ELSEVIER

0006-3207(95)00105-0

Biological Conservation 76 (1996) 177-185

0006-3207/96 $15.00+.00

THE CONSERVATION OF CAVE-ROOSTING BATS IN YUCATAN, MEXICO

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(Received 16 August 1994; accepted 20 June 1995)

Abstract

Seventeen species of bats roost in the caves of Yucatan, Mexico. To identify those caves that would be important in a conservation plan for bats, 36 Yucatan caves were surveyed during a one-year study. Three criteria were considered for the identification of critical sites: a high species richness, an unusually large multispecies population size, and the presence of species of special concern (rare, threatened, or endangered). Most sites were small caves that supported only few (less than five) species, whereas a few caves supported very rich assemblages of more than nine species. The distribution of bat species among caves was highly nested, with smaller assemblages being subsets of larger communities. This distribution produced a pattern in which rare species tend to be present only in those caves with the highest species richness, whereas common species are present in all kinds of caves. A classification of the caves based on the presence or absence of bat species produced six groups. One of such groups included the largest caves, which also harboured the most diverse assemblages, contained the largest populations, and supported several species of concern. Many of these large caves are targetted for development as tourist sites, so a conservation strategy for these sites should take into consideration the social and economic pressures associated with such plans. Copyright © 1996 Elsevier Science Limited.

Keywords: bats, caves, ecotourism, Mexico, nested subsets.

INTRODUCTION

The protection of roosting sites is an essential component of any strategy for the conservation of bats. Because caves are the main roosts for several bat species (Dalquest & Walton, 1970; Kunz, 1982), the preservation of these sites should be of foremost interest for the conservation of chiropteran species. Although many bat species use caves only as alternate refuge, some species rely completely on caves for day roosting. In Mexico, for example, 45% (60 of 134) of bat species are cave dwellers, with 27 using caves as the main roost and 33 additional species using caves occasionally (Arita, 1993b). Obviously, any plan aimed at the conservation of these bats should include the protection of caves.

Several species of cave-dwelling bats are considered endangered or threatened (Culver, 1986). 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 & Bain, 1990). In Mexico, 19 species of cave bats are considered fragile or vulnerable (Arita, 1993*b*). 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 a similar fashion, the presence of bats might be a necessary condition for the subsistence of some cave environments. In passages with no bats, biomass density in a typical North American cave can be as low as 1 g/ha in ponds or 20–30 g/ha in terrestrial areas (Poulson & White, 1969). In contrast, passages covered with bat guano present an overabundance of nutrients and support very diverse communities of arthropods (Barr, 1968; Harris, 1970; Poulson, 1972). Because endogenous primary production by chemosynthetic bacteria is negligible, 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 faeces of trogloxenes, such as cave crickets, birds, bats, and other animals (Harris, 1970; Poulson, 1972; Culver, 1982). In many tropical caves, bat guano is by far the most important source of nutrients. By transporting tons of organic matter to the caves, bats act as mobile links connecting cave environments with the outside world.

Caves are distinctive features of the state of Yucatan, Mexico. The karst landscape of the Yucatan Peninsula is punctuated by numerous caverns and *cenotes* (water-

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filled sinkholes) that are not only a peculiar trait of the area, but also an important link in the cycle of water. Most caves in the state are important archaeological sites that feature splendid pieces of ancient cultures. In a mostly dry environment, caves and their associated dolines are real oases that harbour communities of plants and animals found in no other place.

Yucatan is an ideal setting for a study on cave conservation. The geological and climatic characteristics of the peninsula favour the development of numerous caves. Some of the caves of Yucatan, with their combination of geological, biological, and archaeological attractions, are obvious choices in the new plans by the state government for the development of ecotourism. These caves will constitute a test for the idea that economic development and biological conservation are compatible.

This paper presents data on the patterns of cave use by the bats of Yucatan. In particular, I was interested in identifying those caves that would be of prime importance for the subsistence of bat populations in the area. I considered three criteria for this identification: caves with high diversity of bats; caves with unusually large bat populations; and caves that harbour species of concern.

STUDY AREA

The state of Yucatan occupies the northwestern third of the Mexican portion of the peninsula of the same name. The 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 the state of Yucatan, from sea level to about 20 m. This pattern is broken by the Sierrita de Ticul, a lesser mountain range that consists of a shallow valley surrounded by two narrow ridges reaching a maximum altitude of 200 m (Reddell, 1977). Most caves included in this study are located in this mountain range.

Climate in the Sierrita is hot, subhumid, with summer rains. Mean annual temperature for Tekax, a city located on the north face of the Sierrita, is 26·7°C, and the difference between the minimum and maximum mean monthly temperatures is 6·3°C (23·1°C in December to 9·4°C in May). Rainfall is very seasonal, with the dry season extending from November to April and the rainy season from May to October. Mean annual precipitation at Tekax is 1100·2 mm, with 80·3% falling in the rainy season (García, 1981). The original vegetation of the area, tropical deciduous and semideciduous forest, has been modified in most parts to accommodate human activities (Green *et al.*, 1987). In the study area, vegetation consists of stands of secondary deciduous forest at different stages of succession, with dominance of Leguminosae (*Acacia* spp., *Caesalpinia gaumeri, Enterolobium cyclocarpum, Lysiloma latisiliqua* and *Mimosa bahamensis*) and other species of trees and shrubs (*Bursera simaruba, Ficus* spp., *Vitex gaumeri*).

METHODS

Field work was conducted from July 1989 to August 1990. During 1989, caves included in this project were located and selected, basing the search on previous reports (Reddell, 1977, 1981) on tourist maps and on information from local guides. Caves were surveyed, noting such variables as location, size, number of entrances, ambient temperature, and humidity. Voucher specimens of bats were collected for a reference collection that is deposited in the Institute of Biology of the National University of Mexico (UNAM).

Cave recording

Beginning in January 1990, caves included in this study were systematically surveyed. Each cave was visited at least twice (once during the dry season, once during the rainy season). Smaller caves were visited only twice, but larger sites were surveyed as many as eight times during the study. The 36 sites included in the study constitute a diverse sample of caves, from short tunnels of <10 m to a large system of >1·5 km (Table 1).

Caves were mapped using standard survey procedures (Ellis, 1976), but fixing the distance between surveying stations at 10 m. At each station, measurements were taken of the width of the passage at right angles to the survey line, the height of the passage, the bearing to the next station, and the ambient temperature and relative humidity. Topographic measurements of distance and angles from the mapping procedure provided data to calculate several morphometric variables for the caves. L' is the total horizontal length of all passages in the cave, L_k is the maximum horizontal extent between two points in the cave, H_k is the amplitude of the cave, the maximum vertical distance between two points in the cave, C_v (= H_k/L_k) is the coefficient of verticality, ID (= L'/L_k), is the index of development, a measurement of complexity of passages.

Bat recording

Colonies of bats were located by systematic searches, catching individuals using a hand-held net. Additional information was gathered by capturing flying individuals using mist nets set in strategic locations in the caves. The reference collection made in advance allowed the identification of all species in the field.

Population sizes were estimated for each species. When the number of bats in a group was small (<30, for *Peropteryx macrotis, Micronycteris megalotis, Diphylla ecaudata*, and *Myotis keaysi*) all individuals were usually counted. For bats forming larger colonies (e.g. *Mormoops megalophylla* and *Natalus stramineus*), the density of individuals per m^2 was estimated by direct count and the total area covered by bats was determined using data from the cave surveys. Total population size was calculated by multiplying these values. For species that occupied wide sections of a cave but

Table 1. Morphometric and biological data for 36 Yucatan caves

The key corresponds to the one used in Fig. 2, calculation of morphometric data (L_k, maximum horizontal extent; L', total extent of passages; H_k, amplitude; *ID*, index of development; C_v, coefficient of verticality) is explained in the text. *A*, the total inter-species abundance of bats is the logarithmic value detailed in the text. Groups correspond to the results of the association analysis using the distribution of bat species among caves.

Key	Cave	Entrances	Chambers	L_k (m)	L' (m)	H_k (m)	*ID* (m)	C_v	Bat species	*A* (Total bat abundance)	Group
A	Ruins of Kabah	1	1	6·9	7·1	1·0	1·03	0·14	1	3·00	I
B	Zorro Cave	1	1	7·1	8·6	1·5	1·21	0·21	1	2·00	I
C	Cave "A"	1	1	9·9	9·9	3·04	1·00	0·31	1	2·00	I
D	Actun Chac-Xix	1	1	16·2	28·5	29·3	1·76	1·81	1	2·00	I
E	Aguacate Cave	1	1	18·6	20·6	2·5	1·11	0·13	1	2·00	I
F	Actun Kan-Lol	multiple	1	—	—	—	—	—	1	3·00	I
G	Actun Dzonot	1	1	34·3	36·5	19·8	1·06	0·58	1	2·00	I
H	Actun Kab	1	1	37·4	42·3	22·1	1·13	0·59	1	3·00	I
I	Actun X-Maasit	1	1	40·0	44·1	9·4	1·1	0·24	1	2·00	I
J	Actun On	1	1	10·0	10·0	1·2	1·00	0·12	2	3·00	I
K	Porcupine Cave	1	1	13·0	15·0	3·5	1·15	0·27	2	3·30	I
L	Doña Blanca Cave	1	2	14·8	15·0	1·5	1·01	0·10	2	3·04	I
M	Actun Tolok	1	1	16·9	17·1	6·1	1·01	0·36	2	2·30	I
N	Guayaba y Aguacate	1	1	21·1	22·5	6·8	1·07	0·32	2	3·04	I
O	Acanceh Cave	1	1	26·2	39·4	6·2	1·50	0·24	2	4·00	I
P	Iguana Cave	1	2	27·5	47·5	15·2	1·73	0·55	2	2·30	I
Q	Actun Chunkunab	1	1	33·1	33·5	24·7	1·01	0·75	2	2·30	I
R	Actun Maas	1	1	47·7	51·0	34·4	1·07	0·71	2	2·30	I
S	Kabahchen Cave	3	4	59·9	158·7	6·9	2·65	0·12	2	2·30	II
T	Actun Sitz	1	2	94·1	114·6	27·5	1·22	0·29	2	2·04	III
U	Chocantes Cave	1	>6	183·4	261·6	49·9	1·43	0·27	2	4·04	IV
V	Cave "B"	1	1	26·3	28·6	4·9	1·09	0·19	2	2·48	II
W	Bejucos Cave	1	1	32·9	41·2	10·8	1·25	0·33	3	2·48	II
X	Actun Oxpehol	2	3	55·5	97·5	12·1	1·76	0·22	3	3·48	I
Y	Ramonal y Naranja	2	3	120·6	155·7	11·9	1·29	0·10	3	3·32	II
Z	Roble Cave	1	2	30·2	62·4	18·8	2·07	0·58	4	3·11	II
AA	Flor de Mayo Cave	2	2	74·0	79·6	9·3	1·08	0·13	4	3.34	V
BB	Ramonal Cave	1	3	83·3	103·2	6·0	1·24	0·07	4	4·01	VI
CC	Ruins of Mayapan	1	3	108·3	164·0	31·3	1·51	0·29	4	4·30	V
DD	Cinco de Mayo Cave	1	2	55·9	76·7	2·5	1·37	0·04	5	3·15	II
EE	Bat Cave	1	3	100·8	160·2	20·0	1·58	0·20	7	6·36	V
FF	Hoctun Cave	1	1	136·5	147·9	21·7	1·08	0·16	8	5·09	VI
GG	Actun Sabak-ha	2	4	240·3	410·0	30·0	1·71	0·12	8	5·37	VI
HH	Tzab-Nah Cave	2	4	157·7	372·5	21·3	2·36	0·13	9	4·52	VI
II	Actun Spukil	2	>10	—	—	—	—	—	9	4·81	VI
JJ	Actun Lol-Tun	5	>10	500	1560	45	3·12	0·09	12	4·80	VI

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, the rate of captures in mist nets was used as an indirect estimator of relative abundance. Because all these methods provide only approximate values of abundance, a logarithmic scale of abundance was used to make comparisons: 0 (1 individual), 1 (2–10), 2 (11–100), 3 (101–1000), 4 (1001–10,000), 5 (>10,000).

To estimate the combined abundance of bats in each cave, variable *A* was calculated as:

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

where a_i is the abundance of species *i* in the logarithmic scale described above, and *S* is 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.

Analyses

A classification of Yucatan caves on the basis of use by bats was produced by conducting an association analysis. For each pair of species, a two-by-two contingency table of presence–absence was used to feed a BASIC program 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 $\chi^2 = (O-E)^2/E$ (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 & Reynolds, 1988). The degree of nestedness in the distribution of bats among caves was estimated using the algorithms proposed by Patterson and Atmar (1986) and Wright and Reeves (1992).

RESULTS

The caves

Caves in Yucatan are comparatively small (Table 1). Twenty-three (64%) of the caves in the sample had L' <100 m, and only one (Actun Lol-Tun) had an extent >1000 m. As is the case in other karst areas (White, 1988), the frequency of cave dimensions in the sample follows a log-normal distribution. Most caves had simple development as indicated by the low values of the index of development. The mean value for this parametre (1·40, s^2 = 0·25) is close to the average reported for karst regions in Europe (1·35 for France, 1·33 for Crimea, Dublyansky *et al.*, 1987). Observed values for Yucatan varied from 1·00 or 1·01 for simple tunnels to 3·12 for the complex system of tunnels of Lol-Tun. The amplitude of the caves was in all cases <50 m. All caves but one (Actun Chac-Xix) had a coefficient of verticality between 0·1 and 1·0 (mean = 0·32, s^2 = 0·11), indicating that in general the Yucatan caves are more developed horizontally than vertically. Both total extent and depth of explorable sections of Yucatan caves are limited by the closeness of the water table to the surface. It is possible that some of the many flooded caves in Yucatan extend underwater for several kilometres. This speculation, however, is hardly relevant for bats.

As predicted by models of thermal equilibrium (Tuttle & Stevenson, 1976; Culver, 1982), the average ambient temperature at the deepest part of the caves (26·9°C, s^2 = 2·4, n = 30 caves) was very close to the mean annual surface temperature (MAST) in the area (26·7°C for Tekax). Ambient conditions in the deepest sections 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.

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 (as low as 24·0°C). In contrast, tunnels with a positive slope normally showed mean temperatures higher than the MAST (as high as 30·0°C). Caves with narrow entrances or with constrictions tended to have temperatures close to the MAST.

In most caves with an extent >30 m the relative humidity in the deepest section was always >85%. Exceptions were caves with wide openings or with more than one entrance,

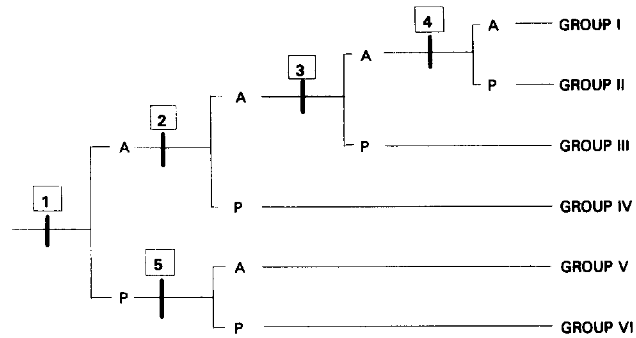

Fig. 1. Association analysis of the caves of Yucatan based on the relationship among bats. A, divisor species is absent; P, divisor species is present. Divisor species are: 1, *Natalus stramineus*; 2, *Pteronotus parnellii*; 3, *Mormoops megalophylla*; 4, *Glossophaga soricina*; 5, *Diphylla ecaudata*.

in which humidity was as low as 81·5%. In small caves, relative humidity was more variable and considerably lower, as low as 66%. Constrictions produced noticeable changes in temperature and relative humidity. For example, in the cave of the Ruins of Mayapan temperature varied from 25·6 to 27·2°C and relative humidity from 83 to 92% in opposite sides of a 10-m long constriction.

The bats

Fourteen species of bats were found using Yucatan caves as day roosts, and another two species were captured during night netting at the entrances to the caves (Arita & Vargas, 1995). Species include one emballonurid, three mormoopids, eight phyllostomids, one natalid, and one vespertilionid.

The association analysis classified the caves in six groups based on the relationship among the bat species (Fig. 1). The procedure identified five divisor species (*N. stramineus, P. parnellii, M. megalophylla, Glossophaga soricina* and *D. ecaudata*). The 19 caves classified in Group I are small and simple sites that harbour 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 harbour large 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.

A one-way ANOVA, excluding groups III 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 in the other groups and that groups II and VI are also different (in all cases, p <0·05).

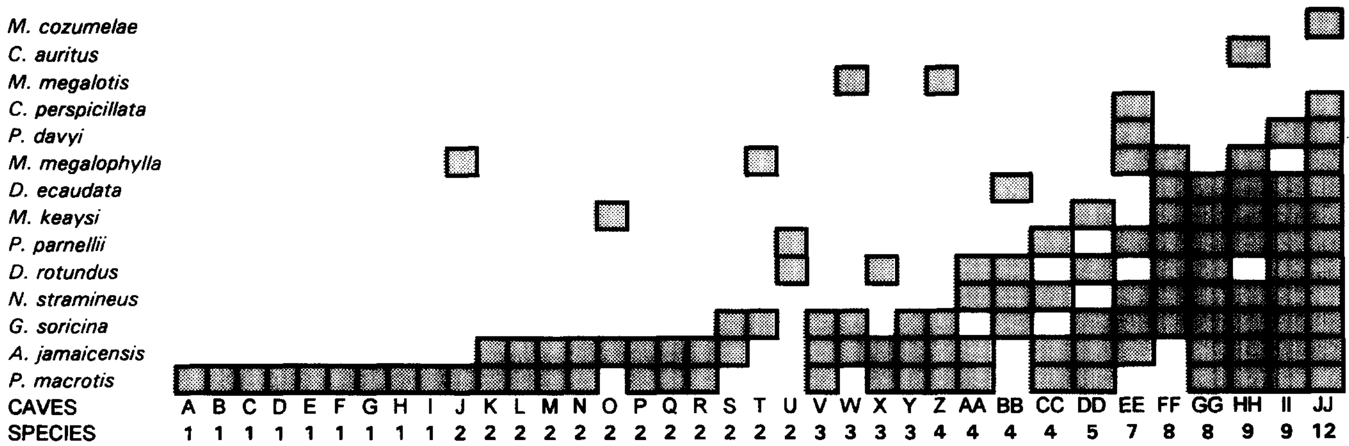

Fig. 2. Nested distribution of bat species among caves in Yucatan. Filled squares show the presence of a given species in a given cave. Caves are arranged along the horizontal axis in increasing species richness. Bat species are ordered along the vertical axis by the number of caves in which each species is found. Key to the caves corresponds to the one used in Table 1.

In contrast, the groups did not differ in terms of cave amplitude (one-way ANCOVA; test for homogeneity of slopes, $F = 2{\cdot}50$, d.f. = 3/28, $p = 0{\cdot}102$; test for effect of Group, $F = 2{\cdot}17$, d.f. = 3/27, $p = 0{\cdot}11$; log-transformed data; Fig. 2). 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, $F = 1{\cdot}79$, d.f. = 3/24; $p = 0{\cdot}18$; test for effect of group, $F = 0{\cdot}57$, d.f = 3/27, $p = 0{\cdot}64$; log-transformed data).

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

The distribution of bats in the caves of Yucatan is highly nested (Fig. 2). Rare species, such as *Chrotopterus auritus* and *Mimon bennettii*, are found only in species-rich caves. In contrast, common bats, such as *A. jamaicensis* and *P. macrotis*, were found both in caves with high and low species richness. These tendencies generate a nested pattern in which caves with low species richness are subsamples of richer sites. This pattern is significantly different from random distributions generated using both the original algorithm of Patterson and Atmar (1986) and the continuity correction of Wright and Reeves (1992, $p < 0{\cdot}001$ in both cases).

Most caves studied had low species richness (Fig. 3). The average number of species per cave was 3·28, but 21 (58%) of the caves harboured only one or two species, whereas only six (17%) provided refuge for seven or more species. The frequency distribution for the caves of Yucatan is similar to that for the caves of Mexico (Arita, 1993*b*). Lol-Tun cave is an unusually rich cave; at least 12 cave species use it as diurnal refuge, and another three (*Dermanura phaeotis, Sturnira lilium,* and *Lasiurus intermedius*) have been

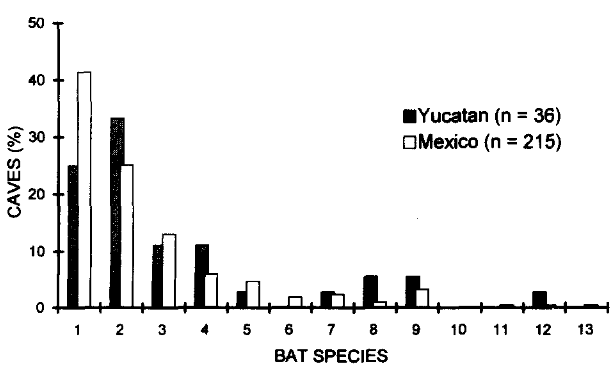

Fig. 3. Frequency distribution of bat species richness for the caves of Yucatan and Mexico.

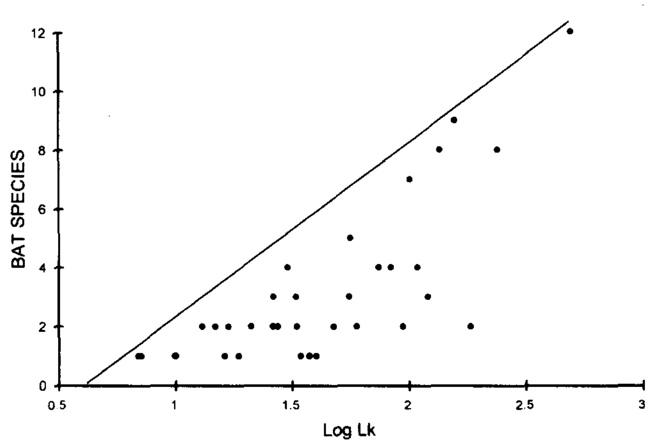

Fig. 4. Relationship between bat species richness and L_k, the maximum horizontal extent of the caves of Yucatan. L_k is a measurement of cave size. Line represents the apparent maximum richness for a given cave size.

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, increasing 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.

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 (Fig. 4, $r = 0{\cdot}78$, $p < 0{\cdot}001$). The upper left triangle in Fig. 4 has no 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 harbour rich assemblages.

Species richness varied among the groups formed by the association analysis among cave bats (Kruskal–Wallis test comparing the four groups with $n > 1$, $c^2 = 23{\cdot}8$, d.f. = 3, $p < 0{\cdot}001$). Caves in Group I had fewer species than the rest of the sample (median S = 1·5; Mann–Whitney test, $U = 245{\cdot}5$, $p < 0{\cdot}001$), whereas caves in group VI were richer than the rest of the sample (median S = 6·0; $U = 3{\cdot}5$, $p < 0{\cdot}01$). 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 $p > 0{\cdot}05$), 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 created by the association analysis form a gradient of species richness. Group I is formed by the shortest and simplest caves that harbour 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 ($r = 0{\cdot}79$, p ($r = 0$) $< 0{\cdot}001$). This result contrasts with the pattern found in the study of Arita (1993*b*) for the caves of Mexico, 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 due as well to the absence in Yucatan of species such as *Tadarida brasiliensis* that form huge colonies in caves with low species richness. In Yucatan, bats that roost in species-poor sites (segregationist species in the nomenclature of Arita, 1993*b*) form small or medium-sized colonies (e.g. *P. macrotis, M. megalotis, A. jamaicensis*), whereas bats that roost in sites of high species richness (integrationist species) tend to concentrate in large and very large groups (e.g. *Pteronotus* spp., *N. stramineus*). As a consequence, caves in Group VI, which have higher species richness, also harbour larger total populations.

DISCUSSION

Criteria for the conservation of bat caves

Three criteria have been proposed for assigning conservation value to caves that harbour bat populations: species richness, abundance, and the presence of species of special concern (Arita, 1993*b*). Here I discuss the patterns of cave use by Yucatan bats in the context of these criteria.

Only 10% of the caves of Mexico harbour ≥6 species of bats. It has been suggested that these caves deserve special consideration for protection because of their unusually high species richness (Arita, 1993*b*). According to this criterion, six (16·7%) of the Yucatan caves under study should be considered relevant in a national conservation plan. Lol-Tun is the second richest cave in Mexico in terms of day-roosting species and the richest in terms of the total number of species using the cave.

Nine of the caves under study support populations of >1000 bats. 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 Mexico forms colonies of several million individuals, is absent from Yucatan. Additionally, in Yucatan the mormoopids (*Pteronotus* spp. and *M. megalophylla*) never form the huge congregations of >100,000 individuals that have been reported from other sites (Bateman & Vaughan, 1974). At the local level, however, these caves deserve special consideration because of their comparatively high population levels.

The bat fauna of Yucatan is a subset of the pool of species of southeastern Mexico and is formed mostly by species with wide distributional ranges (Arita, 1992). Because local abundance and area of distributional range are positively correlated for Neotropical bats (Arita, 1993*a*), the bat fauna of Yucatan 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 Yucatan species would not be considered threatened. In fact, only three of the cave bats of Yucatan are considered fragile or vulnerable at the national level (Arita, 1992).

Two of these species, the spear-nosed bat *M. bennettii* and the woolly false vampire bat *C. auritus*, are rare and form small colonies of <10 individuals (Arita, 1993*b*). During this study both species were found in caves with high species richness (*M. bennettii* in Lol-Tun, *C. auritus* in Tzab-Nah), but other reports (Hatt & 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. bennettii* and *C. auritus* would require special studies to assure their conservation in Yucatan. These studies should focus on the identification of caves that are regularly used by these two species.

The third species, *P. macrotis*, is rare in other tropical areas of Mexico, but in Yucatan 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.

In the case of the caves of Yucatan, 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

The positive correlation between bat species richness and population abundance in the caves of Yucatan implies that a comparatively small number of sites would be necessary to comply with these two conservation criteria. Five of the caves in Group VI (Sabak-Ha, Hoctun, Tzab-Nah, Lol-Tun and Spukil) and one in Group V (Bat Cave) have both the highest species richness and the largest populations. These results contrast with the observation that abundance and richness are uncorrelated in the case of caves in Mexico as a whole (Arita, 1993*b*).

The highly nested pattern of cave use by bats produces a fauna in which most species are integrationist; that is, they tend to occur in caves with high species richness. If the criterion of protecting caves with unusually high species richness is met, most cave bat species of Yucatan 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 *A. jamaicensis*. These species would need special conservation strategies tailored to their particular needs.

Caves with the highest species richness and highest population levels are also the largest and most complex. 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-Tun and Spukil) are well-known tourist attractions, and another site, Hoctun 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

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 'colour' 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 compromise 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 divided into 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 colour according to their conservation value.

The 28 (78%) caves that presented low species richness and low population levels were classified in Groups I to IV on the basis of their bat communities. These caves are in general small and difficult to locate, and could be considered green. There are, however, some exceptions. Actun Chac-Xix, Roble Cave, and Kabahchen are only a few metres from main roads and are frequently visited by people. These sites support only small colonies of common bat species, but they are important archaeological sites. Considering caves such as 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 Yucatan, 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 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'.

I propose four caves (11·1 % of the total) for the yellow category, that is, sites that would require some degree of protection. The cave of the Ruins of Mayapan is a typical site in this category. The association analysis classified this cave in Group V, as it supports populations of four species of bats, including sizable colonies of *P. parnellii* and *N. stramineus*. The cave is within the archaeological site of Mayapan 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 archaeological treasures and the bat populations.

I suggest labelling 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 archaeological value. 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.

The three largest and more complex cavern systems call for multipurpose use. Being a popular tourism attraction, an important archaeological and historical site, and the centre of a small protected area, Lol-Tun cave is already an example of a multipurpose system. The fact that this cavern system still harbours 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-Tun is that many of the chambers that support bats are not open to the public and have separate entrances. 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 archaeological 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 archaeological site can be open to the public under a green status.

CONCLUSIONS

The design of a conservation strategy for the cave bats of Yucatan is facilitated by the fact that the three conservation criteria considered here are correlated. Because of the highly nested pattern of species distribution, caves that support a great species diversity also harbour large multispecies populations, and provide roosts for several species of concern.

The implementation of the conservation strategy can be hindered by the fact that the most important sites for the protection of bats are located in the large systems that are so attractive for tourists. However, as the present status of bat populations in Lol-Tun shows, these caves can be successfully managed for multiple purposes. Conservation plans for the bats of Yucatan are inevitably linked to the protection of cave environments. Because of the particular social and historical traits of the state, such conservation plans need to be linked also to the protection of archaeological sites, to the use by sport speleologists, and to the management of caves as tourist sites. Conservation of caves in Yucatan is necessarily an interdisciplinary endeavour.

ACKNOWLEDGEMENTS

Results presented here are part of my PhD dissertation at the University of Florida. I thank G. Ceballos, J. F. Eisenberg, P. Feinsinger, S. R. Humphrey, K. H. Redford, J. Reiskind and O. Sánchez for their helpful commentaries and criticism. Field work was supported by the University of Florida's Program for Studies in Tropical Conservation, by Sigma-Xi, and by a grant-in-aid of the American Society of Mammalogists. I thank the hospitality and help of the people of Tekax, especially M. Novelo, A. Rodríguez and M. Glover. V. Chablé, O. Sánchez, C. Guerrero, Y. Sakurai and A. Noguez helped me in the field. Collecting and working permits were granted by Secretaría de Desarrollo Urbano y Ecología (now Secretaría de Desarrollo Social) and by Instituto Nacional de Antropología e Historia, Merida office.

REFERENCES

Arita, H. T. (1992). Ecology and conservation of cave bat communities in Yucatan, Mexico. PhD dissertation, University of Florida, Gainesville.

Arita, H. T. (1993*a*). Rarity in neotropical bats: correlations with phylogeny, diet, and body mass. *Ecol. Appl.*, **3**, 506–17.

Arita, H. T. (1993*b*). Conservation biology of the cave bats of Mexico. *J. Mammal.*, **74**, 693–702.

Arita, H. T. & Vargas, J. A. (1995). Natural history, interspecific association, and incidence of the cave bats of Yucatan, Mexico. *Southwest. Natur*, **40**, 29–37.

Arroyo Cabrales, J. & Alvarez, T. (1990). Restos éseos de murciélagos procedentes de las excavaciones en las grutas de Lol-Tún. Instituto Nacional de Antropología e Historia, Mexico.

Barr, T. C., Jr (1968). Cave ecology and the evolution of troglobites. In *Evolutionary biology,* Vol. 2, ed. T. Dobzhanski, M. K. Hecht & W. C. Steere. Appleton-Century-Crofts, New York, pp. 35–102.

Bateman, G. C. & Vaughan, T. A. (1974). Nightly activities of mormoopid bats. *J. Mammal.*, **55**, 45–65.

Culver, D. C. (1982). *Cave life, evolution and ecology.* Harvard University Press, Cambridge, MA.

Culver, D. C. (1986). Cave faunas. In *Conservation biology, the science of scarcity and diversity*, ed. M. E. Soulé. Sinauer, Sunderland, MA, pp. 427–43.

Dalquest, W. W. & Walton, D. W. (1970). Diurnal retreats of bats. In *About bats*, ed. B. H. Slaughter & D. W. Walton. Southern Methodist University Press, Dallas, TX, pp. 162–87.

Diamond, J. (1988). Red books or green lists? *Nature, Lond.*, **332**, 304–5.

Dublyansky, V. N., Ilyukhin, V. V. & Lobanov, Y. E. (1987). Some problems of karst morphometry. *Stud. Speleol.*, **7**, 17–22.

Ellis, B. M. (1976). Cave surveys. In *The science of* *speleology*, ed. T. D. Ford & C. H. D. Cullingford. Academic Press, London, pp. 1–10.

García, E. (1981). *Modificaciones al sistema de clasificación climática de Koppen (para adaptarlo a las condiciones de la República Mexicana)*, 3rd edn. Larios, Mexico City.

Green, K. M., Lynch, J. F., Sircar, J. & Greenberg, L. S. Z. (1987). LANDSAT remote sensing to assess habitat for migratory birds in the Yucatan Peninsula, Mexico. *Vida Silv. Neotrop.*, **1**, 27–38.

Harris, J. A. (1970). Bat-guano cave environment. *Science, N.Y.*, **169**, 1342–3.

Hatt, R. T. & Villa-R., B. (1950). Observaciones sobre algunos mamíferos de Yucatán y Quintana Roo. *An. Inst. Biol., Univ. Nacn. Autón. Méx.*, **21**, 215–40.

Howarth, F. G. (1972). Cavernicoles in lava tubes on the island of Hawaii. *Science, N.Y.*, **175**, 325–6.

Howarth, F. G. (1983). Ecology of cave arthropods. *Ann. Rev. Entomol.*, **28**, 365–89.

Humphrey, S. R. & Bain, J. R. (1990). *Endangered animals of Thailand.* Sandhill Crane Press, Gainesville, Florida.

Jones, J. K., Jr, Smith, J. D. & Genoways, H. H. (1973). Annotated checklist of mammals of the Yucatan Peninsula, Mexico, I. Chiroptera. *Occ. Pap. Mus. Tex. Tech. Univ.*, **13**, 1–31.

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

Ludwig, J. A. & Reynolds, J. F. (1988). *Statistical ecology.* John Wiley, New York.

McCracken, G. F. (1989). Cave conservation: special problems of bats. *Natn. Speleol. Soc. Bull.*, **51**, 47–51.

Patterson, B. D. & Atmar, W. (1986). Nested subsets and the structure of insular mammalian faunas and archipelagos. *Biol. J. Linn. Soc.*, **28**, 65–82.

Poulson, T. L. (1972). Bat guano ecosystems. *Bull. Natn. Speleol. Soc.*, **34**, 55–9.

Poulson, T. L. & White, W. B. (1969). The cave environment. *Science, N. Y*, **165**, 971–81.

Reddell, J. R. (1977). Studies on the caves and cave fauna of the Yucatan Peninsula. *Assoc. Mex. Cave Stud. Bull.*, **6**, 1–296.

Reddell, J. R. (1981). A review of the cavernicole fauna of Mexico, Guatemala, and Belize. *Bull. Tex. Mem. Mus. Univ. Tex. Aust.*, **27**, 1–327.

Tuttle, M. D. & Stevenson, D. E. (1981). Variation in the cave environment and its biological implications. In *Cave gating*, ed. G. Hunt & R. R. Stitt. National Speleological Society, Hunstsville, AL, pp. 46–59.

White, W. B. (1988). *Geomorphology and hydrology of karst terrains.* Oxford University Press, New York.

Wright, D. H. & Reeves, J. H. (1992). On the meaning and measurement of nestedness of species assemblages. *Oecologia (Berl.)*, **92**, 416–28.