NATURAL HISTORY, INTERSPECIFIC ASSOCIATION, AND INCIDENCE OF THE CAVE BATS OF YUCATÁN, MÉXICO

HÉCTOR T. ARITA AND JORGE A. VARGAS

Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, 04510, México, D. F., México
Facultad de Ciencias, Universidad Nacional Autónoma de México, 04510, México, D. F., México

ABSTRACT—The cave bats of the state of Yucatán, México, consist of 17 species. During a one-year study that included the exploration of 36 caves, 14 species were found using caves as day roosts and another two were captured at cave entrances by netting at night. Some species, such as *Natalus stramineus,* and three species of mormoopids, were found only in the deepest, hottest, and most humid sections of caves, forming large colonies. Conversely, species such as *Peropteryx macrotis* and *Artibeus jamaicensis* were found in more exposed areas, forming small groups. There was an overall positive association among the species in terms of cave use, and several pairs showed significant association. This is a consequence of species selecting similar sites and not an indication of any interspecific ecological interaction. Most species in Yucatán are integrationist, occupying caves where species richness is high. Contrary to what has been recommended for the country of México, a local conservation strategy for the cave bats of Yucatán should concentrate on large caves that harbor several species.

RESUMEN—La fauna de murciélagos cavernícolas de Yucatán, México, consiste en 17 especies. Durante un estudio de un año de duración, se exploraron 36 cuevas de este estado y se encontraron 14 especies de murciélagos usando las cuevas como refugio diurno. Otras dos especies fueron encontradas volando cerca de las entradas de las cuevas durante la noche. Algunas especies, como *Natalus stramineus* y tres especies de mormoópidos, fueron encontrados formando grandes colonias únicamente en las secciones más profundas, calientes y húmedas de las cuevas. Por el contrario, otras especies, como *Peropteryx macrotis* y *Artibeus jamaicensis* se encontraron formando grupos pequeños o medianos en sitios más expuestos. Se encontró una asociación positiva general entre las especies de murciélagos, y la mayoría de los pares de especies presentaron también una asociación significativa en cuanto a su uso de las cuevas. Esta asociación es resultado de que la mayoría de las especies tienen requerimientos similares y no refleja una interacción ecológica interespecífica. La mayoría de las especies son integracionistas y se refugian en cuevas con una alta riqueza de especies. En contradicción con lo que se ha recomendado para la conservación de murciélagos cavernícolas de todo el país, una estrategia local de conservación deberá concentrarse en la protección de las cuevas más grandes que albergan varias especies de murciélagos.

Caves are the main roosts for many bat species (Dalquest and Walton, 1970; Kunz, 1982; Arita, 1993). In the United States, 18 bat species regularly roost in caves (Culver, 1986; McCracken, 1989), whereas in México 45% (60 out of 134) of bat species are cave dwellers, with 27 using caves as the main roost and 33 additional species using caves occasionally (Arita, 1993). There is substantial information on the ecology of many Nearctic cave bats (Kunz, 1982), but considerably less is known about the natural history of cave bats of other regions, particularly of tropical areas. Available information on cave use by Neotropical bats comes from anecdotal references in faunistic surveys (Goodwin and Greenhall, 1961; Hall and Dalquest, 1963; Villa-R., 1967; Jones et al., 1973; Handley, 1976; Silva Taboada, 1979; Willig, 1983), from a review of collecting techniques (Tuttle, 1976), from ecophysiological research (McNab, 1969, 1982), and from a few ecological and behavioral papers (Goodwin, 1970; Bateman and Vaughan, 1974; Bradbury, 1977;

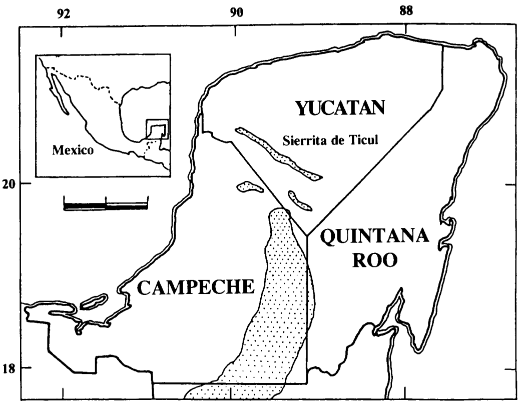

FIG. 1—The state of Yucatán. Dotted pattern indicates areas with elevation >150 m.

McCracken and Bradbury, 1981; Trajano, 1985; Fleming, 1988; Graham, 1988).

Several species of cave bats are endangered or threatened (Culver, 1986; McCracken, 1989; Arita, 1993). The design of adequate conservation strategies depends on a knowledge of the patterns of cave use, along with basic data on the natural history of the species. Unfortunately, this kind of information is scarce for Neotropical bats. For example, in the Neotropics only Bradbury (1977) and Graham (1988) have studied the patterns of interspecific association among bat species sharing roosts. Similarly, the study of Arita (1993) is the only one that has analyzed the incidence of cave bats (i.e., their tendency to occur in species-rich or species-poor sites).

Here we report the results of a study of 36 caves in the state of Yucatán, México. We present information on the natural history of the 16 species of bats that we encountered, and we analyze the patterns of interspecific association and incidence of these species. Many of the caves included in this study will be developed as tourist sites, and we expect that the information presented here will contribute to the design of a developing strategy that will take into account the conservation of bat populations.

STUDY AREA—The Yucatán peninsula is a flat, low-lying limestone shelf that projects from southern México and Central America into the Caribbean sea (Fig. 1). The state of Yucatán occupies the northwestern third of the Mexican portion of the peninsula, extending over an area of 38,402 km^2 (García and Falcón, 1986). Henceforth, we will refer to the state of Yucatán as "Yucatán," and to the physiographic region as "the Yucatán peninsula." The whole peninsula can be considered as a single block of limestone material of various ages. The landscape of Yucatán consists of 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 on underground sources for its water needs. A remarkable feature of Yucatán is the water-filled sinkholes (cenotes, from the Maya *dzonot*) and other types of collapse dolines (Finch, 1973). Caves are very numerous and diverse in morphology (Finch, 1973; Reddell, 1977; Arita, 1992). In 1989 we visited several caves in the *Sierrita de Ticul,* the lesser mountain range that marks the southern border of the state (Fig. 1). During 1990, we made systematic visits to 30 caves in the *Sierrita* and to six additional caves in central Yucatán (Arita, 1992).

Except for the northwestern extreme, where the climate is hot and dry, most of Yucatán is hot, subhumid with summer rains (Aw_o in Koppen's classification modified by García, 1981). Mean annual temperature in Tekax, where most field work was done, is 26.7°C. There is a clearly marked cycle of dry (November to April) and rainy (May to October) seasons. Mean annual precipitation at Tekax is 1,100.2 mm (García, 1981). The original vegetation of the state was tropical deciduous and semideciduous forest (Rzedowski, 1978), but a substantial part of the surface has been modified to accommodate human activities (Green et al., 1987). Present-day vegetation in most parts forms a checkered pattern of stands of secondary deciduous forest at different stages 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*).

MATERIALS AND METHODS—We scheduled at least two visits to each of the 36 caves included in this study, one during the dry season and one during the rainy season. Simple caves with small and easily located bat colonies were visited only twice, whereas complex caves with many bat colonies were surveyed as many as eight times during the study. We mapped the caves using standard cave survey procedures (Ellis, 1976), but we fixed the distance between survey stations at 10 m. At each station, we noted the time and measured the ambient temperature and relative humidity using a portable psychrometer. We systematically searched for groups of bats and, using a hand net, captured individuals to identify the species. Additionally, to verify the identifications, we set mist-nets near entrances and bat colonies to capture flying individuals. Previous experience and a reference collection made in advance (deposited in the Instituto de Biología, Universidad

Nacional Autónoma de México) allowed us to identify all species in the field.

We estimated the population size of the different species in the caves. When the number of bats in a group was small (<30) we were usually able to count all individuals. For bats forming larger colonies, we estimated by direct measurement the density of individuals/m^2 and the total area covered by bats using the maps from the cave surveys. We calculated the total population size by multiplying these two values. For species that occupied wide sections of a cave but formed discrete groups, we estimated by direct count the number of individuals in each group and the number of such groups that were visible. We did not attempt a calculation of absolute population sizes using mist-netting data; rather, we used this information to corroborate identifications of species and to estimate relative abundance.

We analyzed the association between the species using presence-absence data to calculate the pair-wise association index V: $V = (ad - bc)/[(a + b)(c + d) \cdot (a + c)(b + d)]^{1/2}$, 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 for this index go from -1 (complete segregation) to 0.0 (no association) to 1 (perfect positive association). We tested the statistical significance of the associations using Fisher's exact test for two-by-two contingency tables. To visualize the relationships among all species in terms of their association, we conducted a cluster analysis using an average-linkage algorithm (Pielou, 1984), using the values of V as a measure of distance between the species.

We used the variance-ratio test (Schluter, 1984) to analyze the overall association among the 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, 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

$$Vt = s_T^2 \Big/ \sum^n s_i^2,$$

where n is the total number of species, as an index of species association. Under the null hypothesis of no association, $Vt = 1.0$. Values of $Vt > 1$ indicate an overall positive association, whereas values of $Vt < 1$ suggest a negative association. The parameter $W = N \cdot Vt$ follows a χ^2 distribution with N degrees of freedom, allowing the null hypothesis of no association to be tested.

To estimate the incidence of species in the caves of Yucatán (Arita, 1993), we wrote a BASIC program to analyze the distribution of 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 the 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. Observed values for this median larger than the expected value of 2.0 would indicate a tendency of the species to occur in caves with high species richness (i.e., to be integrationist; Arita, 1993). Conversely, an observed value lower than expected would indicate a tendency to occur in species-poor caves (i.e., to be segregationist; Arita, 1993).

RESULTS—We found 14 species, belonging to five families, using the caves surveyed as day roosts (Appendix I). Another two species were captured by netting at the entrances of the caves.

We found the lesser sac-winged bat (*Peropteryx macrotis*) in 28 of the surveyed caves, always at a distance <20 m from the entrance ($\bar{X} = 11.3$ m, $n = 28$). This bat has always been reported in groups of <12 individuals (Goodwin and Greenhall, 1961; Hall and Dalquest, 1963; Willig, 1983). In our caves, average group size was 18.6 individuals ($n = 31$; n is >28 because in some caves there was more than one group), but varied from a single individual to >80. In most cases, sex ratio was close to 1:1, but in July and August the composition of the groups changed and juveniles were mixed in the groups. For example, on 23 July, the groups 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] = 0.02, binomial test). Typically, groups of *P. macrotis* were located on vertical or very inclined walls. Ambient temperature in rooms occupied by this bat varied from 24.4 to 28.8°C. At all sites but one relative humidity was <93%, and at one site it was as low as 67% (Fig. 2).

We found the ghost bat (*Mormoops megalophylla*) in six caves. As with other mormoopids, the ghost bat tends to occupy the deepest sections of caves where temperature and humidity are high (Bateman and Vaughan, 1974). In Murciélagos Cave, near Ticum, the ghost bat formed a

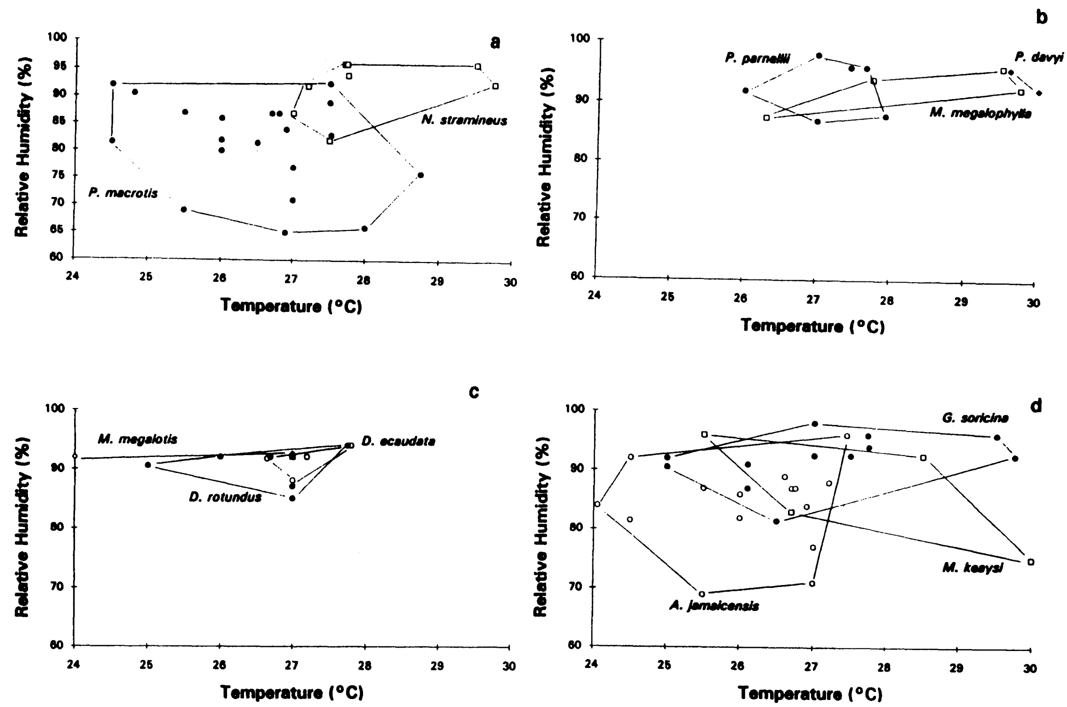

FIG. 2—Temperature and relative humidity of Yucatán caves, by species. Each point represents a single cave and may be an average for several observations.

mixed group with *Natalus stramineus* on the walls and speleothemes (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. Total population size in the cave was >5,000 individuals. In Hoctún Cave, a group of about 50 individuals roosted on an inclined ceiling near a water pool approximately 70 m from the entrance. At least five other species roosted in this cave, but the *M. megalophylla* were always segregated. We documented no sex segregation in *M. megalophylla,* but the sex ratio was significantly skewed. On 17 April we netted 81 ghost bats at Murciélagos Cave; 52 were pregnant females, seven were non pregnant females, and 22 were adult males (P[sex ratio = 1:1] < 0.001, binomial test).

We found the naked-backed bat (*Pteronotus davyi*) in only three of the caves. We captured most individuals with mist-nets and were unable to locate the exact position of the main roosting groups, despite careful searches. In was clear, however, that these bats occupied higher areas of the deepest chambers of the caves, where ambient temperature was >29°C, and relative humidity >90%. Netting trends in Murciélagos Cave indicate the presence of a colony of at least 5,000 individuals.

The mustached bat (*Pteronotus parnellii*) was found in the hot and humid sections of seven of the caves surveyed. In Murciélagos Cave, several groups of moderate size (30 to 50 individuals) roosted in the solution holes located in a chamber where temperature was 26.1°C and relative humidity was 92%. In this cave, mustached bats roosted as close to the entrance as 40 m, whereas in Chocantes Cave they were found at 210 m from the entrance. Herd (1983) reported that *P. parnellii* does not use night roosts. In several nights in Actún Lol-Tún, however, we observed many (>100 individuals) mustached bats flying and roosting in a chamber known as *Salón del Infante,* which during the day harbored no bats.

We located groups of the little big-eared bat (*Micronycteris megalotis*) in two caves. In both cases, the bats formed small colonies (eight and ten individuals) close to the entrance (25 and 35 m) of well-illuminated caves. In Roble Cave, ambient temperature was 24.1°C and relative humidity was 92%. We observed the typical accumulations of bat guano and insect parts that this species forms in other caves, but were unable to find the bats.

The spear-nosed bat (*Mimon bennettii*) was considered a common cave species in Yucatán by Jones et al. (1973). We observed this bat only in Actún Lol-Tún, where we netted one adult female inside the cave, near the main entrance. A specimen of this species, a subadult male that was netted on August 1982 in the open doline at the entrance of Actún Lol-Tún, is deposited in the mammal collection at Instituto de Biología.

The woolly false vampire bat (*Chrotopterus auritus*) was known from Yucatán on the basis of only six specimens from three localities, and it had not been observed there since the early 1960s (Jones et al., 1973). It had also been reported as a fossil and subfossil (Hatt et al., 1953; Arroyo-Cabrales and Alvarez, 1990). On 19 August we 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%. We 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 (*P. macrotis*), and rests of a funnel-eared bat (*Natalus stramineus*). The woolly false vampire feeds mainly on birds and rodents, and there was only one previous record of this species feeding on other bats (Medellín, 1989). Apparently the *C. auritus* used this cave as an alternate refuge. We never saw the bats in any of the four previous visits to the cave, and beneath the group there was no accumulation of guano or prey parts as those described for colonies of this bat (Medellín, 1988). This record confirms the presence of *C. auritus* in the state, and shows that it occurs in the drier areas of central Yucatán, not only in the wet zones where it had been captured before (Jones et al., 1973).

We found Palla's long-tongued bat (*Glossophaga soricina*) in 14 caves, always roosting in small groups (<20 individuals). However, in some caves the combined total population numbered >1,000. Under some circumstances, females segregate to rear the young. On 3 October 1989, all 13 bats of this species netted at the entrance of Actún Lol-Tún were females (P[sex ratio 1:1] = 0.0001, binomial test); two were pregnant, one was carrying a newborn, and five were lactating. Close interspecific associations have been reported between *G. soricina* and *Artibeus jamaicensis*, *Macrotus waterhousii*, and *Carollia perspicillata* (Goodwin, 1970; Graham, 1988). In Yucatán, we found all groups of *G. soricina* segregated from other species during the day. However, just before leaving the roost after sunset, bats of this species were seen in Murciélagos Cave forming large swarming groups intermixed with individuals of *Natalus stramineus*.

The short-tailed bat (*Carollia perspicillata*) is very rare in Yucatán (Jones et al., 1973). We captured two individuals that represent the second and third records of the species for the state. In Murciélagos Cave, one subadult male was netted in the morning close to the colony of *M. megalophylla* described above. A female was netted at 2015 h at the main entrance of Actún Lol-Tún.

The fruit bat (*Artibeus jamaicensis*) was found in 22 caves, under varied situations. We located colonies in small tunnels (Acanceh Cave) and in large cave systems (Actún Lol-Tún, Actún Spukil). Individuals were more frequently observed near entrances (Cave of the Ruins of Mayapán, <20 m from entrance), but in some cases they were roosting as far as 110 m from the entrance (Actún Sabak-ha). Temperatures in areas occupied by this bat ranged from 24.1 to 27.4°C, and relative humidity varied from 69 to 96%. In most sites, *A. jamaicensis* formed small groups (three to 35 individuals) in solution holes on the ceiling of chambers. Small caves were typically occupied by only one group, but total population in larger caves, such as Murciélagos Cave, was estimated at >500.

The only cave record of the dwarf fruit-eating bat (*Dermanura phaeotis*) is that of Villa-R. (1967), who netted one individual at the entrance of a small cave in Tabasco, México. We captured two individuals at night in the open doline of Actún Lol-Tún, but we have no evidence that they were using the cave as a day roost.

The only records of the yellow-shouldered bat (*Sturnira lilium*) using caves are those of Villa-R. (1967), who visually identified one individual in a cave in Puebla, México, and netted another individual at night at the entrance of a cave in Tabasco, México. We netted two females of this species in the open doline of Actún Lol-Tún at night, but it is unlikely that *S. lilium* uses the cave as a day roost.

Although local people consider the vampire bat

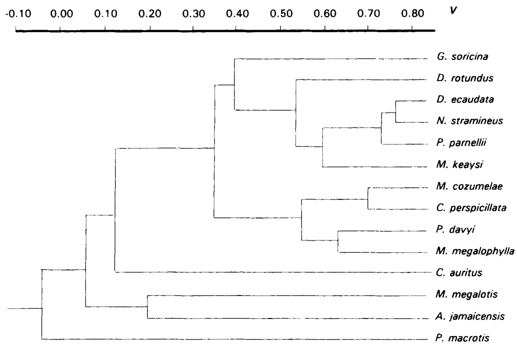

FIG. 3—Cluster analysis of the cave bats of Yucatán based on presence-absence data for 36 caves. Scale indicates distance as measured by the association index *V*.

(*Desmodus rotundus*) a major plague, we found *D. rotundus* in only nine caves and in only one instance—in Actún Sabak-ha—did they form a colony of >1,000 individuals. We found *D. rotundus* more frequently in deep chambers, typically close to a constriction of the cave. This observation contrasts with previous reports (Goodwin and Greenhall, 1961; Villa-R., 1967) of the common vampire roosting in exposed sections of caves, close to the entrances.

We found the hairy-legged vampire bat (*Diphylla 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 pats of its range, this species is uncommon in Yucatán. In Hoctún Cave these vampires formed a small colony of 25 to 35 individuals roosting close to each other but not in direct contact; on 16 August, we captured several pregnant females, and one was delivering a newborn. In Tzab-Nah Cave, these bats formed small groups of 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; the other contained four adult males, three of them with testicles in scrotal position. Temperature at sites occupied by *C. ecaudata* were always >26.5°C and relative humidities were always >87%.

The funnel-eared bat (*Natalus stramineus*) was observed only in deep (>50 m from entrance) chambers where temperature and relative humidity were very high (temperature >27°C, relative humidity >80%). Typically, *N. stramineus* formed medium-sized or large groups (100 to >10,000 individuals), but in Ramonal Cave we found only six individuals. In all cases, bats were close together (20 to 50 cm from each other) but not in direct contact.

We found the black myotis (*Myotis keaysi*) roosting in two contrasting situations. In Hoctún Cave, bats formed large clusters of >1,000 individuals, such as the one described by Villa-R. (1967), on the ceiling of the deepest (>100 m from the entrance) section of the cave, just above a pool. In other caves, the black myotis roosted in small groups of three to five individuals in very small (<20 cm deep) holes and crevices in the walls and ceilings of sections of caves that were close to the entrance. In Hoctún Cave, sex ratio was strongly skewed (1:23.5 males : females, n = 96). Ambient temperature fluctuated at this site from 27.5 to 29.5°C, and relative humidity from 89 to 96%. In contrast, one hole with *M. keaysi* at Actún Sabak-ha was located in an open doline where temperature and relative humidity were 30.1°C and 75%.

Only three of the 17 species of cave bats of Yucatán were not encountered during this study: the fishing bat (*Noctilio leporinus*), the big fruit-eating bat (*Artibeus lituratus*), and the free-tailed bat (*Nyctinomops laticaudatus*). 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* (*R. aeneus,* according to Audet et al., 1993), and *Eumops bonariensis* (Jones et al., 1973; Birney et al., 1974; Bowles et al., 1990).

Positive values of the index *V* predominated in the analysis of pair-wise associations. 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 *P. macrotis–G. soricina* pair—yielded a negative *V* value. The cluster analysis failed to produce clear groupings (Fig. 3). At the level of $V = 0.35$ (the approximate limit for values that have $P < 0.05$ in a Fisher's exact test), ten species form a loose group, whereas four others (*P. macrotis, A. jamaicensis, M. megalotis,* and *C. auritus*) were not grouped. There was significant overall positive association among the species ($Vt = 4.09$, $W = 147.27$, $P < 0.001$, χ^2 test, $d.f. = 36$).

DISCUSSION—The positive association that we observed among species does not imply the existence of a particular interspecific interaction. In the case of the cave bats of Yucatán, it seems clear that the significant V and Vt values are more a consequence of the similarity of ambient requirements for several species than the result of any interaction. For example, several species (*N. stramineus,* the mormoopids) tend to occur together in caves that offer high temperatures and relative humidities, thus contributing to the overall positive association. We agree with the suggestion of Bradbury (1977) and Graham (1988) that most cases of interspecific association in roosting bats are simply the result of similar requirements and should not be interpreted as cases of active interaction. The V index differs from other association indexes, such as Jaccard's and Dice's, in that it includes the sites in which neither of the species occurs (d in formula). We chose to use this index because our interest was to describe the patterns of cave use, not to detect ecological interactions. The use of an index that does not include the d value would have obscured the fact that most caves surveyed harbor very few species (Appendix I).

The four species that were not grouped by the cluster analysis are generalists in their use of caves and can be found in exposed situations and in small caves. Conversely, the 10 species that form the loose group in Fig. 3 tend to occupy medium-sized to large caves with secluded rooms that provide low ventilation and high temperature and relative humidity. These "hot caves" (Silva Taboada, 1977, 1979) are of prime importance to several species of Neotropical bats. For example, several species of *Natalus, Phyllonycteris,* and *Pteronotus* roost only in this kind of refuge (Silva Taboada, 1979).

Cave bats can be classified in three categories of incidence (Arita, 1993). Integrationist species tend to inhabit caves with high species richness, segregationist bats normally share their roosts with few species, and indifferent species occur in both species-rich and species-poor caves. Most species in this study tended to be integrationist (Table 1). 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. In general, these results coincide with the classification of incidence functions for Mexican cave bats presented by Arita (1993). *Peropteryx macrotis,* however, was considered an integrationist species by Arita (1993) but in Yucatán it is an indifferent species, occurring both in species-poor and species-rich caves. It was found roosting alone in small caves and also in large

TABLE 1—Species richness of the caves of Yucatán, by species. For example, the median of species richness for the 28 caves in which *P. macrotis* was found is 2.0. Probabilities are for deviations from a null model based on the distribution of species among caves. Expected median is 2.0. Asterisks = $P < 0.05$.

Species	n[1]	Species richness	
		Median[2]	P[3]
Peropteryx macrotis	28	2.0	1.000
Pteronotus davyi	4	9.0	0.000*
Pteronotus parnellii	8	8.0	0.000*
Mormoops megalophylla	6	8.5	0.001*
Micronycteris megalotis	2	3.5	0.368
Mimon bennettii	1	12.0	0.028*
Chrotopterus auritus	1	9.0	0.077
Glossophaga soricina	14	4.5	0.000*
Carollia perspicillata	2	9.5	0.003*
Artibeus jamaicensis	22	3.0	0.052
Desmodus rotundus	9	5.0	0.006*
Diphylla ecaudata	6	8.5	0.000*
Natalus stramineus	9	8.0	0.001*
Myotis keaysi	7	8.0	0.006*

[1] Number of caves in which the species was found.

[2] Median of the number of species of bat in the caves in which the particular species was found.

[3] Probability based on the distribution of 1,000 random combinations of N caves from the pool of 36.

systems with several other species. Two species that were considered indifferent (*C. perspicillata* and *D. rotundus*) were found in Yucatán only in caves with high species richness. *Mimon bennettii* was considered segregationist by Arita (1993), but in Yucatán it was found only in Actún Lol-Tún, along with 11 other species.

A conservation strategy for the cave bats of Yucatán should concentrate on the larger systems that harbor several species. Arita (1993) suggested that for the entire country of México, the protection of caves with high species richness would not be very beneficial for the rare and endangered species, because these tend to be segregationist, occurring only in caves with low species richness. This study shows that in the particular case of Yucatán, the circumstances are quite different. Because of the overall positive association and because of the related fact that most species are integrationist, protection of caves with high species richness would contribute to the conservation of the majority of the species. For example, Actún Lol-Tún supports populations of 12 of the 14 species, including *M. bennettii,* a species that normally uses roosts with low species richness. Similarly, the rare woolly false vampire (*C. auritus*) was found in a cave with eight other species. Of course, the conservation of these species would require a more detailed study on the viability of the populations.

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Appendix I

Caves included in this study. All sites are in the state of Yucatán, México. Species of bats are as follows: *Peropteryx macrotis* (Pm), *Pteronotus davyi* (Pd), *Pteronotus parnellii* (Pp), *Mormoops megalophylla* (Mom), *Micronycteris megalotis* (Mim), *Mimon bennettii* (Mc), *Chrotopterus auritus* (Ca), *Glossophaga soricina* (Gs), *Carollia perspicillata* (Cp), *Artibeus jamaicensis* (Aj), *Desmodus rotundus* (Dr), *Diphylla ecaudata* (De), *Natalus stramineus* (Ns), *Myotis keaysi* (Mk).

Municipality of Tekax: Roble Cave, 2.5 km W Tekax, 90 m, Pm, Mim, Gs, Aj; Actún Sabak-ha, 4 km S Tekax, 55 m, Pm, Pp, Gs, Aj, Dr, De, Ns, Mk; Actún Chunkunab, 1.5 km SW Ticum, 50 m, Pm, Aj; Actún Maas, 1.5 km SW Ticum, 50 m, Pm, Aj; Murciélagos Cave, 0.5 km SW Ticum, 70 m, Pd, Pp, Mom, Gs, Cp, Aj, Ns; Ramonal Cave, 0.5 km NE Cepeda Peraza, 50 m, Gs, Dr, De, Ns; Flor de Mayo Cave, 2.5 km SSW Tekax, 35 m, Pm, Aj, Dr, Ns; Actún Kab, 2.5 km SSW Tekax, 35 m, Pm; Actún Kan-Lol, 2.5 km SSW Tekax, 35 m, Pm; Porcupine Cave, 2.5 km SSW Tekax, 35 m, Pm, Aj; Chocantes Cave, 0.5 km SW Tekax, 85 m, Pp, Dr; Actún Oxpehol, 0.5 km N Canek, 40 m, Pm, Aj, Dr; Actún X-Maasit, 0.3 km N Canek, 40 m, Pm; Actún Dzonot, 0.5 km S Canek, 30 m, Pm; Iguana Cave, 2.4 km W Tekax, 90 m, Pm, Aj; Doña Blanca Cave, 2 km W Tekax, 55 m, Pm, Aj; Cinco de Mayo Cave, 2.5 km W Tekax, 60 m, Pm, Gs, Aj, Dr, Mk; Cave "A," 2.5 km W Tekax, 60 m, Pm; Ramonal y Naranja Cave, 2.3 km W Tekax, 60 m, Pm, Gs, Aj; Bejucos Cave, 2 km W Tekax, 60 m, Mim, Gs, Aj; Actún Tolok, 2 km W Tekax, 40 m, Pm, Aj; Guayaba y Aguacate Cave, 2 km SW Tekax, 40 m, Pm, Aj; Cave "B," 1 km SE Tekax, 70 m, Pm, Gs, Aj; Actún Chac-Xix, 1 km S Tekax, 75 m, Pm; Zorro Cave, 1 km S Tekax, 60 m, Pm; Aguacate Cave, 1.5 km E Tekax, 65 m, Pm. Municipality of Santa Elena: Cave of the Ruins of Kabah, 60 m, Pm. Municipality of Maní: Kabahchén Cave, 200 m SW Plaza of Maní, 20 m, Gs, Aj. Municipality of Oxkutzcab: Actún Sitz, 1 km SW Oxkutzcab, 60 m, Mom, Gs; Actún On, 1.5 km Oxkutzcab, 50 m, Pm; Actún Lol-Tún, 7 km SW Oxkutzcab, 90 m, Pm, Pd, Pp, Mom, Mc, Gs, Cp, Aj, Dr, De, Ns, Mk. Municipality of Opichén: Actún Spukil, 2 km S Calcehtok, 80 m, Pm, Pd, Pp, Gs, Aj, Dr, De, Ns, Mk. Municipality of Tecoh: Cave of the Ruins of Mayapán, 2 km S Telchaquillo, 20 m, Pm, Pp, Aj, Ns; Tzab-Nah Cave, 1 km S Tecoh, 20 m, Pm, Pp, Mom, Ca, Gs, Aj, De, Ns, Mk. Municipality of Acanceh: Acanceh Cave, 600 m SE Acanceh, 15 m, Aj, Mk. Municipality of Hoctún: Hoctún Cave, 1 km S Hoctún, 10 m, Pd, Pp, Mom, Gs, Dr, De, Ns, Mk.