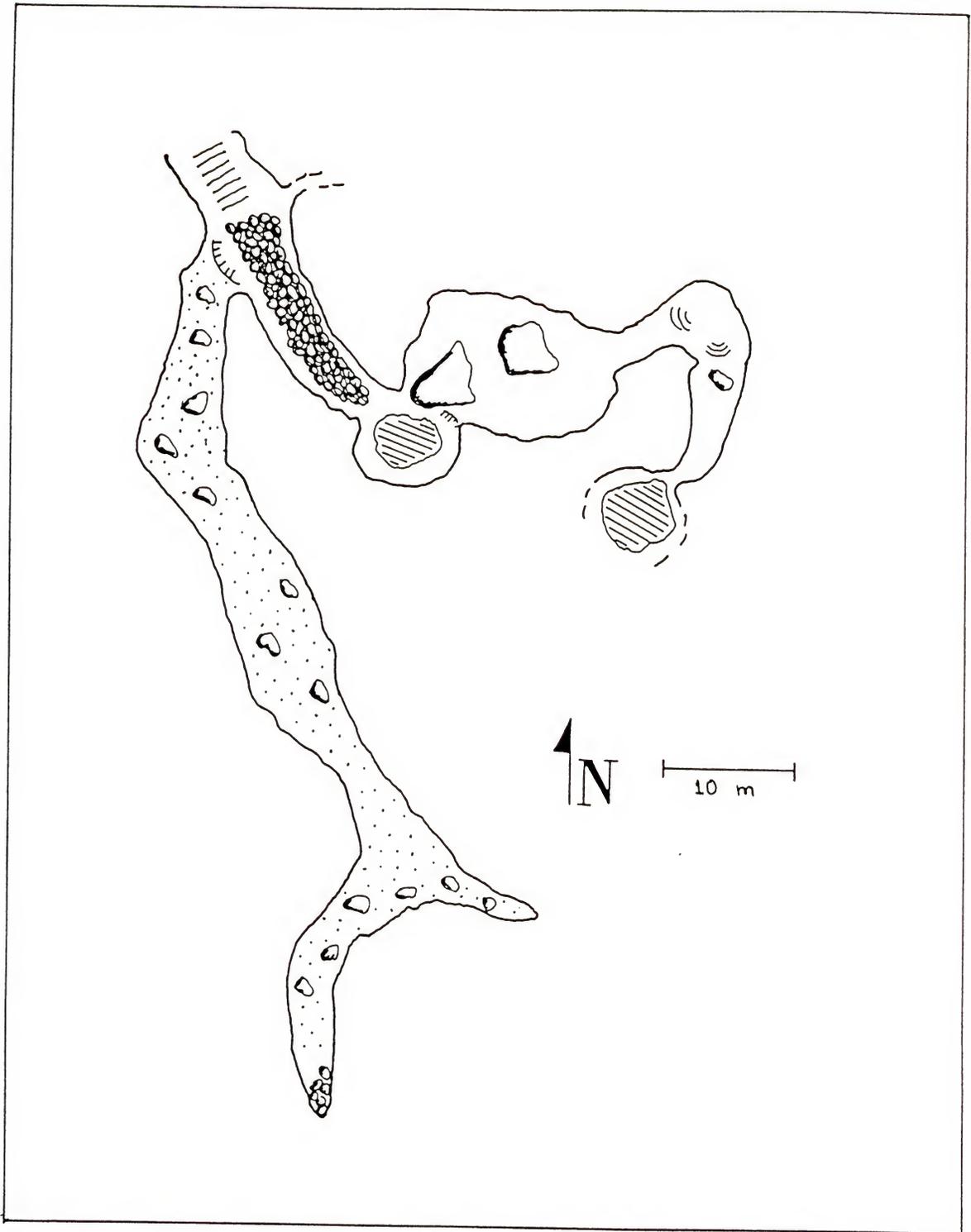


Figure 3.10--Kabahchén Cave, Maní.

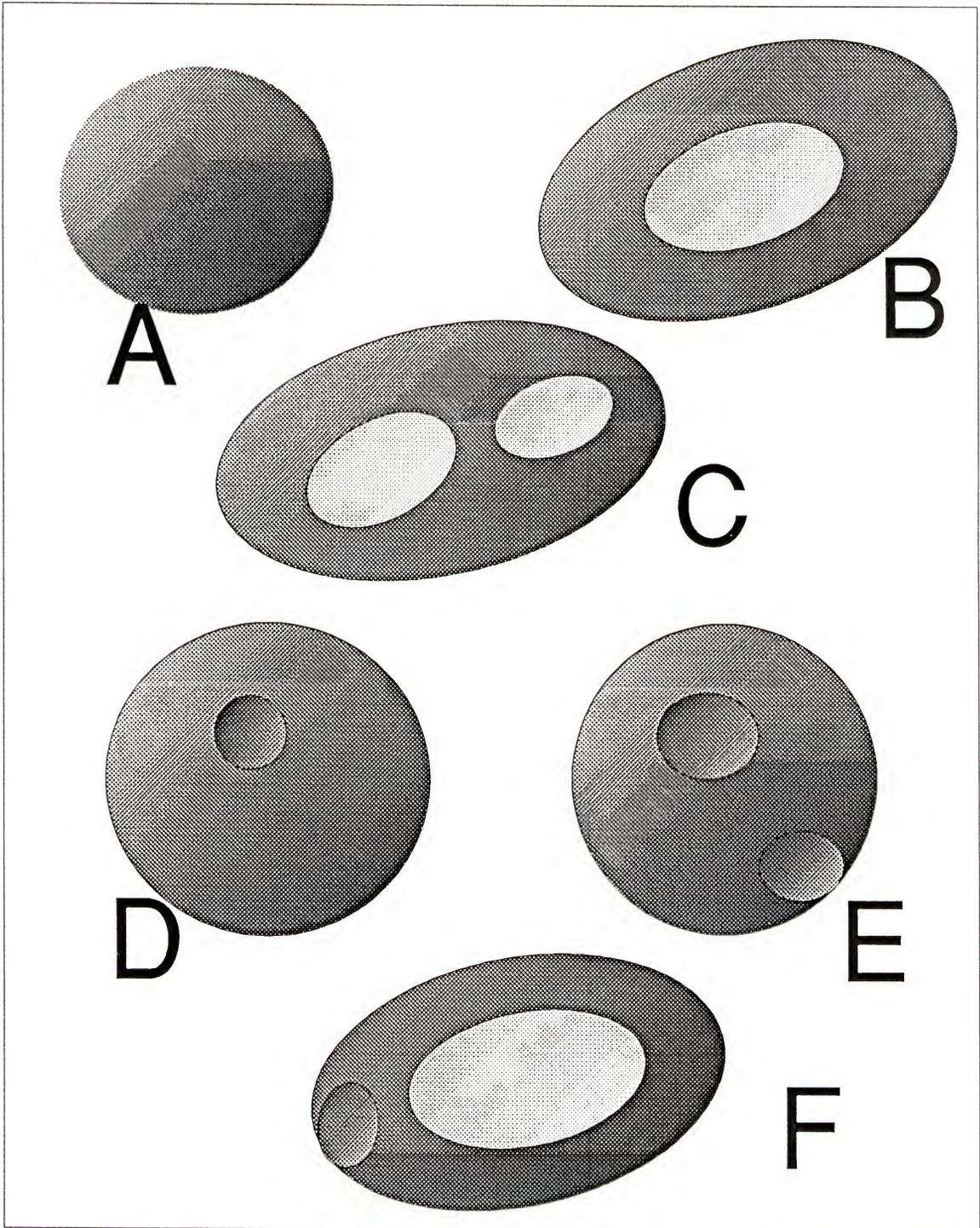


Figure 3.11--Topological classification of surfaces. A: an object of genus 0 (sphere). B: an object of genus 1 (torus). C: an object of genus 2 (pretzel). D: object of genus 0 with one end. E: object of genus 0 with two ends. F: object of genus 1 with one end

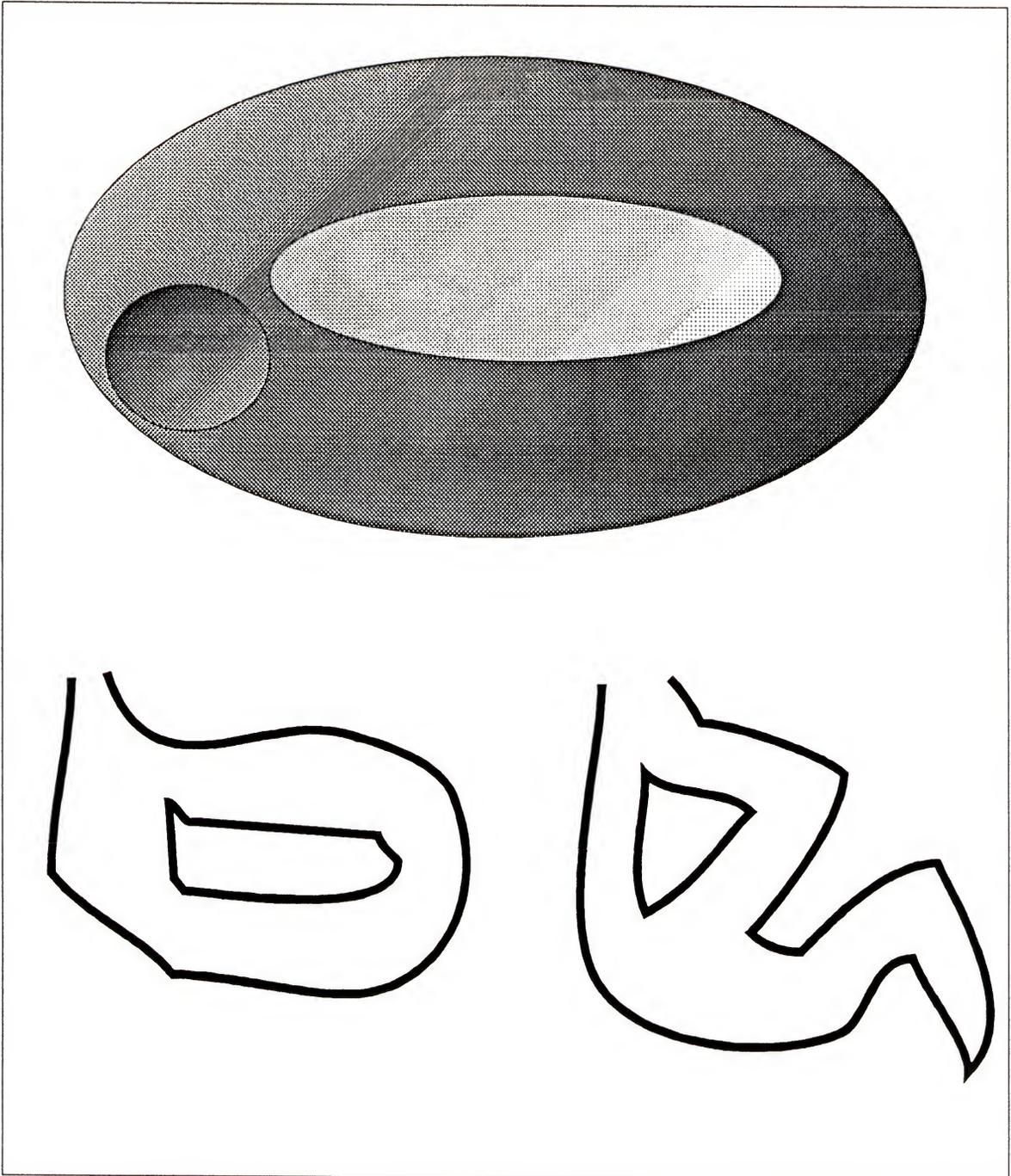


Figure 3.12--Two caves that are topologically identical to an object of genus 1 with one end.

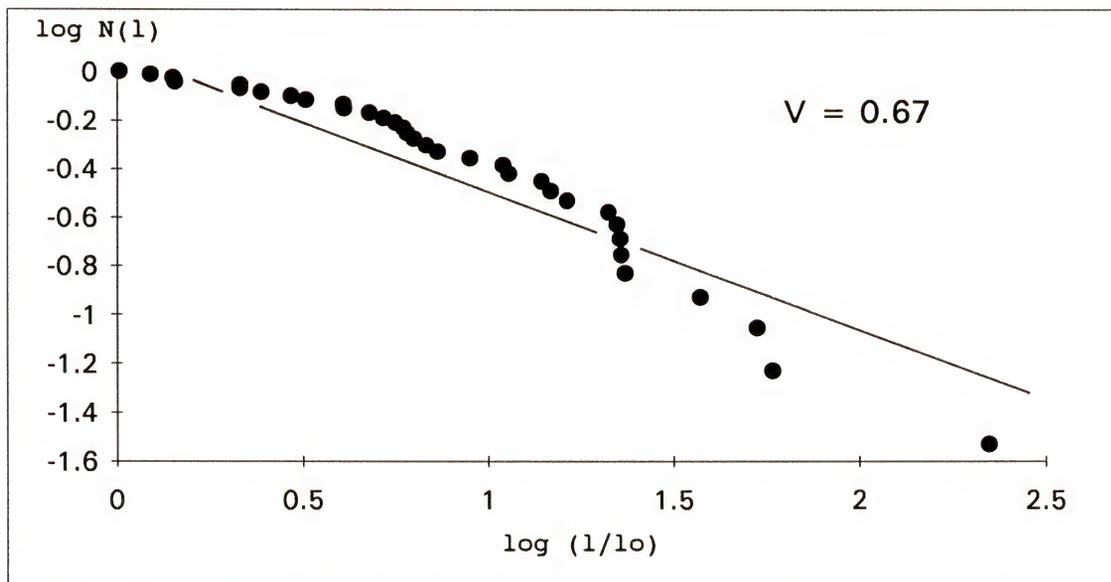


Figure 3.13--Fractal dimensionality of the distribution of cave lengths for Yucatán caves. The fractal dimension is estimated as the slope of the regression line of  $\log N(l)$  as a function of  $\log (l/l_0)$ .

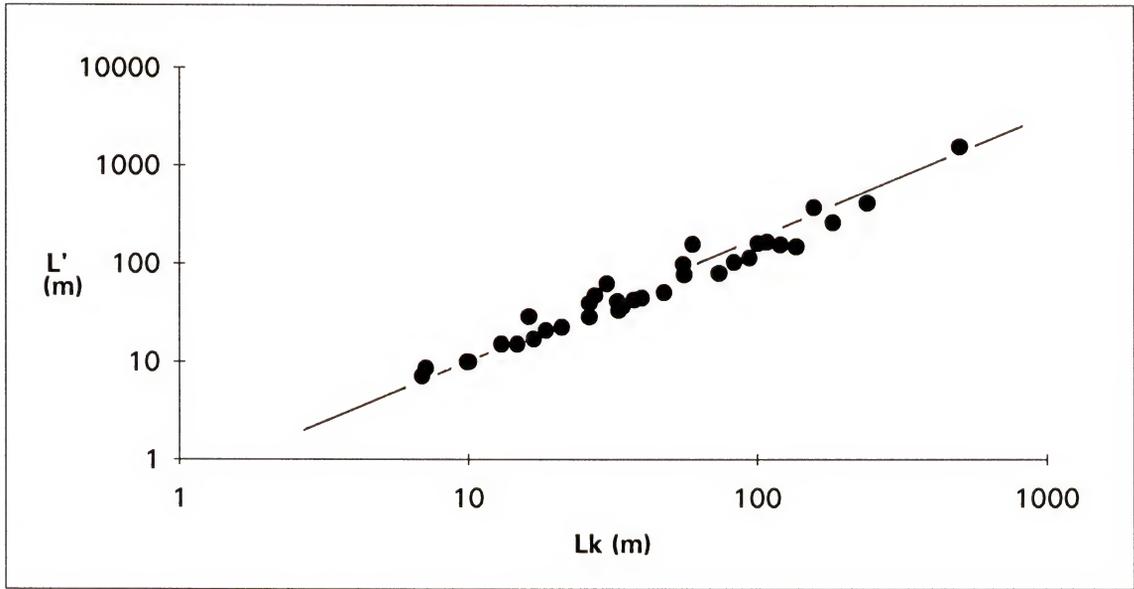


Figure 3.14--Relationship between projected extent of cave passages ( $L'$ ) and maximum horizontal distance ( $L_k$ ). Line marks points for which I.D. = 1.0.

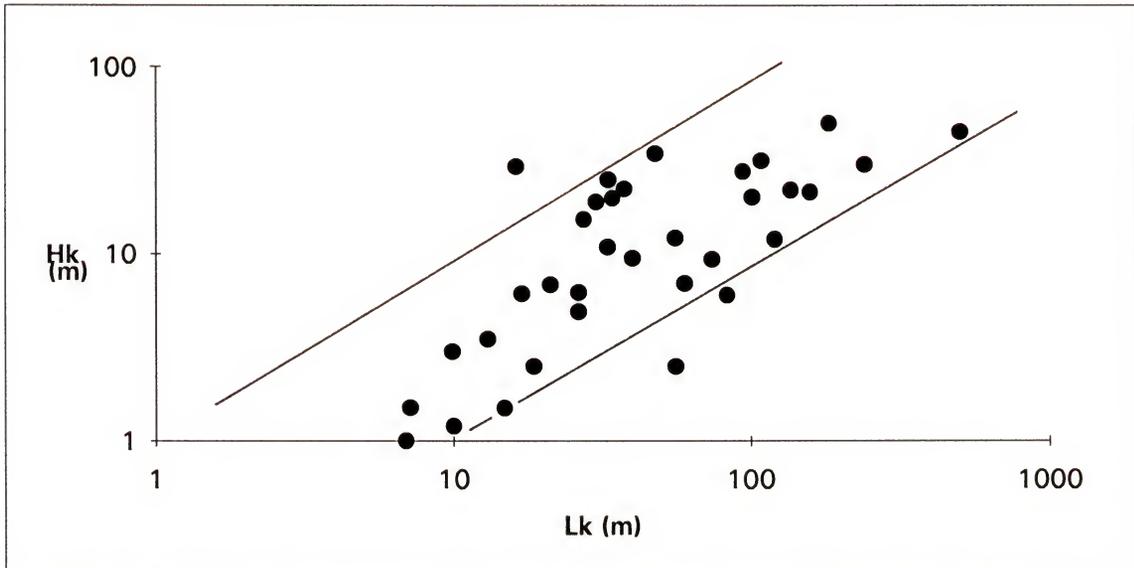


Figure 3.15--Relationship between the amplitude and the maximum horizontal distance for caves of Yucatán. Upper line marks points for which  $C_v = 1.0$ ; lower line marks points for which  $C_v = 0.1$ .

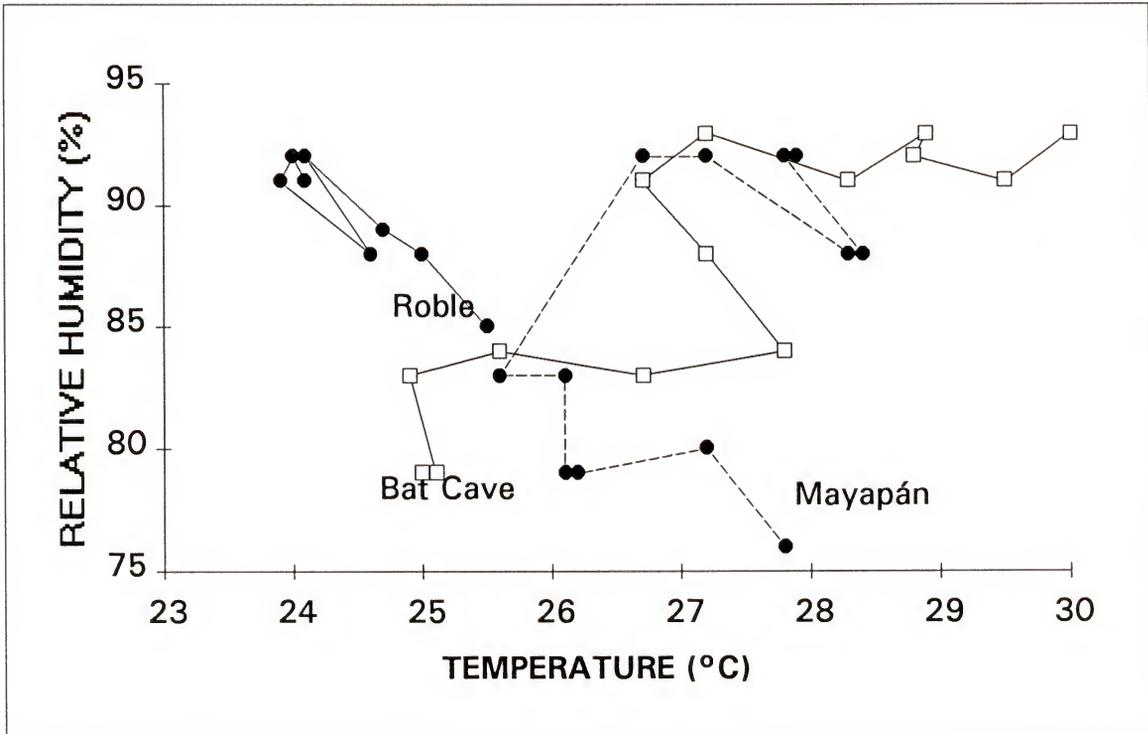


Figure 3.16--Phase diagrams showing ambient conditions for three caves in Yucatán. Beginning with the conditions at the entrance, each survey station is represented by a point which position in the graph corresponds to the coordinates (temperature, humidity). A line connects station  $s_i$  with station  $s_{i+1}$ , so each cave is represented by a network of lines extending from  $s_0$  (the entrance) to  $s_n$  (the end of a tunnel). The name of each cave is shown close to the point representing its entrance. Roble Cave is an example of a cave with wide entrance and negative slope; Bat Cave presents a positive slope; Mayapán is a cave with a constriction.

CHAPTER 4  
CAVE BATS OF MEXICO

Introduction

Caves are essential roosting sites for many bat species (Kunz, 1982a). 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 refuges (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 Kittlitz's hog-nosed bat (*Craseonycteris thonglongyai*), which is known from only six caves in Thailand (Humphrey and Bain, 1990). For species like this, destruction of caves would mean inevitable extinction.

México has a rich bat fauna of 134 species (Jones et al., 1988; Ramírez-P. et al., 1986), many of which are known to use caverns as roosts (Tuttle, 1976; Villa-R., 1967). In this chapter, I review the available literature on use of caves by Mexican bats, providing a list of species that require protection, as well as a catalogue of sites that would be critical in a conservation plan for bats.

A central objective of this review is to analyze the concept that the protection of sites with high biodiversity

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 diversities and abundances. If bats of special concern occur frequently in caverns with rich and abundant communities, then the preservation of these caves also would protect those bats. Conversely, if few or no species of particular concern roost in rich caves, separate strategies would be necessary to protect the caves and the bats.

#### Methods

From a literature survey that included books and articles on distribution, natural history, and taxonomy of Mexican bats (Appendix A), I extracted information for a data base of Mexican cave bats. This data base consists of the list of species that have been reported from each cave, including in some cases information on population density.

I identified the most important caves for the conservation of Mexican cave bats on the basis of their biodiversity and abundance. Biodiversity was estimated by the species richness, 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. Low-abundance caves were defined as sites sheltering bat populations of fewer than 1,000 individuals. Caves with high and very high abundance were defined as supporting

populations greater than 1,000 and 10,000 individuals, respectively. Critical sites were defined as caves presenting 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 refuges but rely frequently on alternative roosts. The third category included species that use caves occasionally but usually roost in other sites, and the last group encompassed 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 the sources on Appendix A, and from personal experience. To be consistent in the classification, I followed some special criteria. For some poorly known species, a single or a few reports of cave use in México were enough to consider them category II 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 I grouped it with the species that use caves as alternative refuges. Similar cases are those of Allen's big-eared bat (*Idionycteris phyllotis*, Czaplowski,

1983) and the free-tailed bats of the genus *Nyctinomops* (Carter and Davis, 1961; Jones et al., 1972). Conversely, species that in the United States use caves as hibernacula but that use other types of sites for summer refuge were generally not considered cave species in México. For most of these species there is no report of hibernacula in México. Examples include the eastern pipistrelle (*Pipistrellus subflavus*) and several species of mouse-eared bats (genus *Myotis*; Humphrey 1982; Schowalter, 1980).

A list of cave species of special conservation concern was developed using the list of Medellín and Arita (in press) for the whole Mexican bat fauna. Medellín and Arita (in press) proposed the terms "fragile" (of some concern) and "vulnerable" (of greater concern) based on the degree of susceptibility of the species to human perturbation. Additionally, I included the species that are endemic to Middle America (México and Central America) and those that are virtually endemic to this area, barely entering the United States (the California leaf-nosed bat, *Macrotus californicus*, the Mexican long-nosed bat, *Leptonycteris nivalis*, and the 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 frequency-

distribution graphs of the proportion of caves occupied by a given species among categories based on the richness of the sites. These graphs are analogous to the incidence functions first used by Diamond (1974, 1975) to study the distribution of birds in archipelagoes in relation to the species richness of the islands. In the case of caves, incidence functions test the use of species richness as a criterion to protect a site. They can be used to identify the species that tend to occur in caves with different levels of species richness.

## Results

### The Caves

The literature survey yielded a total of 215 Mexican caves with information on bats. In these caves, species richness ranged from one to 13 species. The frequency distribution graph follows a negative exponential curve, with several caves supporting few species and few caves harboring many species. Only 10% of the caves contained six or more species, whereas 80% sheltered three or less (Figure 4.1).

Most caves had low abundance of bats; caves with high and very high abundances were comparatively rare. Sites with the largest populations were refuges for the Mexican free-tailed bat (*Tadarida brasiliensis*), which in México forms colonies ranging from a few thousand to more than one million individuals (Cockrum, 1969). Other species that

frequently form large colonies (>1,000 individuals) in Mexican caves include some mormoopids (the mustached bat, *Pteronotus parnellii*, the naked-backed bat, *Pteronotus davyi*, and the ghost-faced bat, *Mormoops megalophylla*; Bateman and Vaughan, 1974), some phyllostomids (Palla's long-tongued bat, *Glossophaga soricina* and the little long-nosed bat, *Leptonycteris curasoae*; Villa-R., 1967; Wilson et al., 1985), the funnel-eared bat (*Natalus stramineus*), and the cave myotis (*Myotis velifer* and *Myotis peninsularis*; Villa-R., 1967; Woloszin and Woloszin, 1982).

The list of critical sites for the conservation of Mexican cave bats included 12 caves (Table 4.1). All these sites sheltered more than seven species of bats and supported large or very large populations.

### The Bats

Sixty (45%) of the 134 Mexican bat species can be considered cave species. Of these, 27 roost primarily in caves, whereas 33 use caves as alternative refuges (Table 4.2). Of the remaining species, 18 use caves only occasionally or rarely and 56 do not use caves at all.

The distribution of cave and non-cave bats among taxa was not random. All mormoopids, desmodontines, and natalids were classified as cave species, as were the majority of glossophagines (ten of 12 species, binomial test with expected  $p = 0.45$ :  $P < 0.01$ ). Conversely, fewer vespertilionids and molossids than expected by chance were

considered cave dwellers (14 of 43 of the former, four of 18 of the latter; binomial test,  $P < 0.05$  for both).

Fifteen fragile and four vulnerable species use caves regularly. There was no demonstrable association between use of caves and fragility or vulnerability; the distribution of species of concern among cave and non-cave categories did not deviate from expected by chance (contingency table analysis,  $\chi^2 = 0.36$ ,  $P > 0.05$ , 1 d.f.). Eleven of the Mexican cave bats are endemic to Middle America, and three others penetrate just barely into United States. There was no association between cave dwelling and endemism among Mexican bats (contingency table analysis,  $\chi^2 = 0.06$ ,  $P > 0.05$ , 1 d.f.).

Mexican cave bats can be classified in three categories of incidence (Figure 4.2). Species like *P. davyi*, which tend to occupy caves with high richness, are here called "integrationists." Species that tend to be found in caves with few species, like the Mexican big-eared bat (*Plecotus mexicanus*) are named "segregationists." Finally, species with no apparent preference for rich or poor caves, such as the common vampire bat (*Desmodus rotundus*) are named "indifferent" (Figure 4.2, bottom).

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 showed no significant deviation from a random distribution of species among incidence types ( $\chi^2 = 2.63$ ,  $P > 0.05$ , 2 d.f.).

Most species occur in caves in small colonies. Of the 60 cave species, 35 never form colonies of more than 100 individuals. Typical species of this class include the spear-nosed bat (*Mimon cozumelae*), the wooly false vampire (*Chrotopterus auritus*), and *M. harrisoni*. Of the remaining 25 species, only seven form very large populations of more than 10,000 individuals. Among these are *T. brasiliensis*, *P. parnellii*, *P. davyi*, *M. megalophylla*, and *N. stramineus*. There was no clear association between incidence and population density (Table 4.3, contingency-table analysis,  $\chi^2 = 3.21$ ,  $P > 0.05$ , 2 d. f.).

### Discussion

Many current conservation efforts concentrate on the protection of areas with high biodiversity (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 biodiversity and the presence of threatened species is less well established. The data

presented in this chapter show the inadequacy of the approach based on species richness to the conservation of Mexican cave bats.

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: species richness, population density, 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 critical sites because they have low species richness. 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 occurs because threatened species normally exist at low population levels, but it also shows that species of concern in general are not associated with other species with higher population densities. Species such as *M. cozumelae*, the long-legged bat (*Macrophyllum macrophyllum*) and *M. harrisoni* always occur in small groups, but they also are seldom or never 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. cozumelae* and the fringe-lipped bat (*Trachops cirrhosus*). These species almost always occur in caves by themselves or sharing the roost with few other species. Other bats of special concern, such as *T. brasiliensis* and *M. peninsularis*, are less segregationists but seldom occupy caves with more than five species. In the case of Mexican cave bats, species richness 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 4.3). Entries in the lower right cell of the table (integrationist bats that form colonies of more than 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 *Leptonycteris* species) are fragile, vulnerable, or endemic. Conversely, half of the species in the upper left cell of the table (segregationists that never form colonies of more than 100 individuals) are fragile or vulnerable (*M. macrophyllum*, *M. cozumelae*, *T. cirrhosus*, *I. phyllotis*, and

the fish-eating bat, *Myotis vivesi*). These species would benefit very 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 species richness and population levels and the management of cave bats of special concern (fragile, vulnerable, and endemic). The data presented in this chapter demonstrate that the implementation of a conservation plan for caves in Table 4.1 does not necessarily mean that fragile species would be protected. Despite this, caves in the list are important because the concentration of so many species and individuals constitutes a unusual natural phenomenon that deserves protection. Moreover, future research on the invertebrate communities in these caves and on the role of the bats of these caves in the outside ecosystems might find subtle and unique ecological interactions that should be preserved. Richness by itself is a sufficient reason for the conservation of caves in Table 4.1, despite their comparatively low contribution to the protection of endangered species.

Special conservation plans need to be developed 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 4.1 with the preservation of caves that are needed by the species of particular concern.

Table 4.1 Critical Caves for the Conservation of Mexican Cave Bats.

CAVE	S	ABUNDANCE	FRAGILE SPECIES
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	-
PUEBLA			
Cueva de las Vegas	13	high	-
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

S is the number of species, the richness of the cave.

Abundance is the combined population size of all species in the cave.

Table 4.2--Mexican Cave Bats.

Species	Cave Use	Incidence	Population Density	Status
Emballonuridae				
<i>B. io</i>	Main	I	L, M	F, E
<i>B. plicata</i>	Main	S	L, M	E
<i>P. kappleri</i>	Alt.	I	L	F
<i>P. macrotis</i>	Main	I	L, M	F
Noctilionidae				
<i>N. leporinus</i>	Alt.	S	L	
Mormoopidae				
<i>M. megalophylla</i>	Main	I	M, H	
<i>P. davyi</i>	Main	I	M, H	
<i>P. gymnonotus</i>	Main	I	L	F
<i>P. parnellii</i>	Main	I	M, H	
<i>P. personatus</i>	Main	I	M	
Phyllostomidae				
Phyllostominae				
<i>M. californicus</i>	Main	Ind.	M	E*
<i>M. waterhousii</i>	Main	Ind.	M	E
<i>M. brachyotis</i>	Alt.	Ind.	L	F
<i>M. megalotis</i>	Alt.	Ind.	L	
<i>M. sylvestris</i>	Alt.	Ind.	L	
<i>L. aurita</i>	Main	I	L	F
<i>M. macrophyllum</i>	Main	S	L	F
<i>M. cozumelae</i>	Alt.	S	L	F
<i>T. cirrhosus</i>	Alt.	S	L	F
<i>C. auritus</i>	Alt.	Ind.	L	F
Glossophaginae				
<i>G. commissarisi</i>	Alt.	Ind.	L	
<i>G. leachii</i>	Alt.	Ind.	L	E
<i>G. soricina</i>	Alt.	I	L, M, H	
<i>G. morenoi</i>	Alt.	Ind.	L	E
<i>H. underwoodi</i>	Alt.	Ind.	L	F, E
<i>A. geoffroyi</i>	Main	S	L	

Table 4.2--continued.

Species	Cave Use	Incidence	Population Density	Status
<i>L. nivalis</i>	Main	I	L, M	V, E*
<i>L. curasoeae</i>	Main	I	L, M	F
<i>C. mexicana</i>	Main	Ind.	L	E*
<i>M. harrisoni</i>	Alt.	Ind.	L	V
Carolliinae				
<i>C. brevicauda</i>	Alt.	Ind.	L, M	
<i>C. perspicillata</i>	Alt.	Ind.	L, M	
<i>C. subrufa</i>	Alt.	Ind.	L, M	
Stenodermatinae				
<i>D. azteca</i>	Main	S	L	E
<i>A. hirsutus</i>	Main	Ind.	L, M	E
<i>A. jamaicensis</i>	Alt.	Ind.	L, M	
<i>A. intermedius</i>	Alt.	I	L	
<i>A. lituratus</i>	Alt.	I	L	
Desmodontinae				
<i>D. rotundus</i>	Main	Ind.	L, M	
<i>D. youngii</i>	Main	Ind.	L	F
<i>D. ecaudata</i>	Main	I	L	
Natalidae				
<i>N. stramineus</i>	Main	I	M, H	
Vespertilionidae				
<i>M. keaysi</i>	Main	I	L, M	
<i>M. californicus</i>	Alt.	Ind.	L	
<i>M. lucifugus</i>	Alt.	Ind.	L	
<i>M. nigricans</i>	Alt.	I	L	
<i>M. peninsularis</i>	Main	Ind.	M, H	F, E
<i>M. thysanodes</i>	Alt.	S	L	
<i>M. velifer</i>	Main	Ind.	M, H	
<i>M. vivesi</i>	Alt.	S	L	V, E

Table 4.2--continued.

Species	Cave Use	Incidence	Population density	Status
<i>P. subflavus</i>	Alt.	Ind.	L	
<i>E. fuscus</i>	Alt.	I	L	
<i>P. mexicanus</i>	Main	S	L, M	E
<i>P. townsendii</i>	Main	S	L, M	
<i>I. phyllotis</i>	Main	S	L	
<i>A. pallidus</i>	Alt.	S	L, M	
Molossidae				
<i>T. brasiliensis</i>	Main	S	M, H	V
<i>N. aurispinosus</i>	Alt.	Ind.	L	
<i>N. femorosaccus</i>	Alt.	Ind.	L	
<i>N. laticaudatus</i>	Alt.	Ind.	L	

Cave Use: Main, caves are the main roost for the species; Alt. (alternative), other types of roosts are regularly used.

Incidence: I, integrationist; S, segregationist; Ind., indifferent.

Population density: L, low (generally <100 individuals); M, moderate (100 to 10,000 individuals); H, high (>10,000 individuals).

Status: F, fragile; V, vulnerable, E, endemic to Middle America; E\*, restricted to Middle America and a very small portion of Southwestern United States.

Table 4.3--Relationship between incidence and population density among cave bats of México. Values in cells are the number of species in each category.

	Segreg.	Indif.	Integ.	TOTAL
Low density <sup>a</sup>	10	18	7	35
high density <sup>b</sup>	4	11	10	25
TOTAL	14	29	17	60

Incidence: Segreg., segregationists; Indif., indifferent; Integ., integrationists.

a: populations are always <100 individuals.

b: populations are normally >100 individuals.

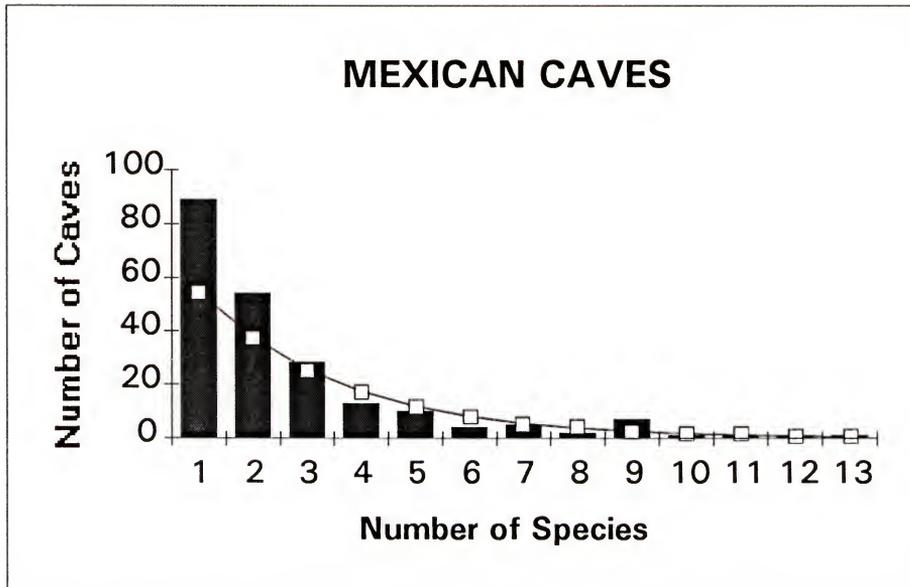


Figure 4.1--Bat species richness of Mexican caves (bars); sample size is 215. Line shows the regression line adjusted to an exponential equation fitting the data ( $F = 92.57$ , 11 *d.f.*,  $P < 0.01$ ).

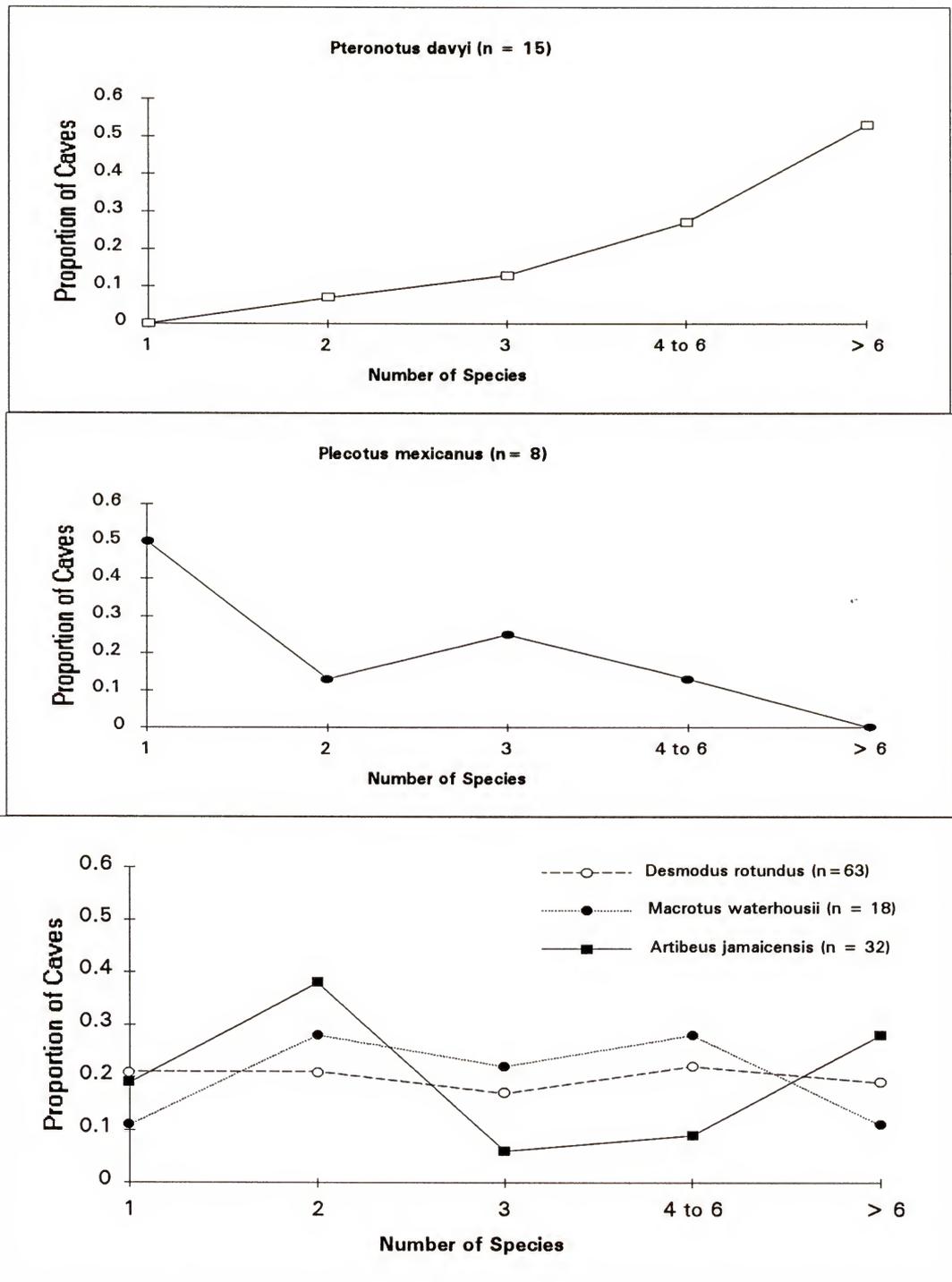


Figure 4.2. Incidence functions of Mexican cave bats. Top: *Pteronotus davyi*, an integrationist species. Middle: *Plecotus mexicanus*, a segregationist species. Bottom: Three indifferent species, *Desmodus rotundus*, *Macrotus waterhousii*, *Artibeus jamaicensis*

CHAPTER 5  
THE BAT FAUNA OF YUCATAN

Introduction

One of the main objectives of community ecology is to understand the organization of assemblages of animal and plant species. One effective approach to the study of communities is the search for patterns that could be interpreted as the effect of one or more ecological forces, such as climate, species interactions, dispersal, or resource availability.

In the last decade, these patterns have been subjected to a more rigorous scrutiny that has debunked many of the early assumptions about community organization. A particularly powerful tool in this endeavor is the use of null models (Harvey et al., 1983). This approach compares some alleged pattern in a given community to a null statistical distribution based on hypothetical communities that are randomly generated from a source pool. The test tries to falsify the null hypothesis that the observed pattern results from purely random processes.

Most attention of recent null-model studies has concentrated on the assessment of the role of interspecific competition in organizing communities. Simberloff and his collaborators (Connor and Simberloff, 1979; Simberloff and

Boecklen, 1981; Strong et al., 1979) used null models to scrutinize previous studies that had claimed to demonstrate the effect of competition in structuring animal communities. Subsequently, several authors have criticized the conclusions and some aspects of the methodology used in these studies and have proposed improved models (reviewed by Harvey et al., 1983; also Colwell and Winkler, 1984; Moulton and Pimm, 1986; Schoener, 1984). The basic idea of using null models as reference points to analyze the apparent organization of animal assemblages, however, has persisted despite this criticism (e.g., Simberloff and Boecklen, 1991).

A considerable proportion of null-model studies has analyzed the faunas of archipelagos or groups of "habitat islands" (see Table 1 in Harvey et al., 1983). These faunas are specially suited for this type of analysis because each island can be treated as a separate entity and compared with the null model developed from the source pool. Studies of continental (non-island) faunas are hindered by the difficulty of defining objective limits to the study assemblages and by the often troublesome selection of an appropriate source pool (Bowers and Brown, 1982; Schoener, 1984; Willig and Moulton, 1989).

In this chapter, I analyze an intermediate case between the archipelago and the continental approaches: a peninsular fauna. A null-model investigation of such a fauna shares with the continental studies the problem of the delimitation

of the study fauna(s), but the source pool can be defined more precisely if it is possible to identify a principal source of colonization. Models of the "peninsular effect" have assumed immigration from a single source, the base of the peninsula (Busack and Hedges, 1984; Gilpin, 1981; Simpson, 1964; Taylor and Regal, 1978). For a null-model study of a peninsular assemblage, it would be reasonable to construct the source pool from the stock of species that is present in the base of the peninsula.

I compare the bat fauna of the state of Yucatán, México, with null models generated from a source pool. The whole fauna of such a large area cannot be considered as a community in the strict sense of the world, because some of the species found in the study area might not be really syntopic. The study fauna can be defined better as a large-scale assemblage of species (Jaksic, 1981; Moulton and Pimm, 1986). Results, however, are no less valid than those derived from studies of small-scale communities or authentic guilds.

The objective of the present study is to analyze the composition of the bat fauna of Yucatán and to search for patterns of organization. The question posed is whether the study fauna shows any particular deviation from what would be expected from an assemblage randomly constructed from a pool.

## Definition of the Fauna and the Source Pool

### The Yucatán Fauna

The study fauna is defined here as the set of bat species found in the state of Yucatán, which occupies the northwestern tip of the peninsula of the same name. The political borders of the state roughly coincide with the limits between the evergreen and the tropical deciduous forests (Rzedowski, 1979). A lesser mountain range, the *Sierrita de Ticul* (<200 m in altitude), marks the southern limit of the state and is the only mountain range in the otherwise flat northern part of the peninsula. Because of these features, the state of Yucatán is treated here as a separate entity from the rest of the peninsula.

The Yucatán bat fauna consists of 31 species in seven families (Table 1). The list is based on the species reported by Ramírez-P. et al. (1986) and a recent record of *Centurio senex* (Bowles et al., 1990). The list is conservative and excludes all species for which there is no definitive proof that they are present in the state of Yucatán. From the list of Ramírez-P. et al. (1986) I deleted the species reported from Yucatán on the basis of erroneously identified specimens (*Rhynchonycteris naso*, *Micronycteris schmidtorum*, *Myotis nigricans*, and *Tadarida brasiliensis*; see Jones et al., 1973; Hall, 1981; LaVal, 1973).

I also excluded two species whose presence in Yucatán is doubtful. Gaumer (1917) reported *Macrotus waterhousii* from the Yucatán peninsula, but the specimens on which he based his report are lost. Anderson and Nelson (1965) and Jones et al. (1973) accepted Gaumer's record on the basis of his description of the specimens, but the fact is that there is no available specimen of *M. waterhousii* to corroborate its presence in the Yucatán peninsula.

Koopman (1974) reported *Plecotus mexicanus* from a cave in northern Yucatán. *P. mexicanus* is a temperate bat, and all records for the species, except the one from Yucatán, are from above 1,500 m. Koopman's (1974) locality is more than 600 km apart from the closest locality for *P. mexicanus* in the highlands of central México. The specimen is one of a series of bats from several localities in México that were donated to the American Museum of Natural History, and it is possible that the specimen of *P. mexicanus* was actually collected somewhere else in México and mislabeled as coming from Yucatán. As Koopman (1974) speculated, even if the record is valid, *P. mexicanus* might not be a year-around resident in Yucatán.

Neither *M. waterhousii* nor *P. mexicanus* has been recently recorded from Yucatán despite extensive collecting efforts (Jones et al., 1973; Birney et al., 1974; Bowles, 1990; Arita, chapter 6; M. Engstrom, personal communication). I am not completely ruling out the possibility that *M. waterhousii* or *P. mexicanus* are present

in Yucatán, but given the conservative criterion to define the study fauna in this study, I decided to exclude both species from the list until their presence in Yucatán is indisputably documented.

### The Source Pool

An important step in the construction of null models is the correct definition of the source pool from which species are to be drawn. In studies dealing with archipelagos, pools have been constructed from the faunas of the mainland adjacent to the islands (Grant, 1966; Simberloff, 1970; Graves and Gotelli, 1983) or using the combined fauna of the archipelago itself (Connor and Simberloff, 1979; Gotelli and Abele, 1982). For a study of continental faunas of neotropical bats, Willig and Moulton (1989) created nested source pools based on the whole fauna of South America.

As discussed by Graves and Gotelli (1983), none of these approaches is completely objective. Habitat and topographic differences between islands and the source area are frequently ignored, and the geological and climatological history of the region is rarely considered. Special problems arise with large archipelagos in which distances among islands are great or in cases where islands can be colonized from several mainland areas. Further complications are differences in habitat preference and dispersal ability of the potential colonizer species (Graves and Gotelli, 1983). The definition of pools should be done

very carefully, taking into account all of these complications. The appropriate source pool should be defined as a larger fauna from which the study subfauna(s) could reasonably have derived, considering the present and past geological features of the region, the past and present habitats available, and the particular ecological features of the potential colonizers.

As the first step in constructing the appropriate source pool for the bat fauna of Yucatán, I considered the base of the peninsula and four other possible sources of species. I defined the base of the Yucatán peninsula as the lowlands (altitude <1,000 m) of the Gulf and Caribbean versants of southeastern México, Belize and Guatemala (Jones, 1966; MacCarthy, 1987; Medellín, 1986). The alternative sources included the state of Florida (bat fauna from Hall, 1981); northeastern México, including the states of Tamaulipas, San Luis Potosí, and Nuevo León (Wilson et al., 1985); the northern extreme of South America (Eisenberg, 1989); and the Greater Antilles, including Cuba, Jamaica, Puerto Rico and Hispaniola (Koopman, 1989).

I used Simpson's index of similarity:

$$S_{(i, j)} = C_{(i, j)} / N_i,$$

where  $C_{(i, j)}$  is the number of species shared by faunas  $i$  and  $j$  and  $N_i$  is the number of species in the smaller fauna, to quantify the faunal similarity between Yucatán and these possible source areas.

The bat fauna of Yucatán showed very little resemblance to that of Florida ( $S_{(f, y)} = 0.21$ ,  $N_f = 14$ ) and that of the Greater Antilles ( $S_{(y, a)} = 0.32$ ,  $N_a = 32$ ). It was moderately similar to the fauna of northeastern México ( $S_{(y, ne)} = 0.65$ ,  $N_{ne} = 62$ ) and very similar to that of northern South America ( $S_{(y, ns)} = 0.84$ ,  $N_{ns} = 148$ ). All bat species in the state of Yucatán are also found in the base of the peninsula ( $S_{(y, bp)} = 1.00$ ,  $N_{bp} = 85$ ).

It is clear that the bat fauna of Yucatán has higher affinity with the neotropics than with the nearctic region. Because the Yucatán fauna is a subset of the stock of species of the lowlands of southeastern México, Belize, and Guatemala, it is reasonable to assume that the bat communities of the northern part of the peninsula were formed by the colonization and subsequent interchange of species from the south.

Zoogeographical evidence supports this assumption. There are no endemic subspecies of bats in Yucatán, and all subspecies and monotypic species in northern Yucatán are shared with the southern portion of the peninsula (Hall, 1981). Conversely, the Greater Antilles have many endemic species, and a large proportion of subspecies differ from the ones found in Yucatán (Hall, 1981).

According to the geomorphologic, palynologic, and phytogeographic evidence reviewed by Toledo (1982), the tropical areas of México have gone through marked cycles of temperature and precipitation during the last 40,000 years.

From 9,000 to 2,000 years before present the region was decidedly warmer and drier than at present. Based on this, Toledo (1982) speculated that savannas, tropical deciduous forests, and thorn forests were widespread in areas now covered with more humid forests. Under this scenario, bat species richness in the region should have been lower than at present, because bat faunas tend to be more diverse in more humid habitats (Fleming et al., 1972; Humphrey and Bonaccorso, 1979). As rainfall increased, tropical forests should have expanded and bat species colonized the new habitats from the areas that Toledo (1982) proposed as rain-forest refugia.

If Toledo (1982) is right, the modern bat fauna of Yucatán has a very short history in geologic terms, and it originated as a mixing of those species adapted to the extremely arid conditions that predominated in Yucatán during the dry period and those species that invaded from the refugia as more humid forests expanded. Unfortunately, the paleontological record of Yucatán is too scant to test Toledo's (1982) scenario. Arroyo-Cabrales and Alvarez (1990) examined the fossil bats of a Yucatán cave and found no major differences from present-day faunas. In any event, the available evidence supports the use of the fauna of the southern portion of the peninsula as the source pool for the Yucatán bat fauna.

The second step in constructing the source pool was to control for habitat preferences among the species. As

Harvey et al. (1983) and Graves and Gotelli (1983) have pointed out, source pools should include only those species that really could occur in the habitats available in the study sites.

The southern portion of the Yucatán peninsula is more diverse in habitats than the northern extreme but in general is more humid (García, 1981). The natural vegetation of the state of Yucatán is tropical deciduous and thorn forests, whereas the southern part of the peninsula additionally harbors other more humid habitats (Rzedowski, 1979).

To correct the original source pool, I deleted all species that are not known to occur in dry areas elsewhere in the neotropics. I based the decisions on the lists of species of Ceballos and Miranda (1986) for western México, Eisenberg (1989) for northern Venezuela and Colombia, Koopman (1978) for western Perú, Willig (1984) for southeastern Brazil, and Wilson (1983) for western Costa Rica. Sixteen of the 85 species were deleted using this criterion. The remaining 69 species, representing eight families, constitute the source pool controlling for habitat use, and will be referred to as "the pool" hereafter.

#### Tests for Composition of the Fauna

One type of null-model test for competition in ecological communities is the search for unusual patterns of species composition among islands in an archipelago (Harvey et al., 1983). In this kind of test, species in the study

area are classified into categories defined by some criterion (taxonomic, ecological, behavioral). The frequency distribution of species among the categories in the derived fauna(s) is then compared against the null distribution obtained by randomly sampling from the pool. If significant differences are found, the possible forces that would have produced such deviations can then be considered.

The purpose of this section is to compare the bat fauna of Yucatán with its source pool, searching for assembly rules that could explain its composition. The null hypothesis in the following comparisons is that the bat fauna of Yucatán is a random subset of the source pool.

Comparison I: distribution among taxa. In the first test, I compared the taxonomic structure of the bat fauna of Yucatán with that of the pool. Any deviation from a random distribution among taxa would indicate different colonization abilities, competitive superiority, or simple habitat selection for the different taxa. The null hypothesis is that the different taxa are proportionally represented in the fauna of Yucatán; the alternative hypothesis is that some taxa are over-represented and others underrepresented.

Constructing random communities from a source fauna is analogous to sampling from a finite pool without replacement. Expected number of species in each taxon and

the respective variance can be estimated using the hypergeometric frequency distribution (Hastings and Peacock, 1975; Graves and Gotelli, 1983; Appendix B).

I divided the species in the pool into families and, for the diverse family Phyllostomidae, into subfamilies. Because there was no a priori reason to expect any particular taxa to be over- or underrepresented in the study fauna, the appropriate test involved the probability of a deviation  $\geq$  the expected value in any direction, that is, a two-tailed test. I computed the exact probabilities with formula (4) in Appendix B using a program written in BASIC. (Listings of this and other BASIC programs are available from the author upon request).

There was very little deviation of the proportion of species in the different taxa from the expected values (Table 5.2). In fact, most taxa are represented by the number of species that would be expected in a random draw from the source pool. The largest deviation is that of the Phyllostominae, represented by only three species in the Yucatán fauna. Even in this case the deviation is not significant ( $P > 0.05$ ). In terms of taxonomic structure, the Yucatán fauna can be considered as a random subsample of the source pool.

Comparison II: distribution among feeding categories A similar procedure was used to analyze the composition of the Yucatán bat fauna in terms of the feeding habits of the

species. I used broad categories as classification criterion because the foraging habits of many species are not known in detail, so a finer classification is not feasible.

Species considered here as frugivores base their diet on soft fruits, although in some cases they also take some insects. They are in the subfamilies Stenodermatinae and the Carolliinae. Nectarivores depend heavily on the nectar and pollen of flowers, sometimes complementing their diet with other components (insects or fruit). They belong in the subfamily Glossophaginae. Gleaners are in the subfamily Phyllostominae, and pluck their prey (arthropods or small vertebrates) from a substratum, although many species in this category complement their diets with fruit or nectar (Humphrey et al., 1983). Aerial insectivores are bats that capture their food on the fly, maneuvering to pursue their prey. This category includes most of the vespertilionids, emballonurids, and natalids. Molossid insectivores also capture their prey in the air, but they have a distinct, rapid flight that separates them from the more agile aerial insectivores. Vampire bats (Desmodontinae) constitute the category of hematophagous bats, whereas *Noctilio leporinus* is the only member of the fish-eating category.

These and other similar feeding categories have been used in previous studies of neotropical bat communities (Bonaccorso, 1979; Fleming et al. 1972; LaVal and Fitch, 1977; Willig, 1983; Willig and Moulton, 1989; Wilson, 1973),

and in some cases they have been defined, incorrectly, as feeding guilds. Strictly, these categories cannot be considered true guilds, groups of species using the same resources in a similar fashion (Jaksic, 1981; Root, 1967), because they are based on resource use only, with no information on foraging strategies. In the present study the feeding categories are treated as convenient assemblages of species grouped by similarities in resource use.

As in the case of taxonomic groups, there was little deviation from expected in the observed number of species grouped by feeding categories (Table 5.2). All groups are represented in the Yucatán fauna proportionally to their frequency in the pool. The null hypothesis of no deviation from random structure cannot be rejected.

#### Comparison III: distribution among roosting categories.

The third analysis was performed using roosting habits as the criterion. I used the classification of Mexican bats in terms of cave use presented in Chapter 4. I assigned the species in the pool either to the category of cave bats (species that use caves as main or alternative diurnal roosting sites) or non-cave bats (species that do not use caves or that use caves occasionally).

Because in this case there are only two categories, it suffices to test only the proportion of species in one of them. For example, once the number of cave species is known, the number of non-cave forms becomes fixed as the

total minus the number of cave species. Statistical tests are equivalent using either category.

In this case there is an a priori reason to expect a particular direction for the deviation of the number of species from the expected value. Caves are very abundant in the Yucatán peninsula, so it would be reasonable to expect that cave species would be overrepresented in the derived fauna. Furthermore, one would expect non-cave species to be underrepresented in the derived fauna because the dry forests of the northern part of the peninsula provide a lower diversity of sites for plant-roosting species, especially those that use palms as refuges. To test for a non-random arrangement of species in terms of roosting habits, a suitable alternative hypothesis is that there are more cave species in the Yucatán fauna than expected by chance. A one-tailed test is the appropriate procedure in this case.

Of the 69 species in the pool, 31 are cave forms. In Yucatán, 17 out of 31 use caves regularly. The expected number of Yucatán cave species based on a random draw from the pool is 14.78. The probability of drawing 17 or more cave species from the pool in a sample of 31 is  $P = 0.197$ . The apparent over-representation of cave species in the Yucatán fauna is not statistically significant ( $P > 0.05$ , hypergeometric distribution test).

Comparison IV: species-to-genus ratio. Several studies have shown that communities with lower species richness tend to have fewer species per genus than richer assemblages (reviewed by Harvey et al., 1983 and Jarvinen, 1982). Since Darwin (1859), competition has been assumed to be stronger between closely related species (e.g., species in the same genus), so lowered species-to-genus (S/G) ratios in simpler communities could be interpreted as evidence for competition because that would show that similar (= competing) species are less likely to coexist in smaller assemblages.

It can be shown statistically, however, that communities with few species have lower S/G ratios simply because of their smaller sample size as compared with that of more complete communities. In fact, real assemblages tend to have higher S/G ratios than expected on the basis of adequate sampling models (Gotelli and Abele, 1982; Simberloff, 1970; and see Jarvinen, 1982 for a historical account involving earlier controversies). An appropriate test for competition involving the use of S/G ratios must be derived from carefully posed models based on the hypergeometric distribution.

I wrote a BASIC program to calculate the expected value and the variance for the S/G ratio of the Yucatán fauna based on the pool, using rarefaction formulas (Heck et al., 1975; Simberloff, 1978). The expected number of genera in a 31-species sample from a pool of 69 species in 44 genera is

24.52. The observed value for the Yucatán fauna is 24 genera (probability of a deviation  $\geq$  observed is  $P > 0.05$ ). S/G ratio analysis provides no evidence of any deviation from random sampling from the source pool.

Comparison V: the effect of dispersal ability.

Undoubtedly, colonization potential affects the probability of a given species to be present in a derived fauna. Unfortunately, species-specific demographic characteristics that permit successful dispersal are very difficult to quantify and remain unknown for most species. Attempts to estimate the dispersal ability of species in null-model studies include the use of incidence functions for archipelagos (Diamond, 1974; Simberloff and Connor, 1978) and the measurement of the area of the distributional range, with the implied assumption that widespread species have better colonization potential than species with restricted distributions (Graves and Gotelli, 1983). Here, I use a modified version of the latter method.

For each species in the pool, I recorded its presence or absence in eight discrete zoogeographical areas of the Neotropics: (1) the Pacific versant in western México (Ceballos and Miranda, 1986), (2) the Gulf of México versant in northeastern México (Hall, 1981; Ramírez-P. et al., 1986), (3) the West Indies (Koopman, 1990), (4) the northern Neotropics (Eisenberg, 1989), (5) the Amazon basin, (6) eastern Brazil, (7) the Pacific versant of South America,

(8) the Patagonia (these last four areas as defined by Koopman, 1983). For each area in which a species is present, I added 1 point, so a given species could have any value from 0 (endemic to the Yucatán peninsula and its pool) to 8 units (present in all areas). The use of this scale provides a better resolution than the binary classification (widespread vs restricted species) that has been used in other studies.

For species in the pool, the frequency distribution of the number of occupied geographical areas was approximately normal (Fig. 5.1). This allowed me to test the null hypothesis that the Yucatán fauna does not differ in terms of dispersal ability of its constituent species, by using the statistical distribution of the mean of samples from finite populations (Freund and Walpole, 1987; Appendix C). The mean for the pool was 4.26 units with a variance of 3.65. The observed mean for the Yucatán fauna was 5.35 units with a sample variance of 2.92 (Figure 5.1). The probability of observing a mean  $\geq 5.35$  for a sample of  $n = 31$  is very low ( $z = 4.26$ ,  $P < 0.001$ ). The null hypothesis is clearly rejected; species with larger areas of distribution are overrepresented in the bat fauna of Yucatán.

#### Summary of Tests for Composition

The Yucatán bat fauna does not differ in species composition from the pool in terms of taxonomic structure, feeding habits, roosting habits, or S/G ratio. The only

apparent difference in composition is that the faunal subset present in Yucatán is composed of more widespread Neotropical species than is the faunal subset that is absent. If one accepts the correlation between area of distributional range and colonization ability, then it can be said that the bat fauna of Yucatán is constituted primarily by those species with superior dispersal capabilities.

#### Morphological Comparisons

Results of the comparisons based on species composition in the previous section showed little evidence for non-random patterns in the Yucatán bat fauna. Such comparisons, however, provide only a crude perspective of subtle ecological differences that might exist between communities of the pool and the derived faunas. Ideally, comparative studies in community ecology are to be based on detailed information on the ecological characteristics of the member species. The collecting of adequate ecological data for large assemblages of species, however, is prohibitively difficult in most cases, limiting the use of this approach.

A compromise is the use of morphological characters as indicators of ecological features of the species, in what is known as the ecomorphological approach (Karr and James, 1975). Ecomorphological studies assume that variation in morphology is associated with variation in ecological or behavioral traits. Significant correlation between

morphology and ecology has been shown for several animal groups, including insects (Gilbert, 1985; Harder, 1985), fish (Gatz, 1979), lizards (Losos, 1990), birds (reviewed by Leisler and Winkler, 1985), and bats (reviewed by Findley and Wilson, 1982; also Fleming, 1991). Other studies have criticized the approach or have found no significant association between morphology and ecology or behavior (Wiens and Rotenberry, 1980).

Morphology has been used to test the competition hypothesis of community organization. The idea that competition affects the morphology of interacting species goes back at least to Lack (1947), who observed that bill size in Darwin's finches varied according to the number of potential competitors in the islands of the Galápagos Archipelago. Brown and Wilson (1956) coined the term character displacement to refer to the phenomenon that related species tend to be less similar to each other when sympatric than when allopatric. Hutchinson (1959) reported a remarkably constant ratio between the measurements of trophic structures of similar (and potentially competing) sympatric species, suggesting a divergence caused by interspecific competition. Subsequently, several studies reported communities with morphological patterns apparently consistent with the theory of character displacement (reviewed by Simberloff and Boecklen, 1981).

In recent years, upon more skeptical inspection, the conclusions of most of these studies have been challenged.

The empirical evidence for character displacement was critically reviewed by Grant (1972, 1975), who concluded that few of the reported examples could be considered genuine cases of competitive displacement. Similarly, the majority of the published cases of alleged constancy of size ratios were dismissed when tested against appropriate null models (Simberloff and Boecklen, 1981; Roth, 1981). Finally, Strong et al. (1979) found little evidence for community-wide character displacement in the two island faunas that they compared with pool sources.

More recently, other authors have criticized the early null models and have proposed new ones, with mixed results (Case et al., 1983; Colwell and Winkler, 1984; Moulton and Pimm, 1983; Schoener, 1984). At this point, competition-driven morphological structure in communities seems to be a real phenomenon, although not as widespread as believed before.

Because ecological information on bats is very difficult to gather in the field, several researchers have relied on morphology to study chiropteran communities. That variation in ecological features of bat species is correlated with morphological characteristics seems to be well established (reviewed by Findley and Wilson [1982]; also Arita [1990], Fleming [1991], and Humphrey et al. [1983]).

Inspired by Hutchinson (1959), early studies of bat communities searched for patterns based on the constancy of

size ratios of potentially competing species (Fleming et al., 1972; LaVal and Fitch, 1977; McNab, 1971; Tamsitt, 1967). Subsequently, Simberloff and Boecklen (1981) re-analyzed the data of some of these studies and found very little evidence for constancy of size ratios.

Beginning with Fenton (1972) and Findley (1976), other researchers have studied the structure of bat communities by analyzing the distribution of bat species in morphological bivariate or multivariate space (e.g. Crome and Richards, 1988; Findley and Black, 1983; Humphrey et al., 1983; McKenzie and Rolfe, 1986; McKenzie and Start, 1989; Schump, 1984; Willig and Moulton, 1989). All of these studies but one (Willig and Moulton, 1989) have reported some degree of organization (non-randomness) for the communities analyzed. The details of the methods used vary considerably, however, and it is difficult to compare the results of the different papers. Willig and Moulton (1989), for example, examined large faunas, whereas the other studies concentrated on more particular communities or guilds.

In this section, I use the ecomorphological approach to analyze the bat fauna of Yucatán. I compare the distribution of the species of Yucatán in morpho-space with that of the source pool, providing new tests for the null hypothesis that the derived fauna is a random subsample of the pool.

## Measurements

I examined museum specimens deposited in the collection of the National University of México (UNAM) for all bat species in the pool. Five external and five skull measurements were recorded for each specimen. Length of the forearm (FA) is a measure of overall size. Length of the tip of the wing (TIP = lengths of the metacarpal and the phalanges of the third digit) and length of the fifth digit (D5) correlates with wing span and wing width, respectively. Length of the tibia (TIB) measures the size of the uropatagium in the species that have one. The length of the ear (EAR) is an index of auditory and echolocation capabilities in bats (Arita, 1990; Fenton, 1972). The greatest length of the skull (GLS), the depth of the braincase (DBC), and the mastoid breadth (MB) quantify the size of the skull in the three dimensions, whereas length of maxillary toothrow (MTR) and width at the level of the last molars (MM) measure the size of the trophic apparatus. All variables except EAR were measured directly from museum specimens following the standard procedures (DeBlase and Martin, 1981). The length of the ear was recorded from the collectors' tags.

I measured adult specimens both from the pool area and from Yucatán. For most species reported from Yucatán, sample size included at least five males and five females from each area. For a few very rare species, such as

*Phyllostomus stenops*, only one or few specimens were available from the area of study.

### Sexual Variation

Sexual dimorphism can pose special problems for comparative studies of community ecology, leading to the necessity of creating separate "morphospecies" for males and females (e.g., Dayan et al., 1989, 1990). In some cases, this convention is an artificial arrangement, because even if measurements for males and females of the same species are different, they may be correlated (Ralls and Harvey, 1985), violating the assumption of independence inherent in null models (Dayan et al., 1989, 1990). The use of morphospecies, however, can provide information on the relative importance of intra- and interspecific competition (Dayan et al., 1989, 1990).

I performed preliminary tests for non-geographic sexual variation. For the species with a sufficient sample size, I compared males against females by performing one-way analyses of variance (ANOVAs) for individual variables and multivariate analyses of variances (MANOVAs) for external and for skull variables. Separated analyses were made for the pool and the derived fauna.

Of the 52 MANOVAs for external variables, five (9%) showed significant sex differences ( $P < 0.05$ ). Species showing differences included the fishing bat (*Noctilio leporinus*), the phyllostomid *Micronycteris brachyotis*, and

three emballonurids (*Rhynchonycteris naso*, *Peropteryx kappleri*, and *Saccopteryx bilineata*). Eight of the 52 MANOVAs for skull characters showed significant sexual dimorphism. Species included *N. leporinus*, one mormoopid (*Pteronotus parnellii*), three stenodermatines (*Artibeus jamaicensis*, *Dermanura phaeotis*, and *Vampyressa pusilla*), and three molossids (*Molossus ater*, *Molossus sinaloae*, and *Nyctinomops laticaudatus*). Besides these species, another 13 showed significant sex differences for at least one character in univariate ANOVAs. Altogether, 80 (20%) of 396 univariate ANOVAs showed significant sex differences.

Results suggest that, overall, sexual dimorphism is not very marked among bats in the study area; the number of significant MANOVAs was relatively low and did not warrant the creation of morphospecies that could lower the effective sample sizes in subsequent analyses. Even when statistically significant, intraspecific sexual differences are negligible when compared with the interspecific variation. In North American mustelids, the average of the female:male ratio for condylobasal length is 1:1.13 (from Table 1 in Dayan et al., 1989). In contrast, the ratio smaller-sex:larger-sex for variables showing significant ANOVAs in bats was as low as 1:1.03 and was >1.1 only for some molossids and for *Noctilio leporinus*. Because *N. leporinus* is treated here as the only member of the piscivorous guild, its marked sexual dimorphism does not affect the results. I decided not to use morphospecies for

molossids despite their sexual dimorphism because my sample sizes would not have been large enough to provide reliable results if sexes were separated. For the remaining groups, the effect of sexual differences is minimal and, for studies of ecological communities, can be safely ignored.

### Tests for Morphological Shifts

Theoretically, competition can lead to differences in the morphological structure between a pool and its derived faunas by two different processes. One process is competitive exclusion, the selective elimination of certain species that are less able to compete. The other is character displacement, a shift in morphology within a species to minimize competition with another species. (The opposite process, competitive release [Van Valen, 1965], that would appear if competition is milder in the derived fauna, is normally not considered in null-model analysis of competition). The final outcome is the same for both processes: less overlap in the morphological space of the derived fauna.

Most studies have failed to differentiate between the effects of the two processes. In null-model studies of bat faunas, both McKenzie and Rolfe (1986) and Willig and Moulton (1989) used a single mean or a single range of measurements for each species for both the source and the derived faunas without testing for morphological shifts. By

doing so, they tested for the effect of competitive exclusion, but not for character displacement.

To test for morphological shifts, I performed two-tailed *t*-tests and MANOVAs comparing samples from the pool and from Yucatán for the 18 species with sufficient sample sizes.

Results showed little evidence for geographic variation. In external measurements, four of the 18 species showed a consistent pattern of variation (at least two significantly different variables and significant MANOVA). The species were *Myotis keaysi*, *Natalus stramineus*, *Pteronotus davyi*, and *P. parnellii*. In all species, the mean for the pool was > than the mean for Yucatán.

Similarly, four species showed consistent variation in skull measurements. *Artibeus jamaicensis*, *Diphylla ecaudata*, and *P. parnellii* were larger in the pool than in Yucatán, whereas *Peropteryx macrotis* was larger in the derived fauna.

Even if significant, most differences between samples were negligible when compared with interspecific variation. As an example, in *Pteronotus parnellii*, the species with the clearest pattern of variation, the maximum mean-size ratio was 1:1.07 for TIB. For the same variable, the ratio between the mean for *P. parnellii* and its congeneric *P. davyi* in the pool is 1:1.25. For other significantly different measurements in other species, the ratio was as low as 1:1.03 and in most cases was <1:1.05. No consistent

pattern of intraspecific morphological difference between the pool and the Yucatán fauna can be claimed.

With morphological shifts dismissed, one can safely test for competitive exclusion. In the following analyses I assumed no intraspecific differences in morphology between the pool and the derived fauna and combined their samples to form a single unit for each species.

### Univariate Tests for Morphological Structure

One way of testing for the effect of competition in animal communities is to search for segregation among the species when they are arranged along a size gradient. The premise is that if species are segregated in a morphological dimension, that would suggest differentiation in resource use and niche separation among them. A particular hypothesis regarding size segregation is the constancy of size ratios first reported by Hutchinson (1959) for pairs of closely related sympatric species and extended to assemblages of more species by subsequent authors (Holmes and Pitelka, 1968; see review by Simberloff and Boecklen, 1981). One methodological advantage of Hutchinson's proposed arrangement to test for competition is that it can be stated in the form of simple and potentially testable hypotheses. In the last decade, several specific statistical procedures have been developed to test directly the hypothesis of size-ratios constancy in communities (Arita, M.S.a; MacNally, 1988; Pleasants, 1990; Roth, 1981;

Schoener, 1984; Simberloff and Boecklen, 1981; Strong et al., 1979; Tonkyn and Cole, 1986).

To test for competitive displacement in the Yucatán bat fauna, I use here several parameters that have been proposed in previous studies. For a community of  $n$  species arranged along a logarithmic size gradient, let  $x_i$  be the log value of the size of the species, so  $x_1$  corresponds to the smallest and  $x_n$  to the largest species. Define  $d_i$  to be  $= x_{i+1} - x_i$  ( $1 \leq i \leq n-1$ ), the distance between adjacent species. Because subtraction of logarithms is equivalent to division of raw numbers,  $\text{antilog } d_i = x_{i+1}/x_i$ , the size ratio between species  $i$  and its larger neighbor in the size line. Under the hypothesis of size-ratio constancy among contiguous species, all  $d$  values should have about the same magnitude.

The parameter Mean is the average distance between adjacent species in the morphological dimension [Mean =  $1/(n-1) \sum d_i$ , where the summation goes from  $i = 1$  to  $n-1$ ]. Pleasants (1990) defined Mean as a community-wide parameter, meaning that its value is determined by the position of all species. As pointed out by Arita (M.S.a), however, if species are arranged on a line, the value of Mean becomes fixed by the position of only two of the species, the smallest and the largest. Because of this, Mean is not a community-wide parameter, and it cannot be used to test for constancy of size ratios. Nevertheless, it provides a simple measure of the range of values that the community

occupies along the line because it is directly proportional to the summation of distances.

In comparisons of a fauna with a finite pool, the power of Mean is limited because its frequency distribution depends on the probabilities of drawing particular pairs of species (see discussion by Arita, M.S.a). Being aware of this limitation, I included Mean in the following analyses for the sake of completeness, and to allow comparisons with the multivariate examples.

The parameter Var (Poole and Rathcke, 1979) is the variance of the values of  $d$  [ $\text{Var} = (n-2)^{-1} \sum (\text{Mean}-d_i)^2$ , where the summation goes from  $i = 1$  to  $n-1$ ]. Min is the minimum value of  $d$ , that is the magnitude of the shortest segment of the morphological line.

If distances are arranged in increasing order of magnitude and they are renamed so  $g_1$  becomes the shortest and  $g_{n-1}$  the longest distance, the  $G$  parameters of Simberloff and Boecklen (1981) can be defined as follows:  $G_{r,s} = g_r/g_s$  (the ratio of the  $r$ th smallest to the  $s$ th smallest segments of the morphological line). Simberloff and Boecklen (1981) proposed the use of three of these ratios ( $G_{1,n}$ ,  $G_{2,n}$ , and  $G_{1,n-1}$ ) to test the hypothesis of size-ratio constancy. Pleasants (1990) argued deficiencies in the  $G$  parameters, but Arita (M.S.a) has shown otherwise, and the efficiency of these parameters in detecting character displacement has been demonstrated in recent papers (Dayan et al., 1989, 1990).

I tested for unusual dispersion and for constancy of size ratios in four of the feeding categories of Yucatán bats (frugivores, gleaners, aerial insectivores, and molossids). Sample sizes were insufficient for the fishing ( $n = 1$ ), hematophagous ( $n = 2$ ), and nectar-feeding ( $n = 1$ ) groups. For each category, I constructed morphological gradients for each of the 10 variables defined above. Then, using a program in BASIC, I computed the parameters for character displacement (Mean, Var, Min, and the G parameters) and compared the values against hypothetical communities generated by randomly sampling the pool. For the gleaner and the molossid insectivore groups, I generated all possible assemblages of the same number of species as in the Yucatán fauna (364 possible combinations of 3-species assemblages from a pool of 14 gleaner species; 462 possible combinations of 6-species communities from a pool of 11 molossids). For frugivores and aerial insectivores, I created 1,000 random assemblages. (For frugivores, there are 1,716 possible combinations of 6 species from a pool of 13; for aerial insectivores, with a pool of 23 species,  $>1.35 \times 10^6$  assemblages of 12 species are possible).

The null hypothesis here is that species in the real communities are not particularly segregated along the morphological line. The alternative hypothesis states that species are more uniformly distributed in the logarithmic scale of the real communities than expected by randomly sampling from the pool. In this case a one-tailed test is

appropriate because the alternative hypothesis predicts a definite direction in the deviation from expected. I calculated the one-tailed probabilities by comparing the observed values of the six parameters against the distribution obtained from the hypothetical communities generated from the pool (Table 5.3).

Frugivores showed very little tendency towards segregation. There was no significant ( $P > 0.05$ ) deviation from expected for any of the parameters in any of the variables. Only the arrangement in the DBC line showed a slight, and almost significant ( $P = 0.05$ ), regularity of size ratios as shown by the Min and  $G_{1,n}$  parameters. In this feeding group, there is little support for the size-ratio constancy hypothesis.

For the group of gleaners, none of the external variables indicated any tendency to morphological segregation (all cases  $P > 0.05$ ). Two parameters suggested segregation for MTR and for MB ( $P < 0.05$ ).

In the category of aerial insectivores, only one of the ten variables (MB) showed indication of a regular arrangement of species. For this variable, parameters Min and  $G_{1,(n-1)}$  deviated significantly ( $P < 0.05$ ) from their expected values, but the other parameters did not. Such pattern of significant and non-significant values was shown by Arita's (M.S.a) example of a community in which regularity of sizes was broken by a single outlier. In the present case, the evidence for constancy of size ratios is

too weak to claim competitive displacement, because significant values were observed for only one variable.

Among molossids, one variable (MM) showed an isolated significant deviation ( $P < 0.05$  for  $G_{2,n}$ ), and the parameters for another (GLS) were significantly ( $P < 0.05$ ) different. For GLS, only Mean failed to indicate displacement. As demonstrated by Arita (M.S.a), the Mean parameter is only a weak indicator of segregation. The fact that three of the other parameters showed highly significant deviations from expected is sufficient reason to reject the null hypothesis of a random distribution of GLSs. Interestingly, the regular arrangement showed by GLS does not appear in the other variables.

### Multivariate Tests

The multivariate analysis of structure in ecological communities is a direct extension of the univariate case. The procedure involves the study of the relative position of the different species in an  $n$ -dimensional morphospace that is assumed to mirror the multidimensional niche space (e.g., Findley, 1976; Findley and Black, 1983; Karr and James, 1975; Moulton and Pimm, 1986; Ricklefs and Travis, 1980; Ricklefs et al., 1981; Willig and Moulton, 1989). In an assemblage in which community-wide character displacement is an active force, species would tend to be more separated from each other and more evenly distributed in the morphospace than expected from a random arrangement.

I performed separate analyses for each of the feeding groups described in the previous section, using the skull measurements. I used principal-components analysis of the log-transformed data to reduce the dimensionality of the morphospace and retained only the first two components because they accounted for most (>90%) of the variance of the original variables in all cases. Principal components were extracted from the correlation matrix using PROC PRINCOMP of the Statistical Analysis System (SAS Institute, 1985). Using a BASIC program, I computed the Euclidean distances for each of the  $n(n-1)/2$  pairs of species in the plane of the first two principal components. Because principal components are uncorrelated between each other, Euclidean distances provide a satisfactory measurement of the relative spacing of the points in the plane.

Nearest-neighbor distance analysis. I used mean neighbor distances to quantify the spacing of the elements of the assemblages. I calculated not only the nearest-neighbor distances as in previous studies, but also a complete series of means for the different orders of nearest-neighbors as defined by Manly (1991). For a guild of  $n$  species,  $q_i$  ( $i = 1$  to  $n - 1$ ) is defined as the mean distance from points to their  $i$ th nearest neighbor. The first-order mean distance ( $q_1$ ) is equal to the nearest-neighbor distance used in previous studies to quantify

species packing in the community (Findley, 1976; Ricklefs and Travis, 1980; Travis and Ricklefs, 1983).

As defined here,  $q_1$  tests for patterns of competitive exclusion. An unusually high value for this parameter would indicate a lowered frequency of pairs of very similar species in the derived fauna, suggesting the effect of exclusion of competing species. Parameters for higher orders test for patterns of segregation among more distant species. High values for these parameters would show displacement among species with less similarity, indicating the effect of a more diffuse competition.

For each feeding category, I used a BASIC program to calculate the  $n-1$   $q$  parameters and compared their value against the frequency distribution compiled from 100 randomly-generated communities from the pool. Under the competition hypothesis,  $q$  values should have significantly higher values than expected by chance. I used one-tailed probabilities for testing the null hypothesis of no segregation.

For the group of frugivores,  $q$  values tended to be > expected, with three of them ( $q_2$ ,  $q_3$ , and  $q_4$ ) being significantly so (one-tailed  $P < 0.05$ , figure 5.2, top). For gleaners and for molossid insectivores, all  $q$ s were within the range of expected values (Figure 5.2). For molossids,  $q_1$  is very low, suggesting that pairs of neighbor (similar) species tend to be more similar to each other than

expected. The deviation from the null distribution is not significant, however ( $P > 0.05$ ).

In the aerial insectivore group, all  $q_s$  are within the expected values. The first three are very close to the upper 5% limit, however, suggesting but not demonstrating a tendency of similar species not to coexist in the Yucatán fauna.

Analysis of minimum-spanning trees. In an additional battery of tests, I computed a series of parameters that are analogous to those used in the univariate analyses. First, I wrote a BASIC program to construct the minimum-spanning tree (MST) in the plane of the first two principal components for each feeding category. MST is the series of  $n-1$  segments connecting all species in the community that has the minimum extension. The length of the MST has been used to quantify the dispersion of species in morphospace (Moulton and Pimm, 1986; Willig and Moulton, 1989). Using the lengths of the segments in the MST as the lengths of the morphological lines in the univariate cases, I calculated the same variables: Mean, Var, Min, and the  $G$  parameters.

Although similar, these parameters are not exactly equivalent in the univariate and the multivariate cases. In the univariate analyses the segments are arrayed along a line, whereas in the multivariate case they are arranged in multidimensional space (in the present study, on a plane).

In contrast with the univariate case, the value of Mean is not determined by the position of only two species in the multivariate case. It can assume different values depending on the position of the rest of the species. Mean measures the dispersion of the species because it is directly proportional to the total length of the minimum spanning tree.

The other parameters measure the segregation of the species in the morphological space. Significant values for Var, Min, or the  $G$  parameters would indicate constancy of distances in the morphospace, suggesting an even distribution of the species.

In the present study, the analysis of the minimum-spanning trees demonstrated no tendency for overdispersion or segregation. None of the values for any of the parameters was significantly different from expected in any of the cases (Figure 5.3, Table 5.4).

#### Summary of Morphological Tests

I found no consistent pattern of sexual or geographic intraspecific variation. Univariate comparisons showed no sign of segregation for frugivores and only weak evidence for insectivores and molossids (significant values for one of the variables in each case). For gleaners, there is a non-significant tendency towards segregation.

In the multivariate analyses, the inspection of the  $q$  parameters suggested, but failed to demonstrate clearly, the

exclusion of pairs of very similar species. In the case of the frugivore group, the analysis showed a more subtle segregation of species in the morphological space. Minimum-spanning trees showed no segregation.

## Discussion

### Species Composition

The analyses of composition of the Yucatán bat fauna provided little evidence for any structuring force. The results indicate that the study fauna is a random subsample of the pool in terms of taxonomic composition, feeding strategies, and roosting preferences. Dispersal ability, — — measured by the size of distributional range, is the only characteristic that differentiates the fauna of Yucatán from its source.

In the present study, I used the traditional classification of Phyllostomidae in six subfamilies (Hill and Smith, 1984; Smith, 1972). Baker et al. (1989) proposed a new arrangement that summarizes recent information on the phylogeny of this diverse family. My results are not affected if the new classification is used, because the major groups remained intact in the new arrangement, changing only their position in the phylogenetic tree and their hierarchy from subfamilies to tribes. The only taxonomic group that would yield different results is the Phyllostominae. Baker et al. (1989), acknowledging previous evidence that phyllostomines are a paraphyletic taxon

(Baker, 1967; Honeycutt and Sarich, 1987; Patton and Baker, 1978), split the group in two subfamilies and left *Macrotus* and *Micronycteris* as genera of uncertain position. The Vampyrinae subfamily in the new classification would be represented in Yucatán by one species out of three from the pool, whereas the tribe Phyllostomini would be represented by one of the eight species in the pool. In both cases the deviation from the expected number of species is not significant ( $P > 0.05$ ).

Food categories coincide closely with the taxonomic arrangement of neotropical bats. For example, molossids are in their own feeding group, the gleaners are in the subfamily Phyllostominae, and all frugivores are classified in the subfamilies Carrollinae and Stenodermatinae. Comparative studies of the neotropical bat fauna face the unavoidable mixing of ecological effects and phylogenetic inertia (Felsenstein, 1985). Not surprisingly, the analysis using feeding groups yielded similar results to the one performed with taxonomic groups.

The analysis of the S/G ratio dismissed the significance of some patterns of the Yucatán fauna that would seem striking. For example, only one of the six species of the genus *Myotis* that exist in the pool is present in Yucatán (*M. keaysi*), and the peninsular fauna harbors only one nectar-feeding bat (*Glossophaga soricina*). Other tropical areas of México normally contain several species of *Myotis* and many nectarivorous species (for

example, the tiny state of Colima in western México contains six *Myotis* species and five Glossophaginae in a fauna of 47 bats, Ramírez-P. et al., 1986). Rarefaction demonstrated that the patterns in the Yucatán fauna are not as unexpected as they seem to be. In fact, the probability of getting one or no *Myotis* in random 31-species samples from the pool is  $P = 0.15$  (using the hypergeometric distribution).

Similarly, the apparent underrepresentation of phyllostomines in Yucatán (three species out of 14 in the pool) is not unexpected based on random sampling from the pool. The seeming orderly patterns of species composition in the fauna of Yucatán are simple sampling artifacts.

The failure of tests to show any sign of organization undermines the idea of competition as a structuring force of the study fauna. Under the competition hypothesis, one would have expected differences in taxonomic or ecological composition of the derived community and a significantly lowered S/G ratio. Results showed otherwise.

Widespread bat species are more likely to be present in Yucatán than forms with restricted distribution. This would indicate that colonization ability is the key factor determining the particular combination of species that constitute the study fauna. That could also be a subtle indication of competitive forces structuring the fauna, however. Widespread species might have larger distributional ranges because they are superior competitors, capable of excluding other species in impoverished areas.

Conversely, species with small distributional ranges would be poor competitors, restricted to rich areas in which competition is less strong. Unfortunately, there is no experimental study of competition in Neotropical bats, and it is not possible to establish the relative competitive ability of the different species. The possible correlation between competitive ability and area of distributional range will remain as a speculation until more field data become available.

#### Sexual and Geographic Variation

With few exceptions, sexual dimorphism is low among bats of the study area. Only the fishing bat (*Noctilio leporinus*) and two species of *Molossus* (*M. ater* and *M. sinaloae*) showed differences between the sexes as marked as the interspecific differences.

Dayan et al. (1989, 1990) have discussed the implications of marked sexual dimorphism to the theory of character displacement. They proposed that for some guilds of carnivores, intraspecific competition between the sexes could lead to the strong dimorphism that they documented. They found regular spacing of elements along size gradients when treating sexes within species as independent entities ("morphospecies"). They interpreted this pattern as the result of an interaction between intra- and interspecific competition.

In the bat fauna of Yucatán and the pool, interspecific competition (if acting at all) would seem to be stronger than intraspecific competition, based on the results of the analysis of sexual dimorphism. Competition does not need to be invoked, however, to explain the absence of sexual dimorphism among the bats of the study area. Several other ecological, physiological, and behavioral forces can explain the presence (or absence) of sexual dimorphism in mammals (Findley and Wilson, 1982; Myers, 1978; Ralls, 1976, 1977; Ralls and Harvey, 1985; Williams and Findley, 1979).

Results showed almost no indication of geographic variation between the pool and Yucatán. The only species with a consistent pattern both for external and for skull measurements was *Pteronotus parnellii*. The lack of geographic variation indicates that the fauna of Yucatán has a very recent origin, that it still has a great deal of interchange with the pool, or both. As already discussed, the paleontological record is very scant and at this time is impossible to make clear inferences about the origin of the Yucatán fauna. Given the simple topography of the peninsula and the volant nature of bats, it is reasonable to assume some genetic interchange between the study fauna and its pool. Unfortunately, there are no studies on regular or seasonal movements of bats in this area. Comparisons made in the present study are not affected whether there is such interchange. The question still is if there is some

definitive rule that determines which species exist in the derived fauna.

The competition hypothesis received little support from the analysis of geographic variation. If the bat fauna of Yucatán were organized by competition, one would have expected variations in size consistent with the phenomenon of competitive character displacement. With the exception of *P. macrotis*, the few species that show significant geographic differences are larger in the pool area than in Yucatán. This indicates more a common trend of geographic variation than the effect of competitive displacement (Grant, 1972, 1975). A complete test for character displacement would require data from more sites, specifically for places where species found in Yucatán are absent (see discussions in Brown and Wilson 1956; Grant, 1972, 1975).

#### Ecomorphological Analyses

Results of the ecomorphological analyses varied among the four feeding groups studied. In general, there was little evidence for unusual patterns as indicated by morphology, but some exceptions deserve some discussion.

In the group of frugivores, univariate analyses and the analysis of the MST showed almost no evidence for unusual patterns. Only for one variable (DBC), for which the Min and  $G_{1,n}$  parameters detected some segregation among the species ( $P = 0.05$ ), indicated some degree of separation.

Dayan et al. (1989, 1990) have shown that segregation can occur in some measurement, while others may show a great deal of overlap. They found that segregation in size occurs principally along the line of the diameter of the upper canines, a variable directly associated with the trophic apparatus of the animals.

In the case of the frugivorous bats of Yucatán, it is difficult to interpret the segregation in terms of depth of the braincase, a pattern that is not shown for the variables associated with trophic structures. A more parsimonious interpretation is that the almost significant value for DBC could have originated just by chance. In analyzing ten variables, it is not unlikely that one of them shows significant results just by chance.

Analysis of the neighbor distances did demonstrate the existence of a unlikely pattern. That  $q_1$  is not significantly larger than expected means that pairs of very similar species coexist in the Yucatán fauna. Significant values for the three intermediate  $q_s$  suggest the tendency of more distant species to segregate in morphological space. In terms of competition, these results indicate that there is no demonstrable competitive exclusion between very close (=similar) species, but they do suggest that diffuse competition might determine the spacing among more distant (=less similar) species.

In this group, two pairs of close species (*Sturnira liliium* with *Dermanura phaeotis*, and *Artibeus jamaicensis*

with *A. lituratus*) determined the low  $q_1$  value. High values for the intermediate  $q_s$  were caused by the more spaced separation among these pairs and the remaining two species in the category (*Carollia perspicillata* and *Centurio senex*). This morphological pattern has an ecological explanation. *Carollia* species differ from other frugivorous bats in that they feed primarily on *Piper* fruits (Bonaccorso, 1979; Fleming, 1988; Palmeirim, 1989), whereas many stenodermatines like *Artibeus* and *Dermanura* consume more *Ficus* and *Cecropia* fruits (Bonaccorso, 1979; Palmeirim, 1989; Vázquez-Yáñez et al., 1975). Bonaccorso (1979) suggested that *Centurio senex* has a peculiar feeding behavior and classified it in its own guild. The assemblage of frugivorous bats in Yucatán is constituted by two pairs of species with similar morphology and size (and presumably ecological traits) and two other, more distant, species.

This interpretation is not in conflict with the results of the other analyses. Univariate parameters and the MST analysis focus on distances between nearest neighbors, and their non-significant results are coincident with the non-significant  $q_1$  value. Higher order  $q_s$  refer to distances among more distant neighbors and their significant values do not contradict the previous conclusions.

For the category of gleaners two of the univariate analyses showed segregation (for MTR and MB), whereas the parameters for the rest of the measurements and for the MST did not detect such segregation. Although only two cases

indicated displacement, competition cannot be completely ruled out in this group. Arita (M.S.a) points out that for small assemblages ( $n < 6$ ) most parameters fail to show displacement unless the segregation is nearly perfect. In Yucatán's 3-species assemblage of gleaners, 12 out of 20 probability values for skull measurements are  $< 0.1$ . No deviation can be safely claimed if the probability is larger than the a priori  $\alpha$  value (0.05), but the low observed probabilities with such a small sample size could suggest some displacement. Results presented here, however, cannot prove this suggestion.

The two  $q$  values for gleaners are within the limits of expected values. No deviation from randomness can be claimed. With only three species in the group, however, the power of the analysis is limited, and interpretations have to be made with caution. Aside from the results of the analyses, it can safely be stated that there is little overlap in the diets of the three phyllostomines in Yucatán. *Micronycteris megalotis* is a small bat that feeds primarily on insects and fruit (Gardner, 1977); *Mimon cozumelae* is a medium-sized animal that relies on larger arthropods and small vertebrates such as geckos; and *Chrotopterus auritus* is a large bat that feeds mainly on small mammals and birds (Medellín, 1989).

As in previous groups, there is little evidence of segregation in the aerial insectivore category. Only one univariate variable detected some segregation, and the

parameters of the MST showed none. The first three  $q$  parameters have high values that are very close to the 5% upper limit of the expected distribution. This suggests that pairs of very similar species tend to be absent from Yucatán. The tendency is not significant at the established  $\alpha$  value (0.05), however, so no real trend can be safely claimed.

For the molossids, only GLS showed significant segregation of the species. One could speculate that the length of the skull could be a key dimension for the organization of the assemblage of molossids, but there is no obvious reason why this should be so. Besides, all other univariate variables and the parameters of the MST showed no appreciable pattern. In this group, all  $q$ s were below the upper limit of the expected values. In fact some of them were quite low, suggesting a tendency of pairs of very similar species to coexist in Yucatán.

Overall, the results of this study provide very weak support for the idea that the Yucatán bat fauna is organized by some ecological force. In particular, competition was not clearly demonstrated by the morphological comparisons between Yucatán and the pool. Only the category of gleaners showed some indication of segregation in morphological space, and the group of frugivores appeared to have some organization in intermediate orders of nearest neighbor distances. The bulk of the evidence, however, points to a random assemblage of the fauna of Yucatán.

That almost no particular pattern can be shown for Yucatán when compared with random assemblages from the pool does not mean that the study fauna lacks order altogether. One could argue that some pattern might be already present in the pool, and that the Yucatán fauna simply cannot be more organized than its source. If this is true, any attempt to show a more conspicuous pattern in the Yucatán fauna would be futile. Nevertheless, the analysis of the patterns of the pool was not the objective of this study, and this idea is presented here only as a speculative, alternative explanation.

Table 5.1 List of bat species recorded from Yucatán.

Emballonuridae	Desmodontinae
<i>Peropteryx macrotis</i>	<i>Desmodus rotundus</i>
<i>Saccopteryx bilineata</i>	<i>Diphylla ecaudata</i>
Noctilionidae	Natalidae
<i>Noctilio leporinus</i>	<i>Natalus stramineus</i>
Mormoopidae	Vespertilionidae
<i>Mormoops megalophylla</i>	<i>Eptesicus furinalis</i>
<i>Pteronotus davyi</i>	<i>Lasiurus blossevillii</i>
<i>Pteronotus parnellii</i>	<i>Lasiurus ega</i>
Phyllostomidae	<i>Lasiurus intermedius</i>
Phyllostominae	<i>Myotis keaysi</i>
<i>Chrotopterus auritus</i>	<i>Rhogeessa tumida</i>
<i>Micronycteris megalotis</i>	Molossidae
<i>Mimon cozumelae</i>	<i>Eumops bonariensis</i>
Glossophaginae	<i>Eumops glaucinus</i>
<i>Glossophaga soricina</i>	<i>Molossus ater</i>
Carolliinae	<i>Molossus sinaloae</i>
<i>Carollia perspicillata</i>	<i>Nyctinomops laticaudatus</i>
Stenodermatinae	<i>Promops centralis</i>
<i>Artibeus jamaicensis</i>	
<i>Artibeus lituratus</i>	
<i>Centurio senex</i>	
<i>Dermanura phaeotis</i>	
<i>Sturnira lilium</i>	

Table 5.2.-Expected and observed values for the number of species in taxa and feeding categories of bats of Yucatán. Probabilities are two-tailed exact probabilities of deviations  $\geq$  observed, calculated using the hypergeometric distribution. Expected number of species is based on the proportions in the source pool.

	Species in Yucatán	Expected	<i>P</i>
<u>TAXA</u>			
Emballonuridae	2	2.25	1.00
Noctilionidae	1	0.45	0.45
Mormoopidae	3	1.80	0.32
Phyllostominae	3	6.29	0.07
Glossophaginae	1	1.80	0.62
Carolliinae	1	0.90	0.20
Stenodermatinae	5	4.94	1.00
Desmodontinae	2	1.35	0.58
Natalidae	1	0.45	0.45
Vespertilionidae	6	5.84	1.00
Molossidae	6	4.94	0.53
<u>FEEDING CATEGORIES</u>			
Frugivores	6	5.84	1.00
Gleaners	3	6.29	0.07
Aerial insectivores	12	10.33	0.45
Molossids	6	4.94	0.53
Nectarivores	1	1.80	0.62
Hematophagous	2	1.35	0.58
Fish eaters	1	0.45	0.45

Table 5.3-- Values and one-tailed probabilities (in parentheses) for parameters of competitive displacement for the bat fauna of Yucatán. For  $G$  parameters and for Min, probabilities are for values  $\geq$  than observed. For Mean and Var, probabilities are for values  $\leq$  observed.

<u>FRUGIVORES</u>	(1,000 simulations)				
	FA	TIP	D5	EAR	TIB
Mean	0.127 (0.323)	0.122 (0.204)	0.117 (0.421)	0.093 (0.190)	0.116 (0.536)
Var	0.017 (0.707)	0.016 (0.784)	0.014 (0.698)	0.007 (0.701)	0.010 (0.701)
Min	0.019 (0.417)	0.012 (0.808)	0.007 (0.533)	0.009 (0.279)	0.003 (1.000)
$G_{1,n}$	0.058 (0.423)	0.039 (0.874)	0.024 (0.669)	0.047 (0.442)	0.012 (0.924)
$G_{2,n}$	0.106 (0.499)	0.055 (0.974)	0.041 (0.885)	0.192 (0.425)	0.211 (0.636)
$G_{1,(n-1)}$	0.106 (0.532)	0.063 (0.980)	0.039 (0.700)	0.054 (0.665)	0.016 (0.923)
	GLS	MTR	DBC	MB	MM
Mean	0.110 (0.186)	0.152 (0.162)	0.086 (0.294)	0.105 (0.306)	0.114 (0.217)
Var	0.005 (0.568)	0.010 (0.724)	0.001 (0.199)	0.007 (0.525)	0.010 (0.672)
Min	0.052 (0.055)	0.029 (0.237)	0.052 (0.050)	0.024 (0.152)	0.004 (0.664)
$G_{1,n}$	0.236 (0.172)	0.094 (0.308)	0.374 (0.050)	0.106 (0.199)	0.015 (0.847)
$G_{2,n}$	0.246 (0.434)	0.416 (0.349)	0.396 (0.223)	0.168 (0.382)	0.211 (0.427)
$G_{1,(n-1)}$	0.444 (0.105)	0.185 (0.248)	0.495 (0.074)	0.160 (0.330)	0.031 (0.815)

Table 5.3-- Continued.

<u>GLEANERS</u>	(364 simulations)				
	FA	TIP	D5	EAR	TIB
Mean	0.422 (0.115)	0.430 (0.225)	0.462 (0.115)	0.328 (0.173)	0.431 (0.173)
Var	0.016 (0.396)	0.023 (0.453)	0.020 (0.459)	0.106 (0.901)	0.002 (0.148)
Min	0.332 (0.107)	0.322 (0.159)	0.362 (0.085)	0.097 (0.506)	0.398 (0.071)
$G_{1,n}$	0.648 (0.236)	0.599 (0.286)	0.645 (0.256)	0.174 (0.731)	0.860 (0.107)
$G_{2,n}$	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)
$G_{1,(n-1)}$	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)
	GLS	MTR	DBC	MB	MM
Mean	0.305 (0.288)	0.297 (0.412)	0.336 (0.258)	0.339 (0.157)	0.311 (0.187)
Var	$5 \times 10^{-4}$ (0.113)	$3 \times 10^{-5}$ (0.036)*	0.002 (0.146)	$1 \times 10^{-4}$ (0.071)	0.034 (0.665)
Min	0.289 (0.110)	0.294 (0.110)	0.304 (0.052)	0.331 (0.036)*	0.181 (0.245)
$G_{1,n}$	0.903 (0.077)	0.976 (0.019)*	0.826 (0.096)	0.957 (0.038)*	0.410 (0.459)
$G_{2,n}$	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)
$G_{1,(n-1)}$	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)	1.000 (1.000)

\*  $P < 0.05$

Table 5.3-- Continued.

	<u>AERIAL INSECTIVORES</u> (1,000 SIMULATIONS)				
	FA	TIP	D5	EAR	TIB
Mean	0.057 (0.518)	0.061 (0.787)	0.050 (0.550)	0.065 (0.394)	0.057 (0.260)
Var	0.003 (0.388)	0.003 (0.276)	0.003 (0.825)	0.003 (0.383)	0.002 (0.488)
Min	0.002 (0.596)	0.014 (0.077)	0.007 (0.095)	0.002 (1.000)	0.003 (0.550)
$G_{1,n}$	0.011 (0.584)	0.068 (0.061)	0.045 (0.166)	0.011 (0.848)	0.024 (0.467)
$G_{2,n}$	0.016 (0.747)	0.068 (0.225)	0.051 (0.433)	0.028 (0.703)	0.047 (0.622)
$G_{1,(n-1)}$	0.020 (0.475)	0.144 (0.052)	0.058 (0.166)	0.017 (0.940)	0.025 (0.629)
	GLS	MTR	DBC	MB	MM
Mean	0.050 (0.483)	0.070 (0.405)	0.074 (0.460)	0.049 (0.403)	0.051 (0.589)
Var	0.003 (0.690)	0.003 (0.683)	0.004 (0.397)	0.002 (0.450)	0.001 (0.124)
Min	$1 \times 10^{-4}$ (0.374)	0.001 (1.000)	0.011 (0.087)	0.012 (0.030)*	0.014 (0.074)
$G_{1,n}$	$7 \times 10^{-4}$ (0.433)	0.006 (0.902)	0.060 (0.074)	0.076 (0.058)	0.098 (0.072)
$G_{2,n}$	0.016 (0.544)	0.068 (0.546)	0.051 (0.197)	0.028 (0.117)	0.047 (0.162)
$G_{1,(n-1)}$	$7 \times 10^{-4}$ (0.526)	0.008 (0.939)	0.064 (0.237)	0.140 (0.033)*	0.179 (0.046)

\*  $P < 0.05$ , \*\*  $P < 0.01$

Table 5.3-- Continued.

MOLOSSID	INSECTIVORES (462 SIMULATIONS)				
	FA	TIP	D5	EAR	TIB
Mean	0.082 (0.695)	0.068 (0.771)	0.695 (0.550)	0.638 (0.394)	0.574 (0.260)
Var	0.002 (0.106)	0.001 (0.219)	0.001 (0.058)	0.020 (0.574)	0.005 (0.178)
Min	0.017 (0.448)	0.034 (0.275)	0.028 (0.394)	0.000 (0.818)	0.009 (0.546)
$G_{1,n}$	0.117 (0.442)	0.337 (0.063)	0.248 (0.126)	0.000 (0.818)	0.046 (0.379)
$G_{2,n}$	0.407 (0.212)	0.406 (0.167)	0.398 (0.188)	0.100 (0.885)	0.251 (0.221)
$G_{1,(n-1)}$	0.149 (0.537)	0.351 (0.188)	0.298 (0.247)	0.000 (0.818)	0.076 (0.348)
	GLS	MTR	DBC	MB	MM
Mean	0.067 (0.576)	0.075 (0.619)	0.082 (0.500)	0.075 (0.413)	0.069 (0.424)
Var	$2 \times 10^{-4}$ (0.002)**	0.002 (0.102)	0.007 (0.751)	0.003 (0.379)	0.002 (0.162)
Min	0.051 (0.028)*	0.024 (0.275)	0.007 (0.545)	0.028 (0.249)	0.003 (0.621)
$G_{1,n}$	0.593 (0.002)**	0.186 (0.091)	0.032 (0.788)	0.185 (0.234)	0.025 (0.413)
$G_{2,n}$	0.628 (0.004)**	0.357 (0.165)	0.149 (0.483)	0.298 (0.396)	0.551 (0.043)*
$G_{1,(n-1)}$	0.654 (0.012)*	0.253 (0.126)	0.074 (0.695)	0.280 (0.214)	0.033 (0.448)

\*  $P < 0.05$ , \*\*  $P < 0.01$

Table 5.4--Observed values and expected probabilities (in parenthesis) for six parameters calculated from distances along minimum-spanning trees. Probabilities are from 100 communities generated from the pool. For G and Min probabilities are for values  $\geq$  expected. For Mean and Var, probabilities are for values  $\leq$  expected.

	Parameter	Expected probabilities	
		External	Skull
FRUGIVORES	Mean	1.272 (0.49)	1.792 (0.11)
	Var	0.736 (0.83)	0.732 (0.07)
	Min	0.300 (0.55)	0.861 (0.44)
	$G_{1n}$	0.122 (0.76)	0.275 (0.11)
	$G_{2n}$	0.245 (0.55)	0.441 (0.19)
	$G_{1(n-1)}$	0.188 (0.85)	0.423 (0.13)
GLEANERS	Mean	2.661 (0.13)	2.590 (0.25)
	Var	0.317 (0.08)	0.080 (0.10)
	Min	2.263 (0.29)	2.390 (0.20)
	$G_{1n}$	0.740 (0.13)	0.857 (0.12)
	$G_{2n}$	1.000 (1.00)	1.000 (1.00)
	$G_{1(n-1)}$	1.000 (1.00)	1.000 (1.00)

Table 5.4--Continued

	Parameter	Expected probabilities	
		External	Skull
AERIAL INSECTIVORES	Mean	0.720 (0.73)	1.022 (0.12)
	Var	0.241 (0.34)	0.604 (0.46)
	Min	0.242 (0.46)	0.136 (0.76)
	$G_{1n}$	0.138 (0.38)	0.054 (0.63)
	$G_{2n}$	0.162 (0.52)	0.122 (0.71)
	$G_{1(n-1)}$	0.163 (0.48)	0.065 (0.66)
MOLOSSIDS	Mean	0.798 (0.85)	1.310 (0.59)
	Var	0.192 (0.49)	0.661 (0.66)
	Min	0.220 (0.17)	0.310 (0.33)
	$G_{1n}$	0.181 (0.32)	0.144 (0.53)
	$G_{2n}$	0.369 (0.33)	0.431 (0.17)
	$G_{1(n-1)}$	0.197 (0.54)	0.415 (0.67)

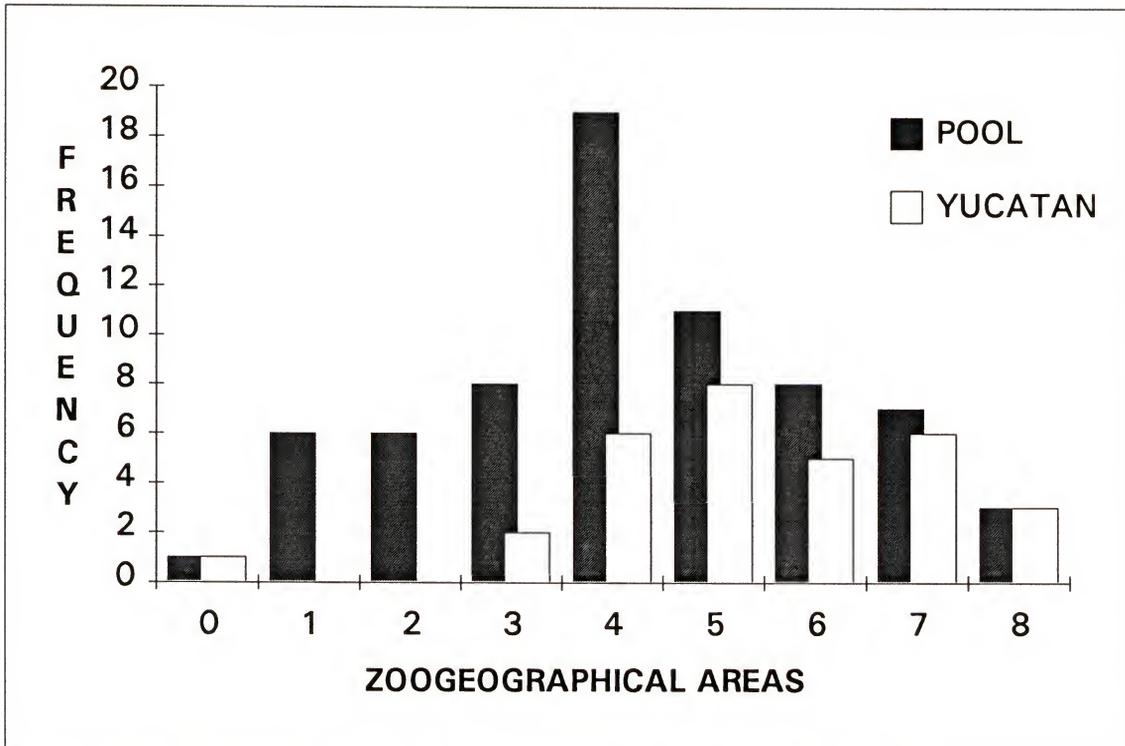


Figure 5.1--Frequency distribution of the area of distributional range for bat species in the pool and the Yucatán fauna. The mean for the Yucatán fauna differs from the expected value ( $P < 0.001$ )

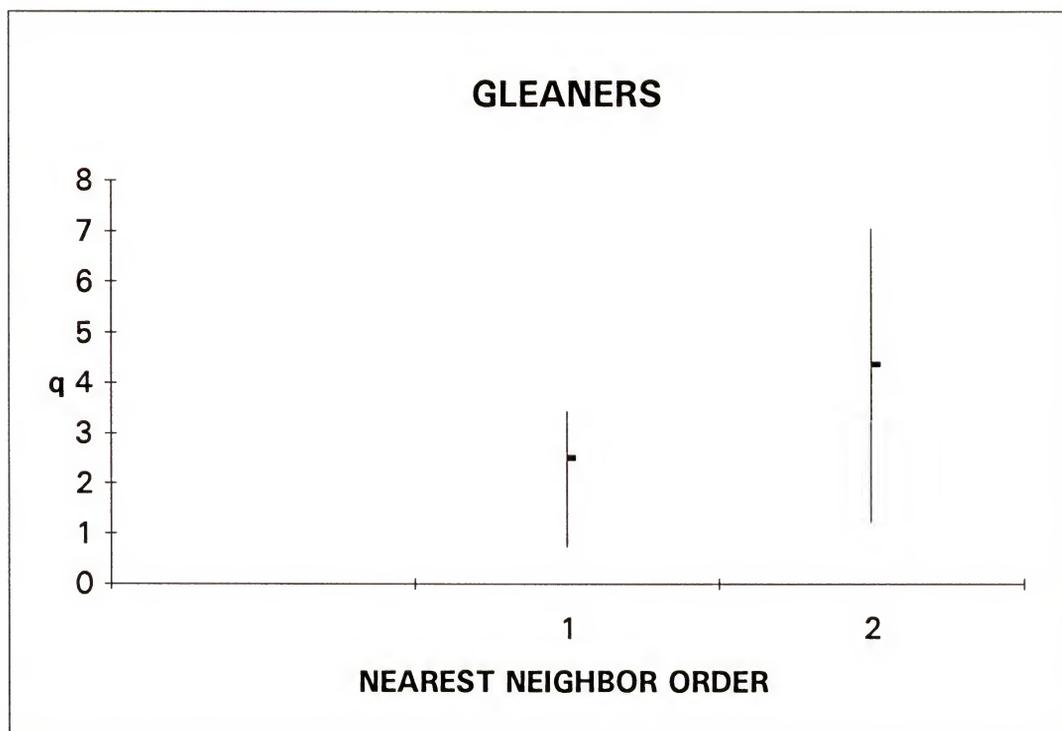
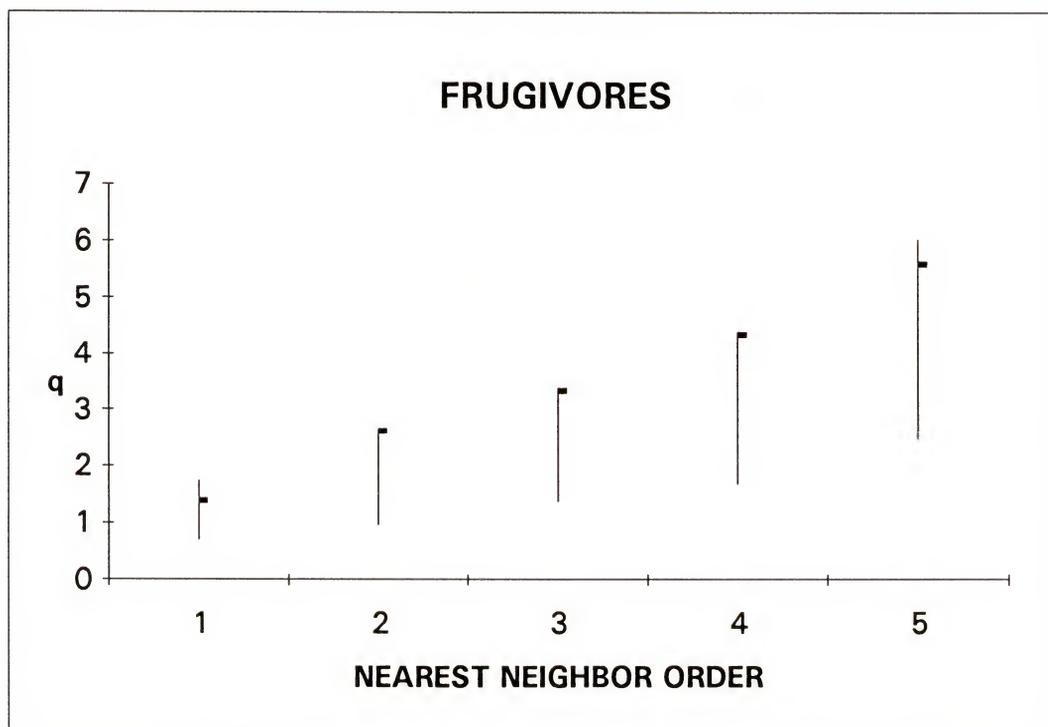


Figure 5.2--Mean nearest-neighbor Euclidean distances in four guilds of bats. Points show values for the Yucatán fauna. Lines are upper and lower 5% limits for expected values obtained from the pool.

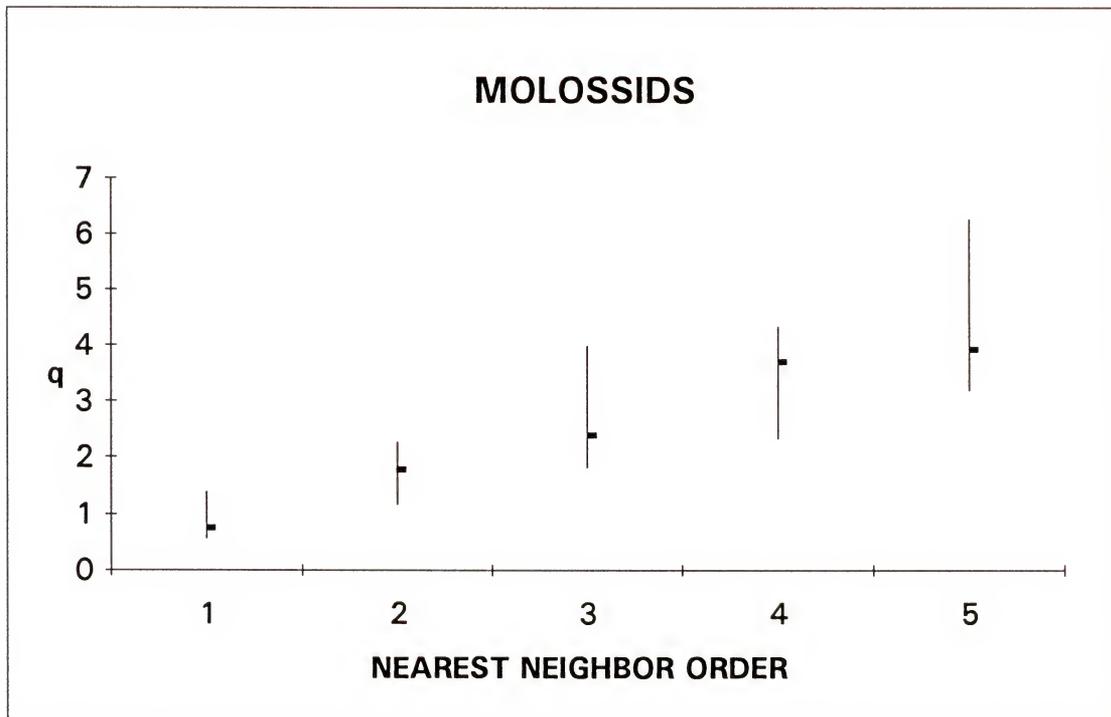
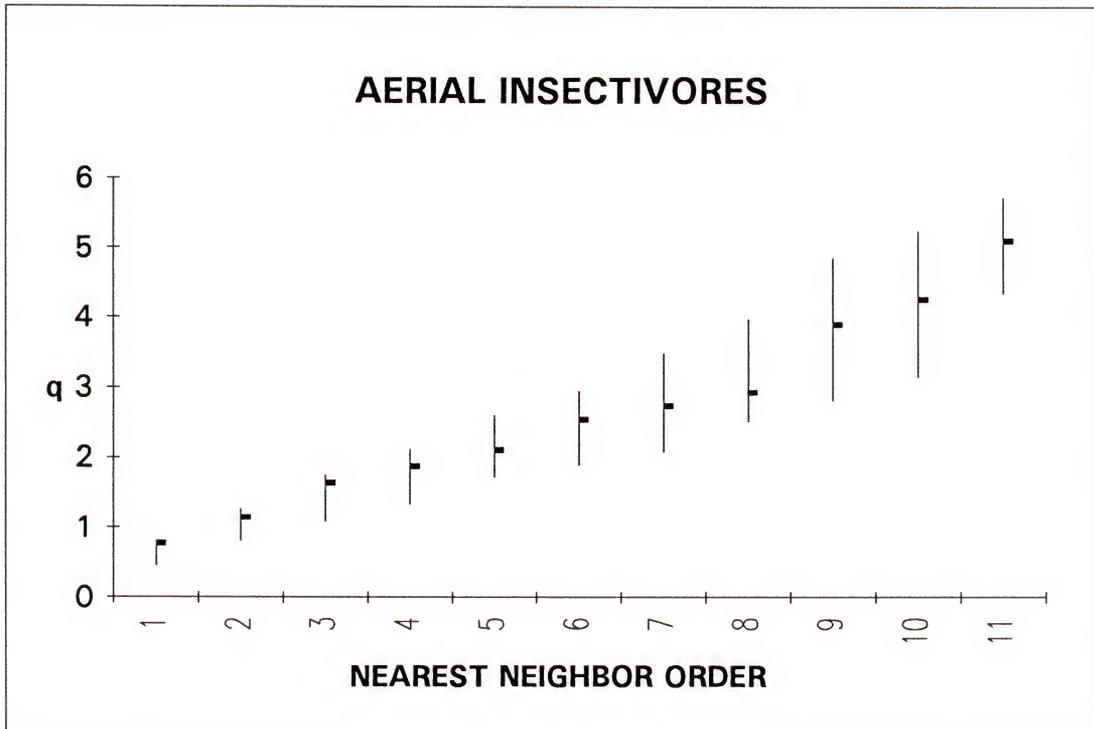


Figure 5.2--Continued.

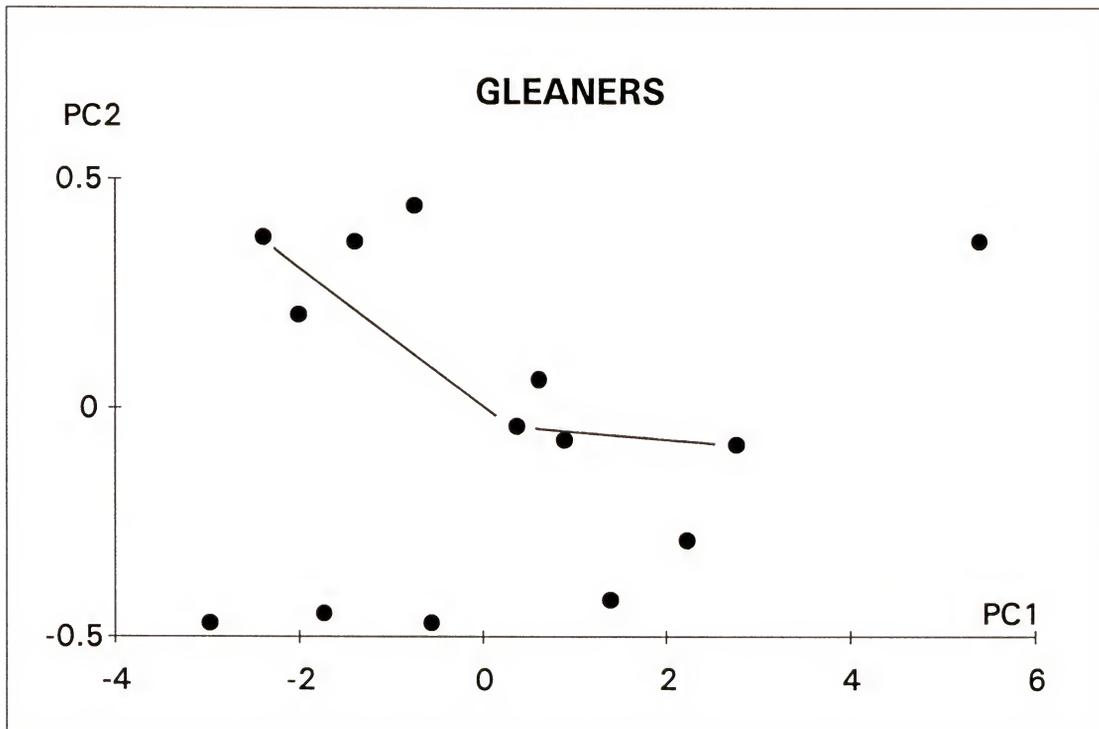
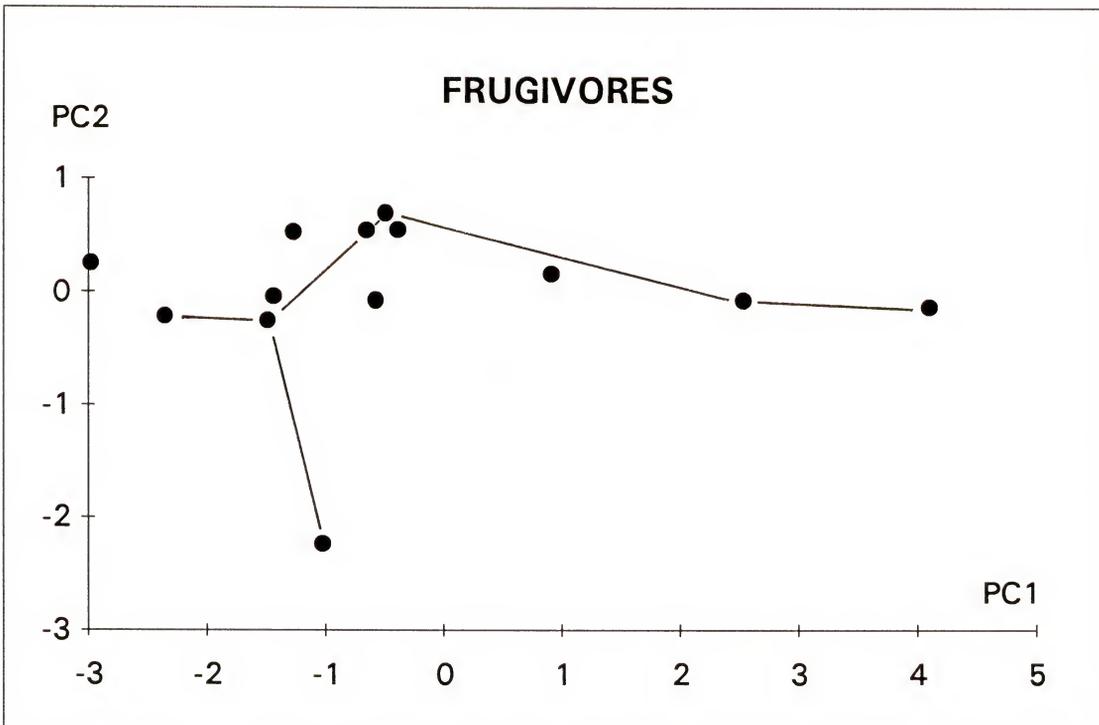


Figure 5.3--Four feeding groups of bats in two-dimensional space for skull variables. Lines are MSTs connecting Yucatán species.

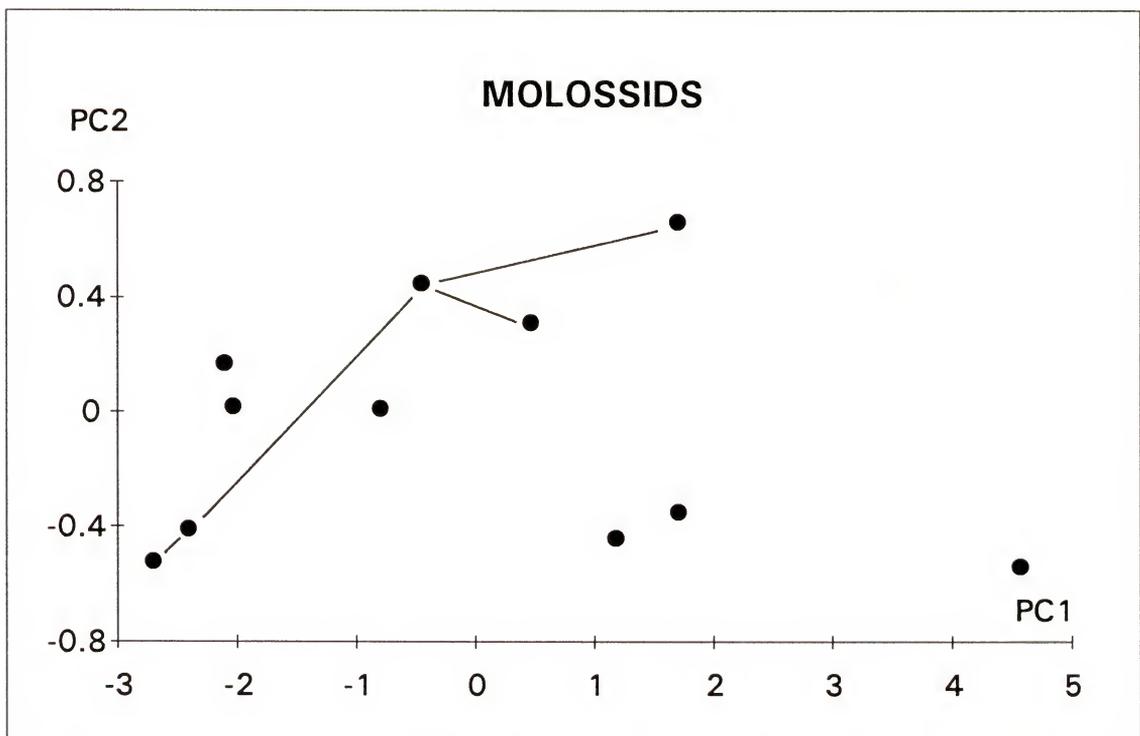
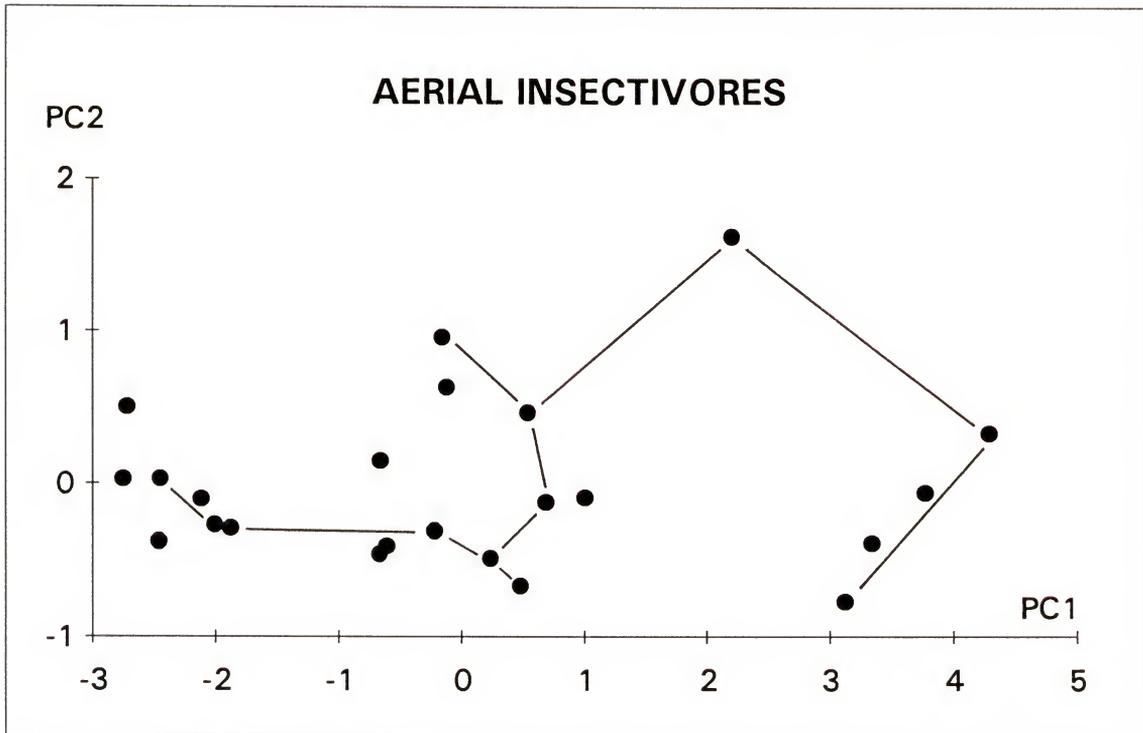


Figure 5.3--Continued.

CHAPTER 6  
ECOLOGY OF CAVE-ROOSTING BATS IN YUCATAN

Introduction

Caves are the main roosts for many bat species (Dalquest and Walton, 1970; Kunz, 1982a). Of the 39 chiropteran species in the United States, 18 regularly roost in caves, and some others use caves as alternative roosting sites (Culver, 1986; Humphrey, 1975; McCracken, 1989). In Mexico, 45% (60 out of 134) of bat species are cave dwellers, with 27 using caves as the main roost; eighteen additional species use caves occasionally (Chapter 4).

There is substantial information on the ecology of many of the Nearctic cave bats (Humphrey, 1982; Tuttle, 1979), but considerably less is known about the natural history of cave bats of other parts of the world, particularly of the tropical areas. For Neotropical bats, available information on cave use by bats come from anecdotal references in faunistic surveys (e.g., Goodwin and Greenhall, 1963; Hall and Dalquest, 1963; Handley, 1976; Jones et al., 1973; Villa-R., 1967; Willig, 1983), from a review of collecting techniques (Tuttle, 1976), from ecophysiological research (McNab, 1969, 1982), and from a few ecological and behavioral papers (Bateman and Vaughan, 1974; Bradbury, 1977; Fleming, 1988; Goodwin, 1970; Graham, 1988; McCracken

and Bradbury, 1981). The approach of most of these studies has been at the individual or population levels, and little is known about community-level parameters such as interspecific association and species diversity. Moreover, few of the published reports provide information on the abiotic conditions and geomorphology of the caves used by bats.

Here I describe and analyze the patterns of cave use by bats in Yucatán, México. First, I present information on the natural history of cave species, examining the physical and biotic factors that determine the suitability of caves to sustain bat populations. Then, I investigate the patterns of interspecific association and species diversity of cave bat communities. Finally, I provide recommendations for the conservation and management of those caves that are important for the conservation of bats.

### Methods

This study was carried out in the state of Yucatán, Mexico. A description of the study area can be found in Chapter 2. The majority of caves surveyed are located in the Sierrita de Ticul, a lesser mountain range that marks the southern border of the state, but some are in the northwestern coastal plain.

## The Caves

The 36 caves included in this study ranged in size from a small tunnel of 7 m to a complex system of >1.5 km of passages and chambers. I made simple maps of the caves using standard survey methods (Ellis, 1976). Topographic measurements of distance and angles from the mapping procedure provided data to calculate several morphometric variables for the caves (Chapter 3).  $L'$  is the total horizontal length of all passages in the cave,  $L_k$  is the maximum horizontal distance between two points in the cave, and  $H_k$  is the amplitude of the cave, the maximum vertical distance between two points in the cave. At each station of the topographic network I measured the ambient temperature and relative humidity using a portable psychrometer.

During each visit to a cave, I systematically searched for groups of bats and, using a hand-held net, I captured individuals to identify the species. Additionally, I set mist nets in strategic positions in the cave to capture flying individuals. Mist-net captures assisted me in the identification of species, but they provided no information on the particular location of the colonies in the cave. Previous experience and a reference collection made in advance allowed me to identify all species in the field. For each individual captured I recorded its species, sex, reproductive status, length of forearm (with a mechanical caliper to the nearest 0.1 mm), and body mass (with a Pesola

dynamometer, to the nearest 0.1 g). I temporarily marked individuals with fluorescent dye to avoid recording the same individual more than once.

I estimated the population size of the different species in the caves. When the number of bats in a group was small (<30; e.g., for *Peropteryx macrotis*, *Micronycteris megalotis*, *Diphylla ecaudata*, and *Myotis keaysi*) I usually was able to count all individuals. For bats forming larger colonies (e.g., *Mormoops megalophylla* and *Natalus stramineus*), I estimated the density of individuals per m<sup>2</sup> (by direct measurement) and the total area covered by bats (from data of the cave surveys, Chapter 3), and calculated the total population size by multiplying these values. For species that occupied wide sections of a cave but formed discrete groups (e.g. *Artibeus jamaicensis* and *Pteronotus parnellii*), I estimated the number of individuals in each group (by direct count) and the number of such groups that were visible. Additionally, I used rate of capture in mist nets as an indirect estimator of relative abundance by recording the proportions of the different species that were caught. Because all these methods provide only approximate values of abundance, and because direct determination of population density was not feasible in all cases, I used a logarithmic scale of abundance to make comparisons: 0 (1 individual), 1 (2 to 10), 2 (11 to 100), 3 (101 to 1,000), 4 (1,001 to 10,000), 5 (>10,000).

### Analysis of Interspecific Association

I used the test developed by Schluter (1984) to analyze the overall association among Yucatán cave bats. If  $p_i$  is the proportion of caves in which species  $i$  is present, the variance of the occurrence of the species is estimated by:

$$s_i^2 = p_i (1 - p_i).$$

If  $N$  is the total number of caves,  $t$  the average number of species per cave, and  $T_j$  the number of species in cave  $j$ , the variance in the number of species is estimated as:

$$S_T^2 = (1/N) \sum_j^N (T_j - t)^2.$$

Schluter (1984) proposed the ratio

$$V = \frac{S_T^2}{\sum s_i^2},$$

where the summation goes from  $i = 1$  to the total number of species, as an index of species association. Under the null hypothesis of no association,  $V = 1.0$ . Values of  $V > 1$  indicate an overall positive association, whereas values of  $V < 1$  suggest a net negative association. Schluter (1984) has shown that the parameter  $W = N \cdot V$  follows a  $\chi^2$  distribution with  $N$  degrees of freedom, allowing the null hypothesis to be tested.

I also tested the pair-wise association between the species using the association index  $I$  (Southwood, 1978):

$$I = \frac{ad-bc}{\sqrt{(a+b)(c+d)(a+c)(b+d)}},$$

where  $a$  is the number of caves in which both species are present,  $d$  is the number of caves in which both species are absent, and  $b$  and  $c$  are caves with only one of the two species. Possible values of this index go from  $-1$  (complete segregation) to  $0.0$  (no association) to  $1$  (perfect positive association). I tested the statistical significance of the associations using Fisher's exact test for two-by-two contingency tables. (The association index is normally represented as  $V$ , but here I use  $I$  to avoid confusion with Schluter's [1984] index).

To visualize the relationship among all species in terms of their association, I conducted a cluster analysis using an average-linkage algorithm. I used the values of  $I$  as a measure of distance between the species.

### Classification of Caves

I conducted an association analysis (Ludwig and Reynolds, 1988; Williams and Lambert, 1959) to produce a classification of Yucatán caves on the basis of use by bats. I used the two-by-two contingency tables from the previous section to feed a computer program written in BASIC that followed the procedures described by Ludwig and Reynolds (1988). First, the algorithm selected those pairs with significant association as shown by a  $P < 0.05$  in a Fisher's exact test. For each species it computed the sum of the parameter  $X^2 = (O - E)^2 / E$  (where  $O$  and  $E$  are the observed and expected values in the contingency table) for all pairs

with significant association. Then, the program selected the species with the highest sum as the "divisor" species and split the caves into two groups: with and without the divisor species. The procedure iterated the sequence for each group until no more significant associations were shown, i.e, when all groups were homogeneous (Ludwig and Reynolds, 1988).

### Correlations of Diversity and Abundance

I estimated biodiversity by using richness, the number of species present in a cave (S). The use of finer estimates of diversity was not possible because there is no reliable way to collect truly random samples of bat communities.

I wrote a BASIC program to analyze the distribution of bat species among the caves in terms of species richness. For each species, the program generated 1,000 random combinations of  $n_i$  ( $n_i$  = number of caves in which species  $i$  was present) caves from the pool of 36 caves. Then, the program calculated the frequency distribution of the median of the number of bat species in the  $n_i$  caves for the 1,000 simulations. Finally, it compared the observed median of the number of species with this distribution to assess the statistical significance of the results.

To estimate total abundance I used the variable A:

$$A = \log_{10} S 10^{a_i},$$

where  $a_i$  is the abundance of species  $i$  in the logarithmic scale described above and the summation goes from 1 to  $S$ , the number of species in the cave. This variable is simply the log value of the sum of the maximum population estimates for each species in the cave. It is gauged against the same logarithmic scale used for abundances of individual species.

### Results and Discussion

#### Natural History of Yucatán Cave Bats

Seventeen of the 31 bat species in Yucatán are cave forms (Chapter 4). During this study I found 14 species using the caves surveyed as day roosts. Another two species were captured during night netting at the entrances of the caves. In this section I provide general information on the natural history of cave use by these species. In each account I first list the caves where the species was found, including the estimate of population size using the categories defined in the methods. Then I mention previous reports of each species in Yucatán caves; the acronym UNAM refers to specimens deposited in the mammal collection of the Instituto de Biología, National University of México. Finally, I review the available information on cave use by each species and report my own observations in Yucatán caves.

## Emballonuridae

*Peropteryx macrotis*. Cueva del Roble (2), Actun Sabakha (3), Actun Chunkunab (1), Actun Maas (1), Flor de Mayo Cave (2), Actun Kan-Lol (2), Porcupine Cave (2), Actun Oxpehol (2), Actun Maasit (1), Actun Dzonot (1), Iguana Cave (1), Doña Blanca (2), Actun Kab (2), Cinco de Mayo Cave (1), Cave "A" (1), Ramonal y Naranja Cave (2), Actun Tolok (1), Guayaba y Aguacate Cave (2), Cave "B" (1), Actun Chac-Xix (1), Aguacate Cave (1), Zorro Cave (1), Cave of the Ruins of Kabah (2), Cave of the Ruins of Mayapán (0), Tzab-Nah Cave (1), Actun On (2), Actun Lol-Tun (2). Additional cave records in Yucatán: Actun Chac-Xix (Pearse and Kellog, 1938); Actun Spukil (Hatt and Villa, 1950; Villa-R., 1967); cave 1 km S Catmís (UNAM); Actun Lol-Tún (fossil, Arroyo-Cabrales and Alvarez, 1990).

The lesser sac-winged bat has been reported from well-lighted sections of caves, always in groups of <12 individuals (Goodwin and Greenhall, 1961, Graham, 1988; Hall and Dalquest, 1963; Jones, 1966; McNab, 1969; Ramírez-P. et al., 1977; Villa-R., 1967; Willig, 1983). In México, the sac-winged bat tends to roost in caves with high species richness ("integrationist species", Chapter 4)

I found *P. macrotis* in 27 of the surveyed caves, always at a distance <20 m from the entrance (mean distance 11.3 m,  $s = 6.8$  m,  $n = 27$ ). Average group size was 18.6 individuals ( $n = 31$ ;  $n$  is >26 because in some caves there were >1 group)

but varied from a single individual found at the Cave of the Ruins of Mayapán to >80 in a colony in Sabak-Ha Cave. Most groups had between eight and 15 individuals. Sex ratio was always close to 1:1 in most groups examined; for example, on January 2 there were eight males and seven females in one group in Sabak-ha Cave ( $P$  [sex ratio is 1:1] = 0.5, binomial test). In July and August, composition of the groups changed and juvenile individuals were mixed in the groups. For example, on 23 July, the group in the cave of the Ruins of Kabah contained two adult males, four adult females, six lactating females, seven juvenile females, and three juvenile males ( $P$  [sex ratio of adults is 1:1] = 0.019, binomial test).

Groups of *P. macrotis* were always in first-order chambers or even in small cracks on the walls of open dolines. In some cases it was possible to spot the bats without using artificial light. Ambient temperature in rooms occupied by *P. macrotis* varied from 24.4 °C to 28.8 °C (Fig. 6.1). At all sites but one relative humidity was <93%, and at one site it was as low as 67%.

Typically, groups of *P. macrotis* were located on vertical or very inclined walls. Individuals normally were close together (<20 cm from each other), but after being disturbed individuals would change their position and became more separated from each other.

## Mormoopidae

*Mormoops megalophylla*. Bat Cave (5), Hochtún Cave (3), Tzab-Nah Cave (2), Actun Sitz (one skull), Actun Lol-Tún (3), Actun Spukil (3). Additional cave records from Yucatán: Balankanchén Cave (Jones et al., 1973); Hochtún Cave (Birney et al., 1974); Actun Spukil (Birney et al., 1974; Hatt et al., 1953, cave deposit; UNAM); Actun Lol-Tún (UNAM; Arroyo-Cabrales and Alvarez, 1990, fossil).

As other mormoopids, the ghost bat tends to occupy the deeper sections of caves where temperature and humidity are high (Bateman and Vaughan, 1974; Goodwin and Greenhall, 1961; Villa-R., 1967; Wilson et al., 1985). It differs from *P. parnellii*, however, in that *M. megalophylla* roosts directly on the ceiling and walls, not inside solution holes like *P. parnellii*. *M. megalophylla* is an integrationist species that normally forms colonies of >1,000 individuals (Chapter 4).

In Bat Cave, *M. megalophylla* forms a very large colony of >10,000 individuals. A precise estimation was not possible because part of the colony roosted in an inaccessible part of the cave, but netting trends indicate that this species is much more abundant in this cave than *P. parnellii*, which numbers >1,000. In this cave I found the ghost bat occupying the deepest parts of a narrow tunnel >100 m from the entrance. It formed a mixed group with *Natalus stramineus* on the walls and speleothems (stalactites

and draperies) of a small chamber where temperature was 29.7 °C and relative humidity was 93%. Individuals of both species were roosting individually, separated from each other by >20 cm. In Hoctún Cave, a small group (<1,000 individuals) roosted on an inclined ceiling near a cenote (pool) approximately 70 m from the entrance. At least five other species roost in this cave, but the *M. megalophylla* were always segregated. Ambient conditions at this site were 27.8 °C and 94% relative humidity.

Apparently there is no sex segregation in *M. megalophylla*, but the sex ratio is significantly skewed. On 17 April I netted 81 *M. megalophylla* at Bat Cave; seven were non-pregnant females, 52 were pregnant females, and 22 were adult males (sex ratio male:female 22:59 = 1:2.68;  $P$  [sex ratio 1:1] < 0.001, binomial test). At other sites, sample sizes were insufficient for statistical tests, but females were always more abundant than males.

*Pteronotus davyi*. Bat Cave (5), Actun Lol-Tún (3), Actun Spukil (3). Additional cave records in Yucatán: Hoctún Cave (Birney et al., 1974; Jones et al., 1973); cenote 2 km NW Dzityá (Birney et al., 1974); Actun Spukil (Birney et al., 1974); Actun Lol-Tún (UNAM; Arroyo-Cabrales and Alvarez, 1990, cave deposit).

The naked-backed bat roosts in humid and dark caves located in dry areas of the Neotropics (Goodwin and Greenhall, 1961; Handley, 1976; Linares, 1987), forming "not

very large" groups (Villa-R, 1967). *P. davyi* is an integrationist species that forms medium-sized to large colonies (Chapter 4).

I found this species in only three of the caves. In Bat Cave, second- and higher-order chambers harbor a population of >1,000 individuals of this species. I captured most individuals with mist nets and was unable to locate the exact position of the main roosting group, although it was clear that these bats occupied only the deepest chambers of the cave. Temperature and relative humidity in these chambers were 29.8 °C and 93%. Similarly, I routinely netted *P. davyi* in Lol-Tún cave but never found its roosting site despite careful searches in most galleries of the cave. I suspect that *P. davyi* roosts in higher areas of chambers, where access by humans is difficult. Jones et al. (1973) and Birney et al. (1974) reported specimens of *P. davyi* collected in Hoctún Cave during the 1960s and 1970s. I never captured this species in Hoctún despite numerous visits to the cave. At Bat Cave, sex ratio did not differ from 1:1 ( $P = 0.249$ ,  $n = 35$ ).

*Pteronotus parnellii*. Actun Sabak-ha (4), Bat Cave (4), Chocantes Cave (3), Cave of the Ruins of Mayapán (3), Tzab-Nah Cave (3), Actun Lol-Tun (3), Actun Spukil (3). Additional cave records in Yucatán (Birney et al., 1974 unless otherwise stated): Balankanchén Cave (Jones et al., 1973, night roost); Hoctún Cave; Actun Spukil (Hatt et al.,

1953, cave deposits); Cave of the Ruins of Mayapán; cenote 2.5 km NW Dzityá (netted at night); Actun Lol-Tún (UNAM; Arroyo-Cabrales and Alvarez, 1990, fossil); cave 1 km S Catmís (UNAM).

The mustached bat typically roosts in large caves that support many other species of bats, forming large colonies of >1,000 individuals (Chapter 4; Bateman and Vaughan, 1974; Goodwin and Greenhall, 1961; Silva-Taboada, 1979; Villa-R., 1967).

I found this species roosting in seven of the caves included in this study. In all cases, mustached bat colonies were located in hot and humid second- or higher-order chambers. For example, in Bat Cave, several groups of moderate size (30 to 50 individuals) of *P. parnellii* roosted in the solution holes located in a second-order chamber where conditions were 26.1 °C and 92% relative humidity. In this cave, mustached bats roosted as close to the entrance as 40 m, but this species was normally found only in deeper sections of caves, up to 210 m from the entrance in Chocantes Cave.

Birney et al. (1974) reported a single specimen of *P. parnellii* from Hochtún Cave, but I never observed this species in this cave despite repeated visits. Jones et al. (1973) reported the use of Balankanchén Cave as a night roost by *P. parnellii*. They netted individuals of this species at night but found none during day visits. In Actun Lol-Tun, I found that mustached bats used certain sections

of the cave only as night roosts. During night visits I saw many (>100 individuals) flying and roosting in a chamber known as Salón del Infante (Room of the Child). During the day, this chamber harbors no bats because it is part of the tourist trail and is artificially illuminated.

#### Phyllostomidae

#### Phyllostominae

*Micronycteris megalotis*. Roble Cave (1), Bejucos Cave (1). Additional cave records in Yucatán: Muruztun Cave, Tizimín (Jones et al., 1973); Xconsacab Cave, Tizimín and X-Mahit Cave, Tekax (Pearse and Kellog, 1938); Actun Lol-Tún (Arroyo-Cabrales and Alvarez, 1990, owl pellet).

The little big-eared bat roosts in the illuminated parts of caves, in culverts, under bridges and other human-made structures, and in hollow trees, rarely forming groups of >12 individuals (Goodwin and Greenhall, 1961; Tuttle, 1976).

I observed eight individuals of this species forming a packed group in one solution hole located in the twilight zone of the Bejucos Cave, about 25 m from the entrance. When disturbed, the group dispersed but readily grouped again in a deeper section of the cave. In the Roble Cave, a group of 10 individuals roosted in a shallow solution hole about 35 m from the entrance. Beneath the groups there was an accumulation of bat guano and insect parts, mostly of Coleoptera and Lepidoptera. Ambient temperature and

relative humidity were 27.0 °C and 93% in Bejucos Cave and 24.1 °C and 92% in the Roble Cave. In Ramonal y Naranja Cave I found an accumulation of guano and insect parts similar to that in the Roble Cave but never observed any *M. megalotis*.

*Mimon cozumelae*. Actun Lol-Tún (1). Additional cave records from Yucatán: cave 8 km NE Tixpehual (Jones et al., 1973); Actun Tuz-Ic, Calcehtok (Hatt and Villa, 1950); Actun Spukil (Hatt et al., 1953, cave deposit); Actun Lol-Tún (UNAM, netted at night).

The spear-nosed bat is a segregationist species that forms small roosting groups in caves and culverts (Chapter 4; Hall and Dalquest, 1963; Tuttle, 1976; Villa-R., 1967). Jones et al. (1973) considered *M. cozumelae* a common cave species in Yucatán. I observed this species only in Actun Lol-Tún, however, where I netted one adult female inside the cave, near the main entrance. On August 1982, a subadult male was netted at night in the open doline at the same entrance of Actun Lol-Tún (Arita, field notes).

*Chrotopterus auritus*. Tzab-Nah Cave (1). Other cave records in Yucatán: cave 6 km N Tizimín (Jones et al., 1973); Actun Spukil and Actun Lara, Yokat (Hatt et al., 1953, cave deposits); Actun Lol-Tún (Arroyo-Cabrales and Alvarez, 1990, fossil).

The wooly false vampire bat forms small groups of <8 individuals in caves, artificial tunnels, and hollow trees

(Davis et al., 1964; Hall and Dalquest, 1963; Jones et al., 1973; McNab, 1969; Medellín, 1988; Villa-R., 1967; Villa-R. and Villa-C., 1971). McNab (1969) reported temperatures ranging from 14 to 22 °C and relative humidities of 77% to 93% in roosts of *C. auritus*. Villa-R. and Villa-C. (1971) registered 20 °C and 80% relative humidity in a cave in northern Argentina that *C. auritus* shared with a colony of vampires (*Desmodus rotundus*).

*C. auritus* was known to occur in the state of Yucatán on the basis of only six specimens from three localities, and it had not been observed since the early 1960s (Jones et al., 1973). It had also been reported as a fossil and subfossil (Arroyo-Cabrales and Alvarez, 1990; Hatt et al., 1953). On 19 August I found three *C. auritus* roosting in a shallow and wide (1.5-m) solution hole on the ceiling of Tzab-Nah Cave, near Tecoh. They were <30 m from the entrance and the area was dimly illuminated. At 0830 h temperature was 27.0 °C and relative humidity was 92%. I captured two of the individuals (one adult female and a juvenile male), but the other individual (presumably an adult male) escaped.

Beneath the solution hole were fresh feces, feathers, a wing of a sac-winged bat (*Peropteryx macrotis*), and a partially eaten funnel-eared bat (*Natalus stramineus*). The woolly false vampire feeds mainly on birds and rodents, and to a lesser extent on other small vertebrates and insects (Medellín, 1988, 1989). Apparently the only previous record

of *C. auritus* feeding on other bats in the wild was by Acosta y Lara (1951, in Medellín, 1989), who observed this bat feeding on *Glossophaga soricina*.

Apparently the *C. auritus* use this cave as an alternative refuge. I never saw the bats in any of the four previous visits to the cave, even though I carefully surveyed the area where the bats were roosting. Additionally, beneath the group there was no accumulation of guano or prey parts as those that have been reported for other colonies of this species (Medellín, 1988).

#### Glossophaginae

*Glossophaga soricina*. Roble Cave (1), Actun Sabak-Ha (3), Bat Cave (4), Ramonal Cave (1), Cinco de Mayo Cave (1), Ramonal y Naranja (1), Bejucos Cave (1), Cave "B" (1), Hochtún Cave (1), Tzab-Nah Cave (2), Kabahchén Cave (1), Actun Sitz (1), Actun Lol-Tún (3), Actun Spukil (3). Other cave records in Yucatán (Jones et al. 1973 unless otherwise noted): Xkyc Cave, Calcehtok (Pearse and Kellog, 1938); Balankanchén Cave; Chapultepec Cenote, Mérida; Muruztun Cave, Tizimín (Pearse and Kellog, 1938); Actun Spukil (Hatt and Villa, 1950); Actun Coyok and Actun Lol-Tún, Oxkutzcab (Hatt et al., 1953, cave deposits); Actun Lol-Tún (UNAM); Cave 1 km S Catmís (UNAM); Hochtún Cave (Birney et al., 1974); Actun Lol-Tún (Alvarez, 1982; Arroyo-Cabrales and Alvarez, 1990, fossil).

Pallas' long-tongued bat is one of the most abundant and widespread cave bats in México (Chapter 4). It forms groups of different sizes, from a few individuals (Goodwin, 1970; Goodwin and Greenhall, 1961) to several thousands (Arita, unpublished data; Villa-R., 1967). *G. soricina* is an integrationist species that shares the roost with many species (Chapter 4).

I found *G. soricina* roosting always in small groups (<20 individuals). However, in some caves the combined total population was >100 or even >1,000. Under some circumstances, females segregated to rear the young. On 3 October 1989, all 13 bats of this species netted at the entrance of Actun Lol-Tún were females ( $P$  [sex ratio 1:1] = 0.0001, binomial test); two were pregnant, one had an attached newborn, and five were lactating. In Kabahchén Cave on 7 October 1989, I captured five lactating females, two females with newborn bats attached, and one juvenile male ( $P$  [adult sex ratio 1:1] = 0.008, binomial test). Conversely, in Bat Cave on 17 April 1990 I netted 8 males and 12 females, one lactating, two pregnant ( $P$  [sex ratio 1:1] = 0.252, binomial test).

Close interspecific associations have been reported between *G. soricina* and *Artibeus jamaicensis*, *Macrotus waterhousii*, and *Carollia perspicillata* (Goodwin, 1970; Graham, 1988). In Yucatán I found all groups of *G. soricina* segregated from other species during the day. However, just before leaving the roost after sunset (1915 h), bats of this

species were seen in Bat Cave forming unusually big groups (>100 individuals) intermixed with individuals of *Natalus stramineus*.

Goodwin (1970) reported finding *G. soricina* in small and dry caves. McNab (1969) reported temperatures from 24 to 27 °C and relative humidities from 70 to 94% in one roost occupied by this species. In Yucatán, the typical roost site was a first-order chamber, generally close to the entrance. For example, in Kabahchén Cave, bats were in a dimly lighted site, <20 m from a wide opening, where temperature and relative humidity were 25.0 °C and 92%. However, other groups were located in second- or higher-order chambers, as far as 120 m from the entrance, where temperature and humidity were >29 °C and >95% (Fig. 1).

#### Carolliinae

*Carollia perspicillata*. Bat Cave (1), Actun Lol-Tún (netted at night).

The short-tailed bat roosts primarily in caves, hollow trees, and artificial tunnels (Fleming, 1988; Goodwin and Greenhall, 1961). McNab (1969) found this species at sites with temperatures ranging from 19 to 26 °C and relative humidity varying from 92 to 98%. In contrast with other sites, where *C. perspicillata* is one of the most abundant species (Fleming, 1988), the short-tailed bat is very rare in Yucatán. The two specimens reported here represent the second and third record of the species for the state (Jones

et al., 1973). In Bat Cave, one individual was netted in the morning close to the colony of *Natalus stramineus* described below. The second specimen was netted at 2015 h at the main entrance of Actun Lol-Tún.

#### Stenodermatinae

*Artibeus jamaicensis*. Roble Cave (1), Actun Sabak-Ha (3), Actun Chunkunab (1), Actun Maas (1), Bat Cave (3), Flor de Mayo Cave (1), Porcupine Cave (2), Actun Oxpehol (2), Iguana Cave (1), Doña Blanca Cave (1), Cinco de Mayo Cave (1), Ramonal y Naranja Cave (2), Bejucos Cave (1), Actun Tolok (1), Guayaba y Aguacate Cave (1), Cave "B" (1), Cave of the Ruins of Mayapán (1), Tzab-Nah Cave (3), Acanceh Cave (3), Kabahchén Cave (1), Actun Lol-Tún (3), Actun Spukil (3). Other cave records in Yucatán (Jones et al., 1973 unless otherwise stated): Balankanchén Cave; Actun Coyok (Hatt, 1938); Actun Spukil (Birney et al., 1974; Davis, 1970; Hatt and Villa, 1950; UNAM); Ebizt, Lol-Tún, Puz, and San Roque Road Caves, Oxkutzcab (Pearse and Kellogg, 1938); Kaua Cave (Pearse and Kellogg, 1938); Chac-Xix, Cinco de Mayo, and Sabak-Ha Caves, Tekax (Pearse and Kellogg, 1938); cave 1 km S Catmís (UNAM); Actun Lol-Tún (Alvarez, 1982; Arroyo-Cabrales and Alvarez, 1990, fossils).

The fruit-eating bat is a generalist species that roosts in a variety of sites, including caves, tunnels, abandoned buildings, culverts, palm leaves, and hollow trees (Goodwin and Greenhall, 1961; Silva-Taboada, 1979; Tuttle,

1976; Villa-R., 1967). It is an indifferent species that roosts in caves with few or many other bat species, forming small to medium-sized colonies (Chapter 4).

In Yucatán, *A. jamaicensis* can be found in very different situations. I located colonies in small tunnels (e.g. Doña Blanca Cave, Acanceh Cave) and in big systems (e.g. Actun Lol-Tún, Actun Spukil). Individuals were more frequently observed near entrances (e.g. Cave of the Ruins of Mayapán, <20 m from the entrance), but in some cases they were roosting in the deepest parts of the caves (e.g. Actun Sabak-Ha, >110 m from the entrance). Temperatures in areas occupied by this bat ranged from 24.1 to 27.4 °C, and relative humidity varied from 69 to 96% (Fig. 1).

In most sites, *A. jamaicensis* formed small groups (three to 35 individuals) in solution holes in the ceiling of chambers. Small caves were typically occupied by only one group, but total population in bigger caves, like Bat Cave, was estimated as >500.

*Dermanura phaeotis*. Actun Lol-Tún (netted at night).

The only cave record of the dwarf fruit-eating bat is that of Villa-R. (1967), who netted one individual at the entrance of a small cave in Tabasco, México. I captured two individuals at night in the open doline of Actun Lol-Tún, but I have no evidence that this bat uses the cave as a day roost.

*Sturnira lilium*. Actun Lol-Tún (netted at night).

Other cave record from Yucatán: Actun Lol-Tún (Alvarez, 1982; Arroyo-Cabrales and Alvarez, 1990, fossils).

The yellow-shouldered bat roosts primarily in hollow trees (McNab, 1969; Tuttle, 1976). Apparently the only records of this species using caves are those of Villa-R. (1967), who visually identified one individual of this species in a cave in Puebla, México and netted another individual at night at the entrance of a cave in Tabasco, México. I netted two individuals of this species in the open doline of Actun Lol-Tún, but I have no evidence that the species uses the cave as a day roost.

#### Desmodontinae

*Desmodus rotundus*. Actun Sabak-Ha (4), Ramonal Cave (3), Flor de Mayo Cave (2), Chocantes Cave (2), Cinco de Mayo Cave (2), Actun Oxpehol (2), Hochtún Cave (2), Actun Lol-Tun (3), Actun Spukil (2). Other cave records in Yucatán (Jones et al., 1973 unless otherwise stated): Balankanchén Cave; Hochtún Cave (Pearse and Kellog, 1938); San Buhla Cave, Motul; Santa Ana Cenote, Valladolid; Actun Spukil (Birney et al., 1974; Hatt, 1938); Actun Lol-Tún (UNAM; Hatt et al., 1953, cave deposit; Arroyo-Cabrales and Alvarez, 1990, fossil); cenote 2.5 km NW Dzityá (Birney et al., 1974, netted at night).

The common vampire bat typically roosts in tunnels, caves, and rarely in hollow trees, forming small to medium-

sized groups (Dalquest, 1955; Goodwin and Greenhall, 1961; Lord et al., 1976; Villa-R., 1967; Wilkinson, 1985). It is an indifferent species that either roosts alone or in caves with many other species (Chapter 4). McNab (1969) registered temperatures from 13 to 25 °C and relative humidities from 78 to 98% in caves occupied by *D. rotundus*.

Although local people consider *D. rotundus* a major plague, I found common vampires in only nine caves and in only one instance--in Actun Sabak-ha--they formed a colony of >1,000 individuals. I found *D. rotundus* more frequently in second- or higher-order chambers, typically close to a constriction. This observation contrasts with previous observations (Goodwin and Greenhall, 1961; Villa-R., 1967; personal observation) of the common vampire roosting in exposed sections of caves, close to the entrances.

Groups of common vampires normally roosted in horizontal cracks and crevices or among thin stalactites on the ceiling of the caves. As someone approached, the animals would walk or leap to higher or deeper sections of their refuges. I found *D. rotundus* sharing the same cave chamber with other five species of bats (*P. parnellii*, *M. megalophylla*, *G. soricina*, *D. ecaudata*, and *N. stramineus*), but in all cases the vampires occupied different sections of the chamber. Temperature at sites occupied by this bat ranged from 25.0 to 28.0 °C, and relative humidity was in all cases >80% (Fig. 1).

*Diphylla ecaudata*. Actun Sabak-Ha (2), Ramonal Cave (1), Hochtún Cave (2), Tzab-Nah Cave (2), Actun Lol-Tún (2), Actun Spukil (2). Other cave records in Yucatán: Oxolodt Cave, Kaua (Pearse and Kellog, 1938); Actun Spukil (Birney et al., 1974; UNAM); Hochtún Cave (Birney et al., 1974); cave 1 km S Catmís (UNAM); Actun Lol-Tún (UNAM; Alvarez, 1982; Arroyo-Cabrales and Alvarez, 1990, fossil).

The hairy-legged vampire bat roosts in caves, forming small groups of <25 individuals (Villa-R., 1967). McNab (1969) found this species at sites with temperatures ranging from 19 to 25 °C and relative humidity from 80 to 98%.

I found *D. ecaudata* in six of the caves. Bats of this species normally roosted in the deepest sections (>70 m from the entrance) where temperature and humidity were high. As in other parts of its geographic range, this species is uncommon in Yucatán. In Hochtún Cave these vampires formed a small (25 to 35 individuals) roosting close to each other but not in direct contact; on 16 August, I captured several pregnant females, and one was delivering a newborn. In Tzab-Nah cave, these bats formed very small groups (three to five individuals) in the solution holes on the ceiling of the main chamber, only 30 m from the entrance. One group consisted of two adult females and one adult male; other contained four adult males, three of them with scrotal testicles. Temperature at sites occupied by *D. ecaudata*

were always  $>26.5$  °C. and relative humidities were always  $>87\%$  (Fig. 1).

#### Natalidae

*Natalus stramineus*. Actún Sabak-Ha (2), Bat Cave (5), Ramonal Cave (1), Flor de Mayo Cave (1), Hochtún Cave (4), Cave of the Ruins of Mayapán (3), Tzab-Nah Cave (3), Actun Spukil (3). Other cave records in Yucatán: Balankanchén Cave (Jones et al., 1973; Pearse and Kellogg, 1938); Hochtún Cave (Birney et al., 1974; Jones et al., 1973; Pearse and Kellogg, 1938); Muruztun Cave, Tizimín (Pearse and Kellogg, 1938); Actun Spukil (Birney et al., 1974; UNAM); Actun Lol-Tún (Birney et al., 1974; Arroyo-Cabrales and Alvarez, 1990, cave deposits).

Bats of the genus *Natalus* roost in the darkest and more humid sections of caves (Goodwin, 1970; Silva Taboada, 1979; Villa-R., 1967), although Goodwin and Greenhall (1961) reported contrasting conditions for *N. tumidirostris* in Trinidad. In one cave in México, McNab (1969) registered temperatures from 27 to 28 °C and relative humidity of 81% where *N. stramineus* was roosting.

The long-legged bat was observed only in deep ( $>50$  m) chambers where temperature and relative humidity were very high (temperature  $>27$  °C, relative humidity  $>80\%$ ). In Bat Cave, where the population of *Natalus* was estimated to be  $>10,000$  individuals, temperature ranged from 29.5 to 30.5 °C and relative humidity varied from 92 to 96%. Typically *N.*

*stramineus* formed medium-sized or big groups (100 to >10,000 individuals), but in Ramonal Cave there were only six individuals. In all cases, bats were close together (20 to 50 cm) but not in direct contact with each other. Population sizes in some cases are probably underestimated because they are based only on colonies actually seen. It is possible that inaccessible parts of these caves harbor other groups of this species. Indirect estimation of population size is not possible for *Natalus* because this species is rarely captured in mist-nets.

#### Vespertilionidae

*Myotis keaysi*. Actun Sabak-Ha (1), Hochtún Cave (3), Tzab-Nah Cave (1), Acanceh Cave (1), Actun Lol-Tún (2), Actun Spukil (1). Other cave records in Yucatán (Jones et al., 1973 unless otherwise stated): Balankanchén Cave; Hunucmá Cenote; Cinco de Mayo Cave (Pearse and Kellog, 1938); cenote 2.5 km NW Dzityá (Birney et al., 1974, netted at night); Actun Lol-Tún (UNAM; Arroyo-Cabrales and Alvarez, 1990, fossil); cave 1 km S Catmís (UNAM).

The black myotis has been reported in volcanic and limestone caves by Villa-R. (1967) and by Medellín and López-Forment (1986). Villa-R. (1967) found a big group of these bats in a cenote in Hunucmá, Yucatán, where temperature was 28 °C and relative humidity was 95%.

I found *M. keaysi* to roost in two contrasting situations. In Hochtún Cave, bats formed large clusters,

like the one described by Villa-R. (1967), on the ceiling of the deepest (100 m) section of the cave, just above a cenote (cave pool). In other caves, the black myotis roosted in small (three to five individuals) groups in very small (<20 cm deep) holes and crevices in the walls and ceiling of sections of caves that were close to the entrance.

In Hochtún Cave, the sex ratio was strongly skewed (1:23.5 males:females,  $n = 96$ ). Ambient conditions at the site of the *M. keaysi* varied from 27.5 °C and 96% relative humidity on 2 March to 29.5 °C and 89% relative humidity on 16 July. In contrast, sex ratio in the small groups was always close to 1:1 and ambient conditions were less favorable. In Actun Sabak-ha, for example, one hole with *M. keaysi* was located in an open doline where temperature and relative humidity were 30.1 °C and 75%.

Only three of the 17 cave species of cave bats of Yucatán were not encountered during this study. The fishing bat, *Noctilio leporinus* occurs only on coastal areas or close to major river systems, and its presence in the areas surveyed is very unlikely. The big fruit-eating bat (*Artibeus lituratus*) is uncommon in Yucatán (Jones et al., 1973) and it uses caves only as alternative roosts (Chapter 4). The free-tailed bat (*Nyctinomops laticaudatus*) is common in the peninsula (Bowles et al., 1990) but has not been reported using caves in Yucatán, although it is known to roost in caves in other parts of México (Carter and Davis, 1961; Chapter 4).

Besides the bats discussed above, another five species have been captured in caves or at the entrances of caverns during night netting: *Eptesicus furinalis*, *Lasiurus ega*, *Lasiurus intermedius*, *Rhogeessa tumida*, and *Eumops bonariensis* (Birney et al., 1974; Bowles et al., 1990; Jones et al., 1973; UNAM). It is not clear if these species use these sites as night roosts or as foraging areas. Skulls of two species, *Lasiurus blossevillii* and *Lasiurus ega*, were found inside caves by Pearse and Kellog (1938). Barbour and Davis (1969) reported that bats of the genus *Lasiurus* in the United States sometimes get lost in caves and die inside. It is possible that the skulls found in Yucatán caves came from such events or were deposited as part of owl (*Tyto alba*) pellets.

Besides the species already mentioned, another 11 were reported by Hatt et al. (1953) or by Arroyo-Cabrales and Alvarez (1990) in Recent and Pleistocene cave deposits. It is not clear how many of these species actually inhabited the caves at one time or whether the bones were deposited in owl pellets.

#### Analysis of Interspecific Association

There was a significant positive association among the cave bats of Yucatán ( $V = 4.09$ ,  $W = 147.27$ ,  $P < 0.001$ ,  $X^2$  test, 36 *d.f.*). In the majority of the studies reviewed by Schluter (1984) there was a positive association among the animal species under consideration. As he pointed out, a

significant result does not imply the existence of a particular interspecific interaction among the species. In the case of the cave bats of Yucatán, it seems clear that the significant positive association is more a consequence of the similarity of ambient requirements for several species than the result of a positive interspecific interaction (mutualism). For example, many species (*Natalus*, the mormoopids) tend to be together in caves that offer high temperatures and relative humidities, thus contributing to the overall positive association.

Positive values of  $I$  predominated in the analysis of pair-wise association. Thirty-one of the 91 possible pairs of species showed a significant association ( $P < 0.05$  in Fisher's exact test), and only one of these--the *Peropteryx macrotis* - *Glossophaga soricina* pair--yielded a negative  $I$  value. The species with the higher number of positive associations ( $>6$ ; the three mormoopids, *Diphylla ecaudata*, *Natalus stramineus*, and *Myotis keaysi*) tend to occupy the same hot and very humid rooms in caves. Again, these positive associations seem to indicate similarities in habitat requirements rather than any particular interspecific interaction.

The cluster analysis failed to produce clear groupings (Fig. 6.2). At the level of  $I = 0.35$  (the approximate limit for values that have  $P < 0.05$  in a Fisher's test), ten species form a loose group, whereas four other (*P. macrotis*, *A. jamaicensis*, *M. megalotis*, and *C. auritus*) stand by

themselves. The ten species in the large group tend to occupy only those caves that have secluded rooms with high temperature and relative humidity. The four independent species were found in more exposed situations in smaller caves.

Results discussed in this section show that most bat species tend to inhabit the same type of caves, those whose particular physical characteristics produce conditions of high temperature and humidity. This similarity in habitat preference produces a positive association among these species, as well as significant positive pair-wise associations in most cases. Three species (*P. macrotis*, *M. megalotis*, and *A. jamaicensis*) and possibly *C. auritus*, do not conform to this rule and are more catholic in their habitat preferences.

### Classification of Caves

The association analysis classified the caves of Yucatán in six groups based on the relationship among the bat species (Fig. 6.2, Table 6.1). The procedure identified five divisor species (*N. stramineus*, *P. parnellii*, *M. megalophylla*, *G. soricina*, and *D. ecaudata*). The 19 caves classified in Group I are small and simple sites that harbor populations of only *P. macrotis* or *A. jamaicensis*. Group II included six caves that provide roosts for *G. soricina* but that also tend to be simple and short. Actun Sitz, a medium-sized cave with an unusually poor bat fauna, is the

sole member of Group III, whereas Group IV is formed by the Chocantes Cave, a large system that provides roosts for only two species of bats. Group V is composed of three medium-sized caves that harbor big populations of at least four species each. Finally, Group VI encompasses six of the largest and more complex caves, each with a diverse and abundant bat fauna (Table 6.2).

A one-way ANOVA excluding groups II and IV (which had only one element each) showed a significant difference among the groups in terms of maximum horizontal extent ( $L_k$ ,  $F = 19.92$ ,  $d.f. = 3/28$ ,  $P < 0.001$ ; log-transformed data). A Tukey's multiple comparison procedure demonstrated that caves in Group I are significantly shorter than caves on the other groups and that groups II and VI are also different (in all cases,  $P < 0.05$ ; see means and standard deviations in Table 6.2).

In contrast, the groups did not differ in terms of cave amplitude (one-way ANCOVA; test for homogeneity of slopes,  $F = 2.50$ ,  $d.f. = 3/28$ ,  $P = 0.102$ ; test for effect of Group,  $F = 2.17$ ,  $d.f. = 3/27$ ,  $P = 0.11$ ; log-transformed data; Figure 6.4). I used analysis of covariance (ANCOVA) to test for the effect of group on  $H_k$  (amplitude), using maximum horizontal extent ( $L_k$ ) as covariate, to control the effect of size that had been demonstrated by the significant differences in  $L_k$ . A similar analysis showed no difference in total extent of passages ( $L'$ ) when controlling for  $L_k$  (ANCOVA; test for homogeneity of slopes,  $F = 1.79$ ,  $d.f. =$

3/24;  $P = 0.18$ ; test for effect of Group,  $F = 0.57$ ,  $d.f = 3/27$ ,  $P = 0.64$ ; log-transformed data; Figure 6.5).

These results indicate that size of the cave (as gauged by horizontal extent) is the key factor explaining the association among bats in the caves of Yucatán. Larger caves, like those in Group VI, are more complex and have higher probabilities of having chambers with the necessary isolation from the exterior to assure the stability in temperature and humidity that is required by most cave bats. Smaller caves, like those in Group I are simple refuges that harbor only those species with less strict ambient requirements, such as *P. macrotis* and *A. jamaicensis*.

#### Correlations of Diversity and Abundance

Most caves studied had a low species richness (Figure 6.6). The average number of species per cave was 3.28, but 21 (58%) of the caves harbored only one or two species, whereas only six (17%) provided refuge for seven or more species. The frequency distribution for the caves of Yucatán is similar to the one for the caves of México (Chapter 4). Actun Lol-Tún is an unusually rich cave; at least 12 cave species use it as diurnal refuge, and other three species (*Dermanura phaeotis*, *Sturnira lilium*, and *Lasiurus intermedius*) have been captured in the open doline. Arroyo-Cabrales and Alvarez (1990) reported bone material from Recent owl pellets or from fossil material corresponding to 13 other species, pushing the total number

of bat species that have been reported from the cave to 28. It is not possible to know if the species found by Arroyo-Cabrales and Alvarez (1990) actually inhabited the cave or if the bones were in fact deposited in owl (*Tyto alba*) pellets. In any case, both the present-day richness and the number of fossil species are remarkable.

Most species tended to inhabit caves with high species richness (Table 6.3). The median for the number of species in caves inhabited by a given species was significantly higher than expected by chance for ten of the 14 species. *Peropteryx macrotis* and *Artibeus jamaicensis* are generalists that use caves of any size and species richness. *Micronycteris megalotis* seems to prefer caves that are not used by other species. *Chrotopterus auritus* was found in only one cave, and it is not possible to infer its preferences.

Results in Table 6.3 coincide with the classification of incidence functions for Mexican cave bats presented in Chapter 4. A discussion of the major discrepancies follows. *Peropteryx macrotis* was considered an integrationist species in Chapter 4, but in Yucatán it rather would be considered an indifferent species that lives in caves both with few and with many other bat species. Two of the species that were classified as indifferent in Chapter 4 tended to be found in Yucatán only in caves with high species richness. *C. perspicillata* is uncommon in Yucatán, and it is difficult to extract meaningful conclusions from the reduced sample size

in the study site. The populations of the common vampire (*Desmodus rotundus*) in Yucatán differ from those of the rest of México in that in Yucatán this bat tends to inhabit caves with many other species (i.e., it is an integrationist species). In half of the cases, there were five or more bat species in caves occupied by common vampires (Table 6.3). *Mimon cozumelae* was considered segregationist in Chapter 4, but in Yucatán it was found only in Actun Lol-Tún, along with other 11 species. Even if significant, the deviation from expected is based on a single observation; a larger sample size would be needed to get a conclusive assessment of the preferences of this species.

There was a positive correlation between species richness and the size of the cave, as measured by  $L_k$ , the maximum horizontal extent of the cave (Figure 6.7 top,  $r = 0.78$ ,  $P < 0.001$ ). The lower right triangle in Figure 6.7 top is empty of points, suggesting that there is a minimum size of a cave to support a given number of bat species, but that large caves do not necessarily harbor rich assemblages.

The relationship between species richness and size of the cave can be modeled using the concepts of fractal geometry (Figure 6.7 bottom; Appendix D). The estimate of the fractal dimension ( $d = 0.54 < 1.0$ ) indicates that a given increment in cave size produces only a small increase in species richness. The full meaning of this dimensionality will not be clear until data from other regions are collected. The parameter  $d$  could be used as a

parameter to measure the relationship between species richness and cave morphology in different zones.

Species richness varied among the groups formed by the association analysis among cave bats (Kruskal-Wallis test comparing the four groups with  $n > 1$ ,  $X^2 = 23.8$ ,  $d.f. = 3$ ,  $P < 0.001$ , Table 6.2). Caves in Group I had fewer species than the rest of the sample (Median  $S = 1.5$ ; Mann-Whitney test,  $U = 245.5$ ,  $P < 0.001$ ), whereas caves in group VI were richer than the rest of the sample (Median  $S = 6.0$ ;  $U = 3.5$ ,  $P < 0.01$ ). Species richness for caves in Groups II and V did not differ from expected (Median  $S$  for Group II = 3.0; for Group V = 4.0; in both cases  $P > 0.05$ ), and Groups III and IV were not tested due to insufficient sample size but their species richness ( $S = 2$  in both cases) is equal to the expected value for the whole sample.

These results show that the categories formed by the association analysis form a gradient of species richness. Group I is formed by the shortest and simplest caves that harbor only one or two species. Groups II to V include caves with more species than those in Group I but fewer than those in Group VI. This last group includes the caves with the highest species richness.

The correlation between abundance and species richness was positive and significant ( $r = 0.79$ ,  $P (r = 0) < 0.001$ , Figure 6.8). This result contrasts to the pattern found in Chapter 4 for the caves of México, in which there was no correlation between abundance and species richness. Perhaps

this reflects a variation in terms of geographical scale, but it could be as well be due to the absence in Yucatán of species like *Tadarida brasiliensis* that form huge colonies in caves with low species richness. In Yucatán, segregationist and indifferent species form small or medium-sized colonies (e.g. *P. macrotis*, *M. megalotis*, *A. jamaicensis*), whereas integrationist forms tend to concentrate in big and very big groups (e.g., *Pteronotus* spp., *N. stramineus*). As a consequence, caves in Group VI, which have higher species richness, also harbor larger total populations.

Table 6.1--Classification of Yucatán caves based on the association among bat species. Caves are fully described in Chapter 4. See Figure 6.3 for the classification criteria.

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Group I	Group II
Actun Chunkunab	Roble Cave
Actun Maas	Cinco de Mayo Cave
Actun Kan-Lol	Ramonal y Naranja Cave
Porcupine Cave	Bejucos Cave
Actun Oxpehol	Cave "B"
Actun Maasit	Kabahchén Cave
Iguana Cave	Group III
Doña Blanca Cave	Actun Sitz
Actun Kab	Group IV
Cave "A"	Chocantes Cave
Actun Tolok	Group V
Guayaba y Aguacate Cave	Bat Cave
Actun Chac-Xix	Flor de Mayo Cave
Aguacate Cave	Ruins of Mayapán
Zorro Cave	Group VI
Ruins of Kabah	Actun Sabak-ha
Acanceh Cave	Ramonal Cave
Actun On	Hoctún Cave
	Tzab-Nah Cave
	Actun Lol-Tún
	Actun Spukil

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Table 6.2--Morphometric and biological data for the six groups of Yucatán caves as classified by the association among bat species. The table shows average values and the standard deviation in parenthesis; values in parenthesis below group number are the sample size. L', total extent of the cave; H<sub>k</sub>, amplitude (maximum vertical distance); I.D., index of development; C<sub>v</sub>, coefficient of verticality; S, number of bat species; A, abundance of bats.

GROUP	L'	H <sub>k</sub>	I.D.	C <sub>v</sub>	S	A
I (18)	30.3 (22.2)	11.1 (10.6)	1.21 (0.27)	0.42 (0.40)	1.53 (0.61)	1.63 (0.61)
II (6)	87.2 (56.7)	9.3 (5.8)	1.62 (0.61)	0.23 (0.21)	3.33 (1.03)	1.81 (0.43)
III (1)	114.6 (-)	27.5 (-)	1.22 (-)	0.29 (-)	2.00 (-)	1.04 (-)
IV (1)	261.6 (-)	49.9 (-)	1.43 (-)	0.27 (-)	2.00 (-)	3.04 (-)
V (3)	134.6 (47.7)	20.2 (11.0)	1.39 (0.28)	0.20 (0.08)	5.00 (1.73)	3.67 (1.54)
VI (6)	518.7 (597.4)	24.8 (14.2)	1.90 (0.84)	0.12 (0.03)	8.50 (2.66)	3.77 (0.47)

Table 6.3--Species richness of the caves of Yucatán, by species. Probabilities are for deviations from a null model based on the distribution of species among caves. Expected median is 2.0.

SPECIES	N	Species Richness	
		Median	P
<i>Peropteryx macrotis</i>	28	2.0	1.000
<i>Pteronotus davyi</i>	4	9.0	0.000*
<i>Pteronotus parnellii</i>	8	8.0	0.000*
<i>Mormoops megalophylla</i>	6	8.5	0.001*
<i>Micronycteris megalotis</i>	2	3.5	0.368
<i>Mimon cozumelae</i>	1	12.0	0.028*
<i>Chrotopterus auritus</i>	1	9.0	0.077
<i>Glossophaga soricina</i>	14	4.5	0.000*
<i>Carollia perspicillata</i>	2	9.5	0.003*
<i>Artibeus jamaicensis</i>	22	3.0	0.052
<i>Desmodus rotundus</i>	9	5.0	0.006*
<i>Diphylla ecaudata</i>	6	8.5	0.000*
<i>Natalus stramineus</i>	9	8.0	0.001*
<i>Myotis keaysi</i>	7	8.0	0.006*

\*  $P < 0.05$

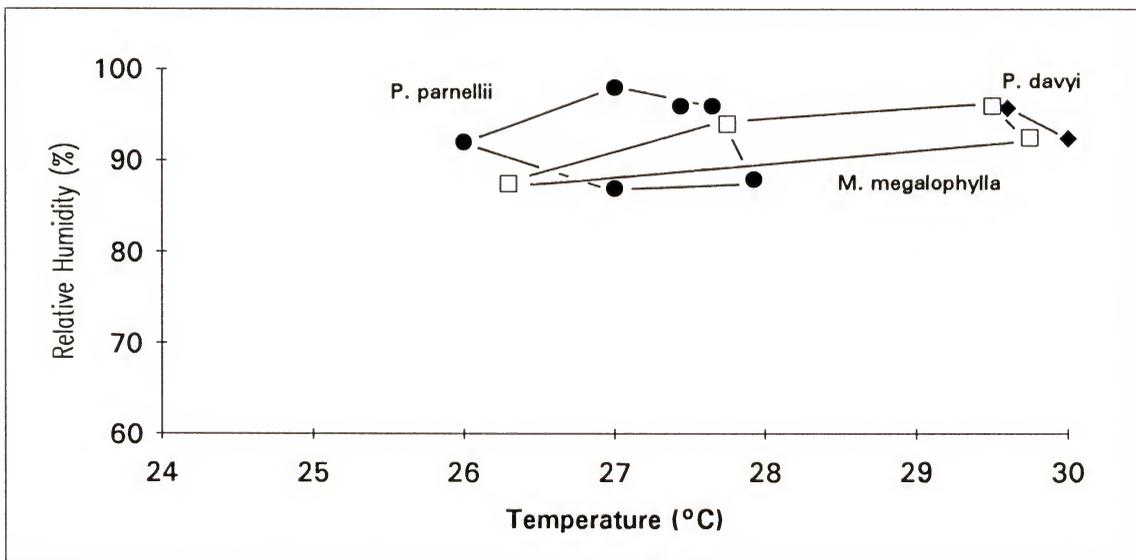
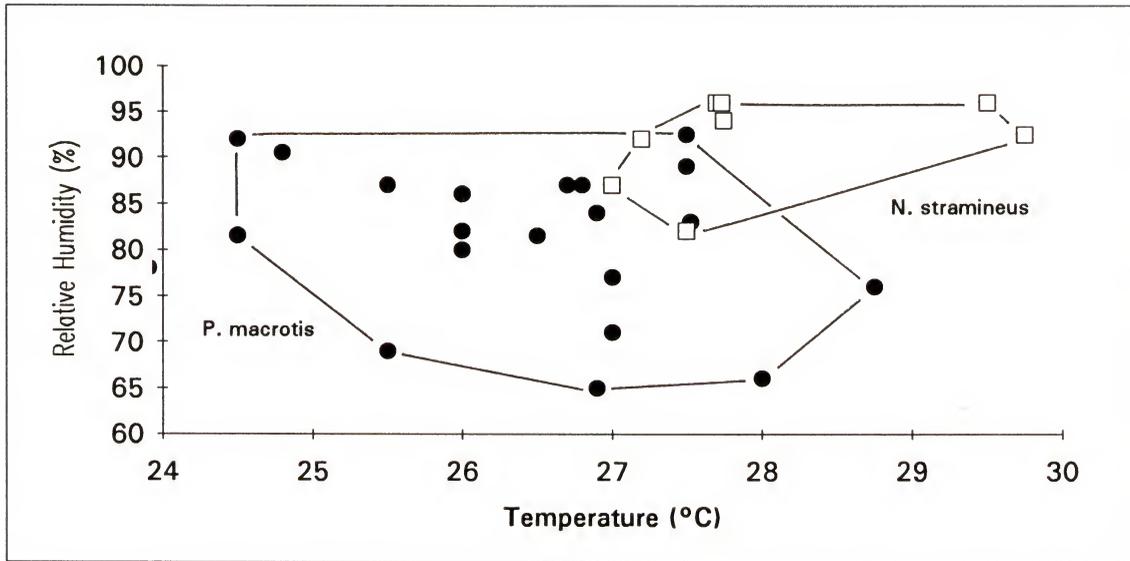


Figure 6.1--Temperature and relative humidity of Yucatán caves, by species. Each point represents a single cave and may be an average for several observations.

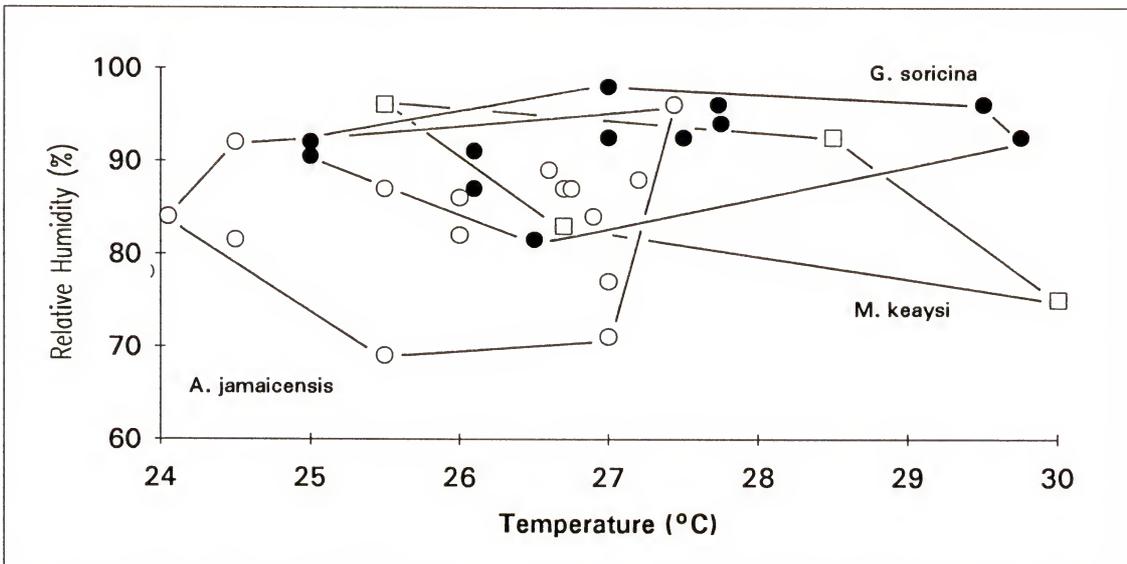
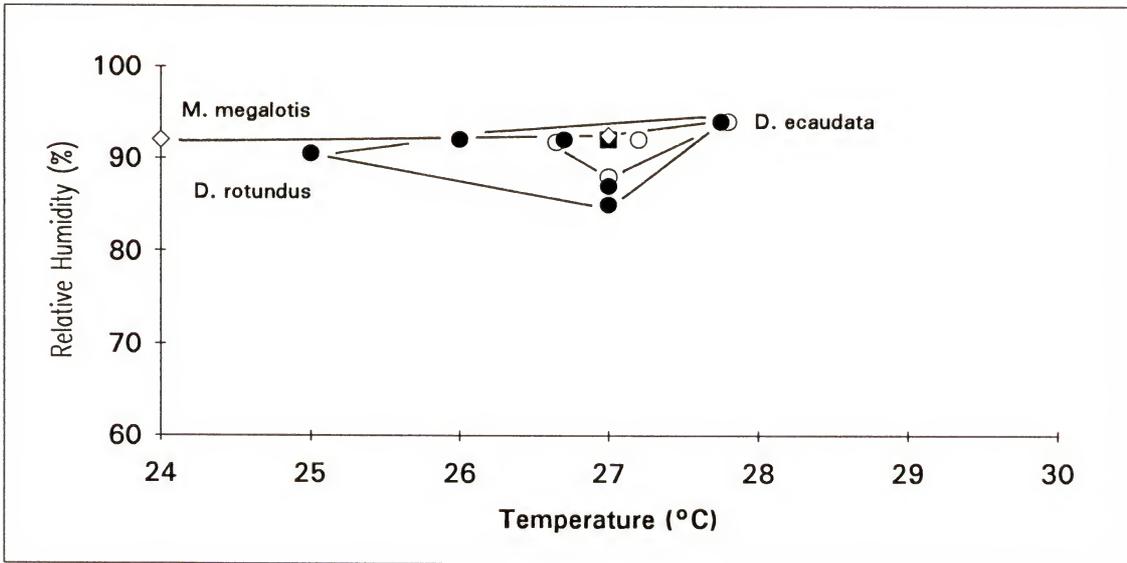


Figure 6.1--Continued.

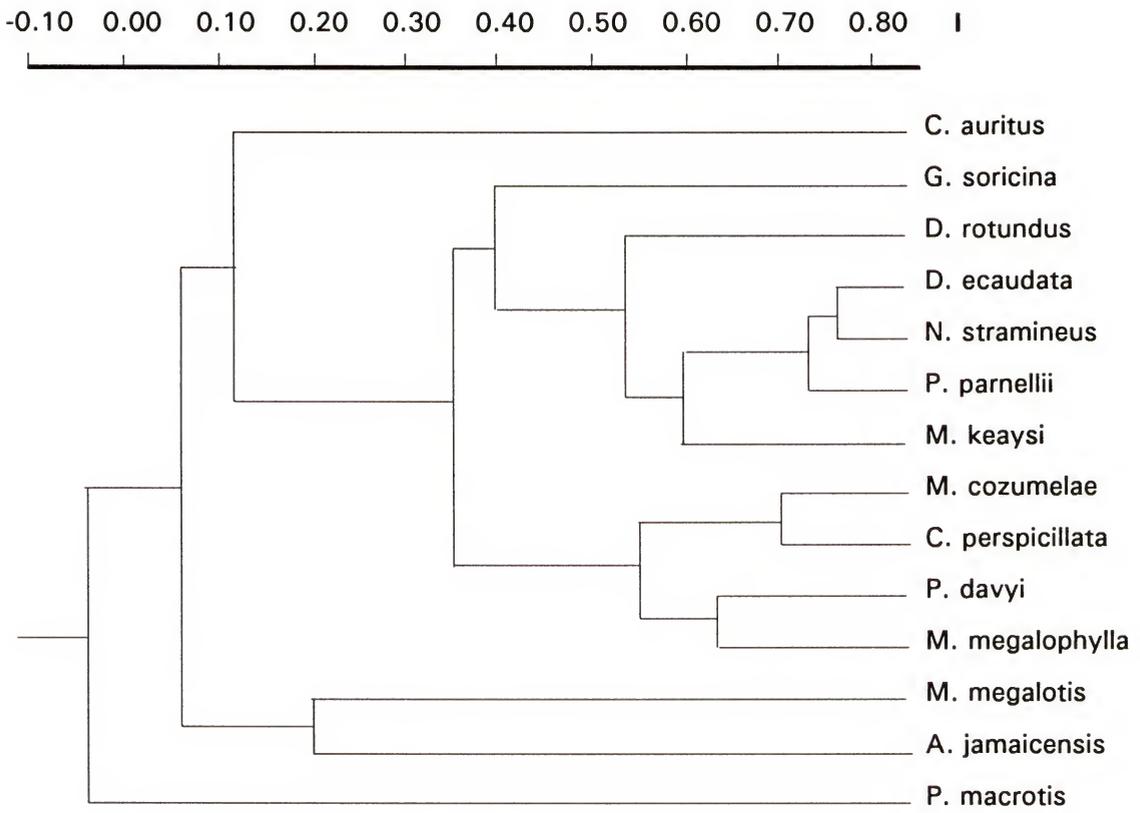


Figure 6.2--Cluster analysis of the cave bats of Yucatán based on presence/absence data for 36 caves. Scale indicates distance as measured by the association index, I.

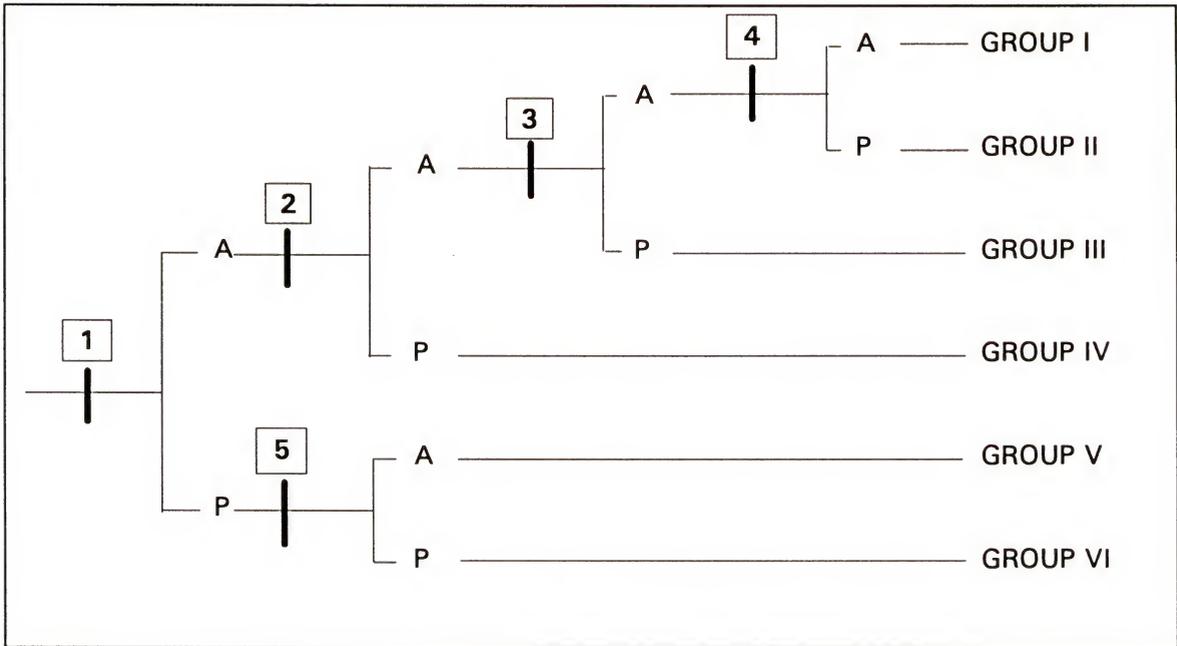


Figure 6.3--Association analysis of the caves of Yucatán based on the relationship among bats. A means that the divisor species is absent, P means that it is present. Divisor species are: 1, *N. stramineus*; 2, *P. parnellii*; 3, *M. megalophylla*; 4, *G. soricina*; 5, *D. ecaudata*.

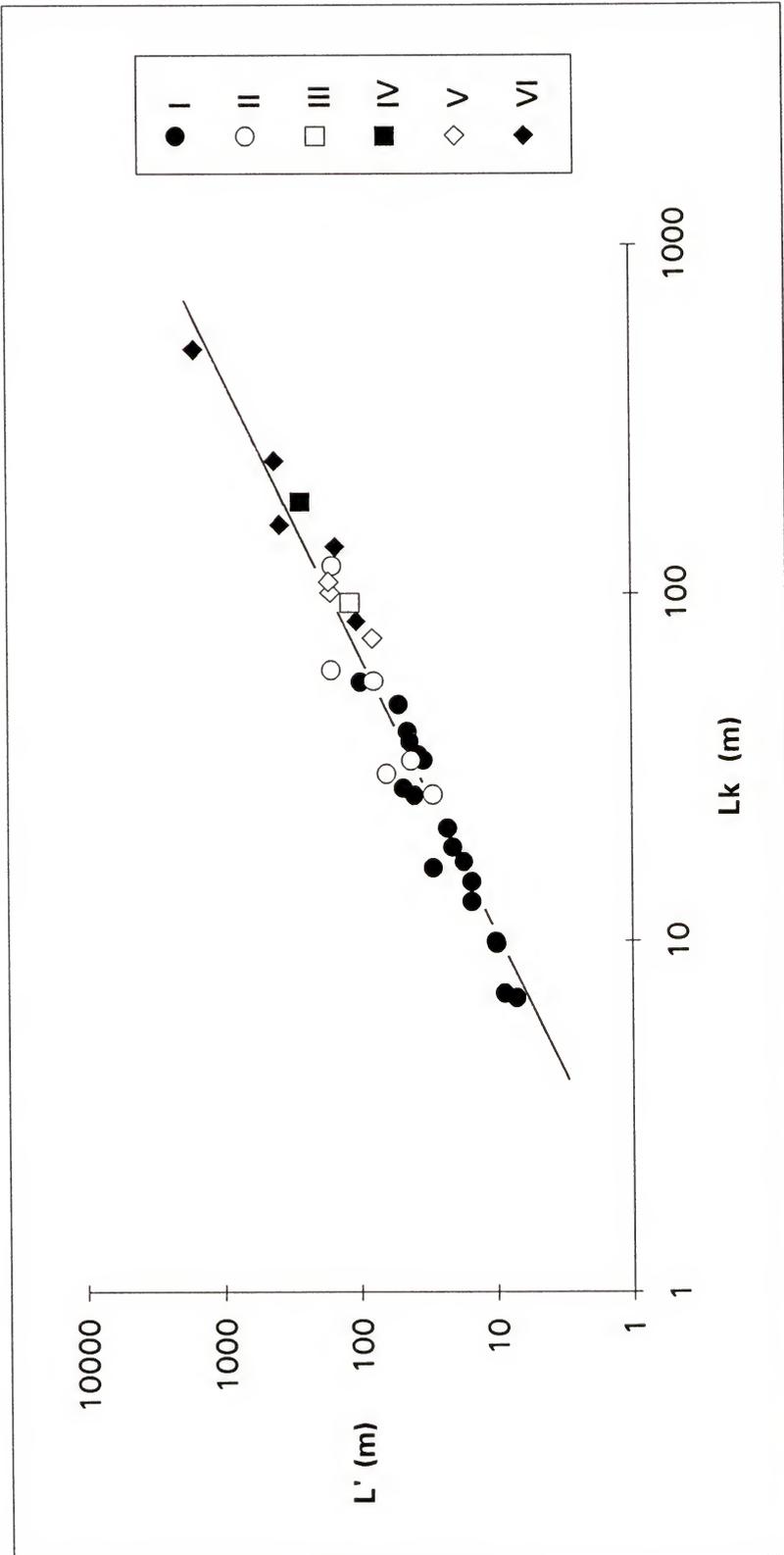


Figure 6.4--Relationship between total passage extent ( $L'$ ) and maximum horizontal extent ( $L_k$ ) for caves of Yucatán classified according to the association among bats. Note logarithmic scales. Regression lines are not different among the groups (see text for details).

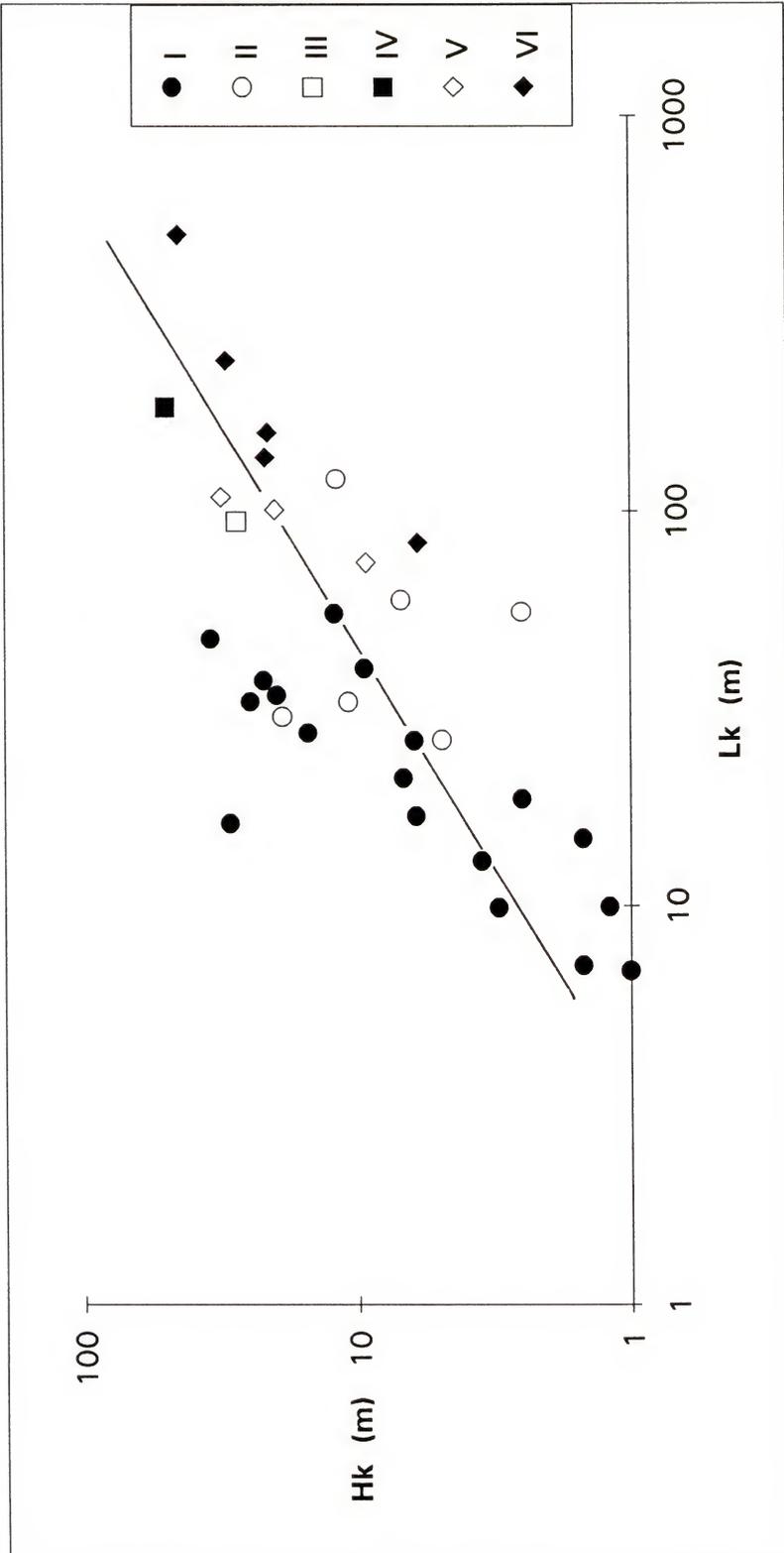


Figure 6.5--Relationship between amplitude ( $H_k$ ) and maximum horizontal extent ( $L_k$ ) for caves of Yucatán classified according to the association among bats. Note logarithmic scales. Regression lines are not different among the groups (see text for details).

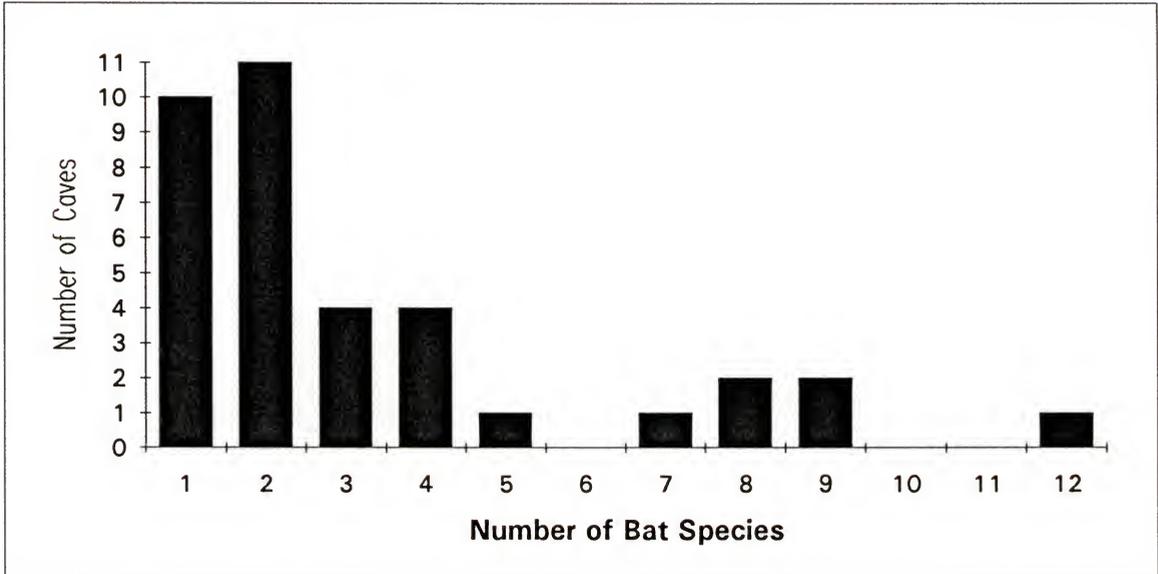


Figure 6.6--Frequency distribution of the number of bat species for the caves of Yucatán.

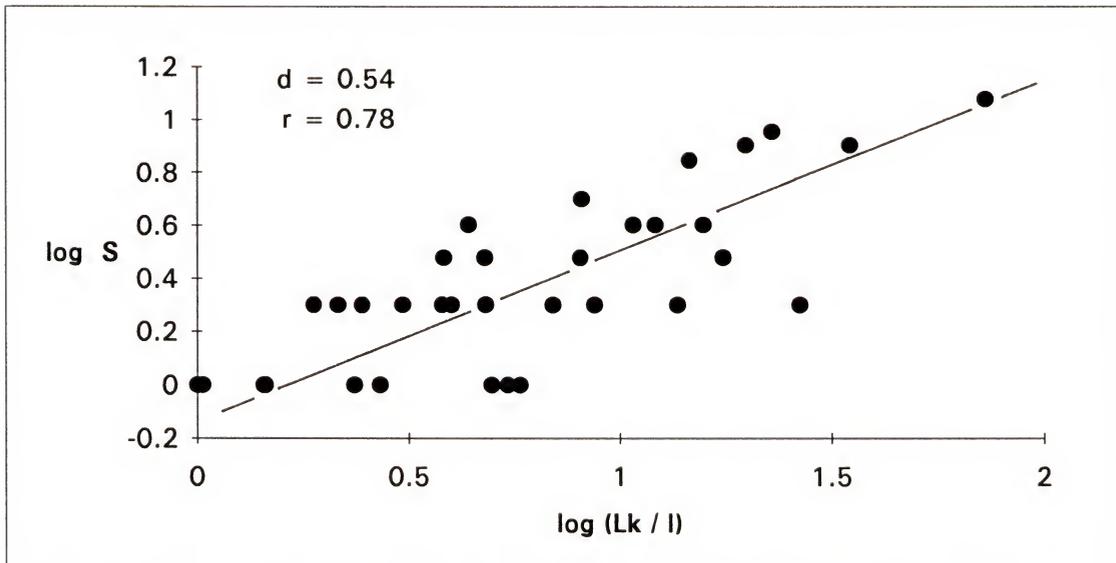
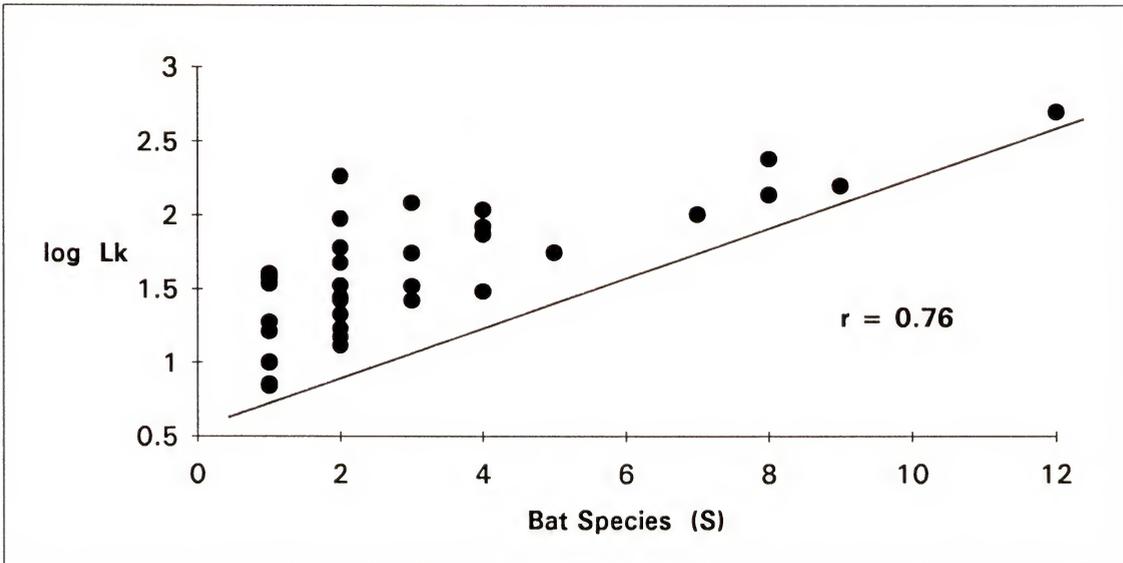
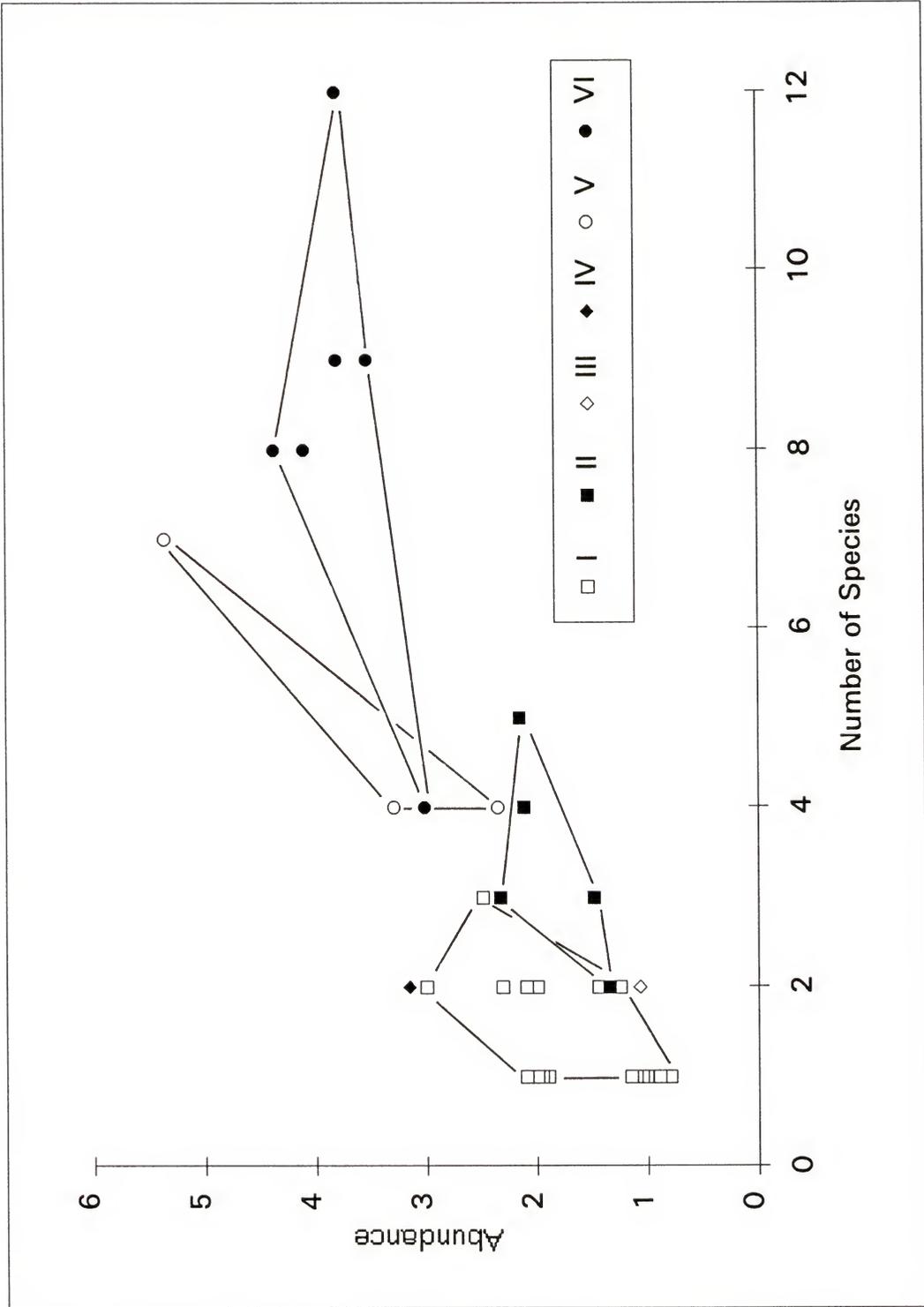


Figure 6.7--Correlation between the species richness and the size of the Yucatán caves. Top;  $S$  is the species richness and  $L_k$  is the maximum horizontal extent of the caves; line shows minimum size required for a given species richness. Bottom, Fractal scaling of species richness in Yucatán caves; line shows the least-square regression line.  $L_k$  is the horizontal extent of the caves and  $l$  is the horizontal extent of the smallest cave in the sample. See Appendix D.

Figure 6.8--Correlation between abundance and species richness for the caves of Yucatán.  
The figure shows the groups of caves as classified by the association analysis of the  
distribution of bats among the caves.



CHAPTER 7  
A PLAN FOR THE CONSERVATION AND MANAGEMENT OF THE CAVES OF  
YUCATAN

In this chapter I summarize the main results of this dissertation and present a series of recommendations for the conservation and management of Yucatán caves. The suggestions presented here are based mostly on the surveys of the caves (Chapter 3) and on the data on Yucatán cave bats presented in Chapter 6. I also use the results of the reviews of the Mexican cave bats (Chapter 4) and of the Yucatán bat fauna (Chapter 5) to support some of the conclusions. The recommendations presented here are intended to contribute principally to the conservation of bats, so they could be criticized for being biased and for neglecting other taxa. Nevertheless, I envision these suggestions as part of a larger plan that should be supported by subsequent surveys by geologists, archaeologists, social scientists, as well as by other biologists. The main contribution of this chapter is that it constitutes the first attempt to design a management plan for a set of caves in Yucatán. The main objective of this dissertation will be accomplished when the conclusions presented in this chapter prompt subsequent studies by other scientists to elaborate a more complete management plan.

### Criteria for the Conservation of Bat Caves

Three criteria have been proposed for assigning conservation value to caves that harbor bat populations: species richness, abundance, and the presence of species of special concern (Chapter 4). In this section I apply these criteria to the case of the caves of Yucatán.

#### Species Richness

Only 10% of the caves of México harbor  $\geq 6$  species of bats (Chapter 4). I suggested that these caves deserve special consideration for protection because of their unusually high species richness. According to this criterion, six (16.7 %) of the Yucatán caves under study should be considered relevant in a conservation plan (Table 7.1). Lol-Tún is the second richest cave in México in terms of day-roosting species and the richest in terms of the total number of species using the cave.

#### Population Abundance

Nine of the caves under study support populations of  $>1,000$  bats (Table 7.1). At a national level, none of these caves can be considered unusual in terms of abundance. This is because the Mexican free-tailed bat (*Tadarida brasiliensis*), that elsewhere in México forms colonies of several million individuals, is absent from Yucatán. Additionally, in Yucatán the mormoopids (*Pteronotus* spp. and *Mormoops megalophylla*) never form the huge congregations of

>100,000 individuals that have been reported from other sites (Bateman and Vaughan, 1974). At the local level, however, the caves in Table 7.1 deserve special consideration because of their comparatively high population levels.

### Species of Concern

The bat fauna of Yucatán is a subset of the pool of species of southeastern México and is formed mostly by species with wide distributional ranges (Chapter 5). Because local abundance and area of distributional range are positively correlated for Neotropical bats (Arita, unpublished data), the bat fauna of Yucatán is formed by species that tend to be not only widespread but also locally abundant. Consequently, using rarity as the criterion for vulnerability, the majority of the Yucatán species are not endangered. In fact, only three of the cave bats of Yucatán are considered fragile or vulnerable by Medellín and Arita (in press).

Two of these species, the spear-nosed bat (*Mimon cozumelae*) and the woolly false vampire bat (*Chrotopterus auritus*), are rare and form small colonies of <10 individuals (Chapter 4). During this study both species were found in caves with high species richness (*M. cozumelae* in Lol-Tún, *C. auritus* in Tzab-Nah), but other reports (Hatt and Villa-R., 1950; Jones et al., 1973) indicate that these species also roost in caves with low species richness.

Because they are rare, both *M. cozumelae* and *C. auritus* would require special studies to assure their conservation in Yucatán. These studies should focus on the identification of caves that are regularly used by these two species.

The third species, *Peropteryx macrotis*, is rare in other tropical areas of México (Medellín and Arita, in press), but in Yucatán it is relatively abundant and was present in a high percentage (75%) of the caves surveyed. Judging from its ubiquity and abundance, *P. macrotis* seems to be in no immediate danger and probably does not require special conservation treatment. Because it is present in a large number of caves, this species would benefit from any conservation action that protects caves or bat cave communities.

In the case of the caves of Yucatán, a conservation approach based on the presence of bat species of special concern would be difficult to undertake and of little practical use. Clearly, a better strategy would be to focus on the conservation of bat communities as a whole. Species richness and total population abundance would be better criteria than the presence of species of concern.

#### Correlations Between the Criteria

There is positive correlation between bat species richness and population abundance in the caves of Yucatán (Chapter 6). This correlation implies that a comparatively

small number of sites would be necessary to comply with these two conservation criteria. Five of the caves in Group I and one in Group V have both the highest species richness and the largest populations (Table 7.1; see Chapter 6 for definition of groups). These results contrast with the observation that abundance and richness are uncorrelated in the case of caves of all México (Chapter 4).

There is an overall positive association among the cave bats of Yucatán, indicating that most species tend to use the same set of caves (Chapter 6). This tendency produces a bat fauna in which most species are integrationist, that is they tend to occur in caves with high species richness (Chapter 4). If the criterion of protecting caves with unusually high species richness is met, most cave bat species of Yucatán would be protected as well. Exceptions would be the indifferent and segregationist species that do not follow the general trend, including *P. macrotis*, *Micronycteris megalotis*, and *Artibeus jamaicensis*. These species would need special conservation strategies tailored to their particular needs.

The caves with the highest species richness and highest population levels are also the largest and most complex (Chapter 6). This poses a potential conflict between cave conservation and economic interests, because large caves are also the most prized as tourist sites. In fact, four of the six caves with the highest species richness (Sabak-ha, Tzab-Nah, Lol-Tún, and Spukil) are well-known tourist

attractions, and another site, Hochtún Cave, is visited on a daily basis by local people. The only exception is Bat Cave, a relatively small and inconspicuous site that is seldom visited.

### Classification of Caves

In this section I assign the caves under study to the categories of use outlined in Chapter 1. I emphasize that the recommendations presented here are based principally with the conservation of bats in mind. This classification should be revised in the future when information on other aspects of cave conservation becomes available.

### Green Caves

The 27 (75%) caves that presented low species richness and low population levels were classified in Groups I to IV on the basis of their bat communities (Chapter 6). These caves are in general small and difficult to locate, and could be considered "green" (of no special concern) sites. There are, however, some exceptions. Actún Chac-Xix, Roble Cave, and Kabahchén are only a few meters from main roads and are frequently visited by people. These sites support only small colonies of common bat species (Chapter 6), but they are important archeological sites. Considering caves like these as green sites would have a negligible effect for the conservation of bats, but would endanger the historical patrimony of the area.

Because caves of this type are ubiquitous and numerous in Yucatán, trying to protect these sites on an individual basis would be a futile effort. Such misguided strategy would have the high opportunity cost of allocating less resources to the protection of other more important sites. An education campaign for the conservation of caves would be a more effective strategy because it would encourage the protection of all kinds of caves, even those that are not known by the planners but that are visited by local people. The adjective "green" should be used as meaning "of no special concern", not as implying that these sites are "dispensable."

#### Yellow Caves

I propose four caves for the yellow category, that is sites that would require some degree of protection.

Flor de Mayo Cave harbors small colonies of four bat species (Chapter 3). The association analysis of Chapter 6 classified this cave in Group V because the funnel-eared bat (*Natalus stramineus*) was observed there. The presence of this species, and direct measurements (Chapter 3), indicate that some sections of Flor de Mayo present the conditions of high temperature and relative humidity necessary for the maintenance of larger populations of other species. In fact, the accumulation of guano in the deepest sections of the cave suggests that larger populations inhabited the cave in the past or that the site is still used on a seasonal

basis. The fact that a large fossil bone (a horse, *Equus conversidens*, tooththrow) was found on a surface stratum suggests a potential for a rich paleontological site. This cave presents a complex system of tunnels that is attractive to sport speleologists. I suggest that this cave requires a yellow status and that it could have access restricted to a limit annual number of speleologists.

The cave of the Ruins of Mayapán supports populations of four species of bats, including sizable colonies of *Pteronotus parnellii* and *N. stramineus* (Chapter 3). The cave is within the archeological site of Mayapán and access is supposed to be restricted, but the graffiti in the cave is evidence of a high rate of visitation. I recommend simply that the restricted access to the cave be enforced to assure the maintenance of both the archeological treasures and the bat populations.

Hoctún and Tzab-Nah caves are problematic cases. They harbor large populations of several species of bats (eight in Hoctún, nine in Tzab-Nah) and their cenotes support populations of several endemic water invertebrates and fishes, so from a strict conservation perspective they should be typical red caves. The caves are, however, sources of water and recreation centers for the towns of Hoctún and Tecoh and a ban to visit the caves would only create political conflicts. The only solution to the dilemma is the compromise of labeling the caves as yellow sites and restricting the entrance to the minimum necessary

for the local people. I suggest that the best solution would be an education campaign to convince the inhabitants of Hochtún and Tecoh of the importance of their caves and the necessity to limit the impact to these ecosystems. If this is accomplished, local people would both limit their visits to the caves and protect them from outsiders.

### Red Cave

I suggest labeling Bat Cave as the only red cave in the set under study. This site is unique in supporting large populations of bats and being almost unknown to local people. The site is a medium-sized cave with no special geological features and no particular archeological value (Chapter 3). The cave supports, however, large populations of seven bat species, many of which form maternity colonies in the cave. Because the cave features no attraction to the general public, and because of its evident importance for bat conservation, Bat Cave is an obvious choice for the category of red caves.

### Multipurpose Caves

The three remaining sites--Sabak-Ha, Spukil, and Lol-Tún caves--are complex cavern systems that call for multipurpose use. Being a popular tourism attraction, an important archeological and historical site, and the center of a small protected area, Actún Lol-Tún is already an example of a multipurpose system. The fact that this cavern system still harbors a large and rich community of bats

despite the visitation by thousands of people every year is encouraging and shows that commercial use is not necessarily anathema for biological conservation. A possible explanation for the existence of these bat populations in Lol-Tún is that many of the chambers that support the bats are not open to the public and have entrances different than the main entrance used by tourists. Besides that, the modifications in the cave for tourist use are minimal (simple natural trails and some artificial light).

I suggest that this multipurpose use can be sustained if different sections of the cavern system are officially assigned conservation status. In particular, sections not open to the public should be given a red status to protect the bat populations and the archeological heritage. The tourism trail can continue to be used under a yellow status provided that the route is not "modernized" (with cement walkways, sophisticated lighting systems, or sound systems). Under federal law, no area in this archeological site can be open to the public under a green status.

A similar multipurpose use has been proposed for Spukil and Sabak-Ha caves. Both cases are complicated because of the topographical features of these two cavern systems. Spukil is an important archeological site and harbors large populations of nine bat species. It also features a complicated topography and spectacular speleothems that attract many speleologists and that prompted local people to request that the cave be developed for a tourism project.

The problem here is that the adaptation of the system for tourist visitation would require substantial alterations of the cave to allow access to the general, non-skilled, visitors. Additionally, because the main section of the system is connected to the exterior through a single access, the development of a tourist trail would necessarily affect the only entrance that is available for the large populations of bats that the cave supports.

A possible compromise is to restrict the tourism visitation to the open dolines and the first few chambers of the system, leaving the deep sections as red sites devoted to the protection of the bats and of the archeological treasures. I suggest a red status for the deep sections instead of a yellow status because the bat colonies are located in an area that makes impossible for humans to gain access to the deepest parts of the system without disturbing the animals. Repeated molestation of the bat colonies by visitors would probably have an unbearable cost in terms of energetic waste and disturbance of the social structure and reproductive performance. In addition, the deepest sections have a rarefied environment that is dangerous to humans to visit. The alteration of the environment to ventilate these areas would certainly have a significant negative impact on the bat populations.

A similar situation is that of Sabak-Ha. The main section of the cavern system has a single, small entrance and the opening of the cave for tourists would require

substantial modifications, perhaps involving the alteration of the circulation patterns within the ecosystem. The relatively simple topography of the system implies that a system of artificial illumination would affect all places inside the cave, making the areas inhospitable for bats. Additionally, because the substrate of the cave is muddy, tourists would require artificial trails that could have a negative impact on the distribution of invertebrates. The bat populations in Sabak-ha are not as spectacularly large as those in Spukil, and in fact one of the most abundant species in Sabak-ha is the common vampire bat (*Desmodus rotundus*). The impact of diminishing the populations in Sabak-ha would probably be less important than a similar effect on the populations in Spukil.

Planners should take into account the recommendations presented here before developing either Spukil or Sabak-ha as tourist sites. They should consider if a second and even a third major cave attraction too close (<30 km) to the already popular Lol-Tún site would really benefit the local people and if those projects are worth losing two of the most important bat communities in the area.

#### Final Recommendations

In this last section of the dissertation I provide specific recommendations for future actions to be taken to enhance the probabilities of conserving the cave bat populations of Yucatán.

A program to create an official state catalogue of caves should be started as soon as possible. This system could be administered by the state government or by one of the newly formed Yucatecan speleological societies. The purpose of the system would be to operate a reliable list of caves with official names, precise locations, details on special (geological, archeological, or biological) features, conservation status, and categories of use. A good planning of use of the extensive cave system of Yucatán is impossible without such a precise catalogue.

Current rates of visitation to caves are very high. Data presented in this dissertation are not adequate to assess with precision the impact of human visits to caves. The effect of vandals and other uneducated visitors to caves is in some cases self evident. Nevertheless, the less conspicuous but persistent visits by other people could have a higher impact in the long run than the noticeable effect of one-time visits by vandals. Entrance to yellow and red caves should be restricted in some way to ameliorate the impact on important cave systems. The particular way that this can be accomplished needs to be studied on a case-by-case basis because each cave presents particular problems to be solved.

Education should be a pivotal part for the conservation plan of Yucatán caves. Different strategies would be necessary to address the two groups that are most likely to interact with caves: local people and tourists (including

"ecotourists"). Because a crusade to ban totally entrance to all the caves that local people have been visiting for centuries is unrealistic, an education campaign would be a much more effective approach to the problem. This campaign should be aimed at convincing local people of the enormous importance that caves have in the cycle of water in karst regions and of the role of cave organisms in tropical ecosystems. A persuaded local population could be a more efficient instrument to protect the caves of Yucatán than a full army of guards. The design of a particular education campaign is beyond the objectives of this dissertation, but I am confident that the information presented here will in some way contribute to such an important endeavor.

Caves could be a central issue for an educational campaign aimed at tourists. Yucatán is particularly suitable for a project of this kind because most visitors are attracted to the state by its natural and cultural richness, not by modern tourist developments. These "enlightened" tourists constitute an easier target for an educational campaign. The state government could take advantage of the incredible richness of geological, historical, and biological treasures contained in caves to launch a program of cultural tourism centered at cave systems.

Local authorities should be encouraged by the state government to create municipal parks that could combine the protection of important caves with the education of both the

local community and the visitors. These parks should include not only the cave itself, but also the surrounding environment to emphasize the fact that caves and the external surroundings are not independent worlds. In this way people could be persuaded that caves are not isolated and extraneous worlds, but that they are part of their everyday life.

Table 7.1--Yucatán caves with high species richness or high population abundance.

CAVE	SPECIES RICHNESS <sup>1</sup>	ABUNDANCE <sup>2</sup>
Lol-Tún	12	very high
Spukil	9	very high
Sabak-Ha	8	very high
Hoctún	8	very high
Bat Cave	7	very high
Tzab-Nah	9	high
Ramonal	4	high
Ruins of Mayapán	4	high
Chocantes	2	high

<sup>1</sup> Species richness: number of bat species that use the cave as a day roost.

<sup>2</sup> Abundance: total bat population. High, >1,000 individuals; very high, >10,000 individuals.

APPENDIX A  
SOURCES FOR THE DATABASE OF MEXICAN CAVE BATS

The following list includes the sources for the database of Mexican cave bats used in Chapter 4.

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Alvarez, 1963	Lay, 1962
Alvarez and González-Q, 1970	Manning and Jones, 1989
Alvarez and Ramírez-P., 1972	Medellín and López-F., 1987
Anderson, 1972	Medellín et al., 1983
Baker, 1956	Medellín et al., 1985
Barbour and Davis, 1969	O'Farrell and Studier, 1980
Birney et. al., 1974	Pearse and Kellog, 1938
Cockrum, 1969	Ramírez-P. and Alvarez, 1972
Cockrum and Bradshaw, 1963	Ramírez-P. et al., 1977
Dalquest, 1953	Schaldach, 1965
Fenton and Barclay, 1980	Silva Taboada, 1979
Hall and Dalquest, 1963	Villa-R., 1967
Harrison, 1975	Watkins, 1972
Hermanson and O'Shea, 1983	Watkins, 1977
Hoffmann et al., 1986	Watkins et al., 1972
Jones and Arroyo-C., 1990	Webster and Jones, 1984
Jones et al., 1972	Webster and Jones, 1985
Jones et al., 1973	Wilson et al., 1985
Kumirai and Jones, 1990	Winkelmann, 1962
Kunz, 1982b	Woloszin and Woloszin, 1982

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APPENDIX B  
THE HYPERGEOMETRIC DISTRIBUTION

Consider a source fauna of  $N$  species and a derived subset of  $n$  species ( $n < N$ ). If the  $i$ th family has  $S_i$  species in the pool, the expected number of species of this family in the subset is:

$$E(s_i) = \frac{n S_i}{N} \quad (1)$$

The probability of drawing exactly  $x$  species of the  $i$ th family in the subset is:

$$P(s_i = x) = \frac{\binom{S_i}{x} \binom{N-S_i}{n-x}}{\binom{N}{n}} \quad (2)$$

Tail probabilities can be calculated by adding the probabilities for the extreme values up to the desired value; for example, the probability of drawing  $a$  or fewer species is:

$$P(s_i \leq a) = \sum_{x=0}^a \frac{\binom{S_i}{x} \binom{N-S_i}{n-x}}{\binom{N}{n}} \quad (3)$$

I used equation (3) to calculate the exact tail probabilities reported in Chapter 5.

APPENDIX C  
THE DISTRIBUTION OF THE MEAN FOR SAMPLES  
FROM A FINITE POPULATION

If  $\bar{x}$  is the mean of a random sample of  $n$  elements from a finite population of  $N$  elements with mean  $m$  and variance  $s^2$ , the expected value and the variance of  $\bar{x}$  are:

$$E(\bar{x}) = m \quad (1)$$

$$\text{Var}(\bar{x}) = \frac{s^2}{n} \frac{N - n}{N - 1} \quad (2)$$

According to the central limit theorem the distribution of

$$z = \frac{\bar{x} - m}{\sqrt{\frac{s^2}{n} \frac{N - n}{N - 1}}} \quad (3)$$

is the standard normal distribution. I used equation (3) in Chapter 5 to calculate the probabilities for observed values in the sample community.

APPENDIX D  
FRACTAL SCALING OF SPECIES RICHNESS

Let  $l$  and  $s$  be the linear size and species richness of small cave and  $L$  and  $S$  the same variables for a larger cave ( $l < L$ ;  $s \leq S$ ). The scaling of species richness can be modeled using the fractal formula:

$$d = \frac{\log S/s}{\log L/l},$$

where  $d$  is the fractal dimension (Mandelbrot, 1983). The equation can be transformed to:

$$\log S = d \log (L/l) + \log s$$

The value of  $d$  can be estimated as the slope of the regression line in a graph of  $\log S$  against  $\log (L/l)$ .  $l$  is arbitrarily chosen as the smallest cave in the distribution.

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## BIOGRAPHICAL SKETCH

Héctor T. Arita was born October 12, 1960, in Mexico City, where he attended elementary and high school. He enrolled in the National University of Mexico (UNAM) in October, 1978, and graduated in February, 1985, with a B.S. in Biology with the thesis "Identification of dorsal guard hair of wild mammals of the Valley of Mexico." He was employed as a part-time assistant in the Laboratory of Photomicrography of UNAM and, later, as a full-time field collector of mammals for the Institute of Biology. His studies were supported in part by a special scholarship from UNAM.

In 1986, he entered the Program for Studies in Tropical Conservation of the University of Florida. His studies centered on the theoretical bases for the conservation of tropical species and communities. He was supported by scholarships from the Mexican Government and the National University of Mexico and by a fellowship from the Tropical Conservation and Development Program (TCD) of the University of Florida.

During his years in Gainesville, he was the recipient of the American Society of Mammalogists Award (awarded to outstanding student presentations), an honorary student

award for his participation in the joint meeting of the American Society of Mammalogists and the Argentine Mammal Society, the Environmental Publication Award of the National Wildlife Federation, and the Pew Scholarship.

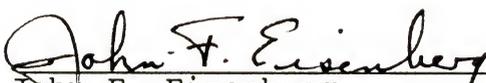
Héctor is a charter member of the Mexican Mammal Society (AMMAC) and has served as coordinator of public relations, associate editor, and vice president. Additional honorary and professional society memberships include American Society of Mammalogists, Bat Conservation International, Ecological Society of America, and Society for Conservation Biology.

After graduation he is planning to join the faculty of the Center of Ecology of UNAM, where he will be teaching and conducting research on the conservation biology of tropical communities.

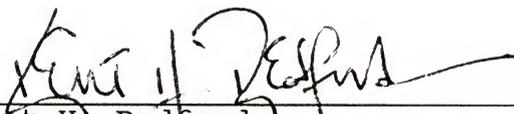
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\_\_\_\_\_  
Stephen R. Humphrey, Chairman  
Professor of Forest Resources  
and Conservation

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

  
\_\_\_\_\_  
John F. Eisenberg  
Katharine Ordway Professor  
of Ecosystem Conservation

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Kent H. Redford  
Associate Professor of Latin  
American Studies

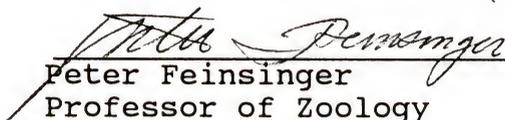
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Jonathan Reiskind  
Associate Professor of Zoology

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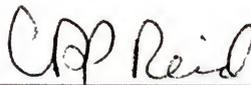


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Peter Feinsinger  
Professor of Zoology

This dissertation was submitted to the Graduate Faculty of the School of Forest Resources and Conservation in the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements of the degree of Doctor of Philosophy.

August 1992



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Director, School of Forest  
Resources and Conservation

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Dean, Graduate School