COMMUNITY STRUCTURE OF BATS ALONG AN ALTITUDINAL GRADIENT IN TROPICAL EASTERN MEXICO

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ABSTRACT.- The changes in species richness, relative abundance, and biomass of bats were monitored along an altitudinal gradient (800 to 2,560 m) in the Sierra Madre Oriental in eastern Mexico. In general, species richness, density, and biomass were correlated with elevation, but the insectivorous bats were more numerous at mid-elevation sites. The frugivorous bats contributed with the majority of the biomass along the gradient. One migratory species (*Tadarida brasiliensis*) was only detected during the summer months. It is hypothesized that the observed changes are correlated to the amount of food availability and thermoregulatory abilities of bats.

RESUMEN.- Los cambios en riqueza de especies, abundancia relativa y biomasa de los murciélagos fueron monitoreados a lo largo de un gradiente altitudinal (800 a 2,560 m) en la Sierra Madre Oriental en el este de México. En general, la riqueza de especies, densidad y biomasa estuvieron correlacionadas con la altitud; sin embargo, los murciélagos insectívoros fueron más numerosos en altitudes intermedias. Las especies frugívoras contribuyeron con la mayor proporción de la biomasa. Una especie migratoria (*Tadarida brasiliensis*) sólo fue colectada en el verano. Se sugiere que los patrones observados están correlacionados con la disponibilidad de alimento y las habilidades termorregulatorias de los murciélagos.

Key words: Chiroptera, community structure, altitudinal gradients, Queretaro.

INTRODUCTION

The changes of animal communities along altitudinal gradients in tropical mountains represent one of the most interesting phenomena to study in community ecology, because several life zones are generally compressed within a relatively short distance, and the results can help to understand the structure of communities. Probably one of the most extensively surveyed areas is the Peruvian Andes Mountain, where studies are available for birds (Terborgh, 1971, 1977; Terborgh and Weske, 1975), reptiles (Duellman, 1979), non-volant mammals (Pearson and Ralph, 1978), and rodents (Pizzimenti and De Salle, 1981).

The changes in a bat community at the Andes showed that species richness is correlated with elevation, climatic factors (temperature) and foliage-height diversity (Graham, 1983). In this paper, we compare the bat community in an altitudinal transect in a tropical mountain of the northern Hemisphere, where a much impoverished bat fauna is present, when compared to the Andes.

METHODS

Eight collecting localities were selected along an altitudinal transect in the Sierra de Pinal de Amoles, which is a part of the Sierra Madre Oriental, State of Querétaro, Mexico. The altitudinal range covers from 800 to 2,650 m and both faces of the Sierra de Pinal de Amoles. Sites were selected to represent the different vegetation as well as climate types.

Alternate field trips to one of the slopes of the mountain were done during one and half years, covering the different seasons for all the localities. Eleven trips were performed from 31 July 1982 to 30 December 1983, and for the purpose of this analysis, the period of one year, from September 1982 to August 1983 was considered.

Bats were mist-netted along streams, ponds and forests. Mist nets were placed for two nights in each locality. External body measurements of bats were taken in the field to all individuals caught. The reproductive condition was determined by autopsy, recording pregnancy, lactation and prominence of teats. Vaginal opening was annotated as closed or open. Testes in males were measured with dial calipers. Body weight is given in grams. Only free-ranging bats were included in this study, therefore bats captured in caves were not considered.

The altitude of the locality, number and size of mist nets utilized were recorded for each trapping month, allowing us to evaluate the number of species, density and biomass of bats captured in every locality weighted against the number and type of mist netting effort in each locality. The unit which allowed us to ponderate the effort was the linear meter of mist net. Relative abundance of bats was approximated as the number of individuals per linear meter of mist net, calculated as the ratio of individuals per linear meters of mist net for a two-night period per locality. The cumulative biomass in grams per linear meter of mist net was calculated for every locality, based on the individual body weights. The number of species, density and biomass of bats was analyzed for the whole group, and for the trophic guilds recorded in every locality.

STUDY AREA

The Sierra de Pinal de Amoles is located in the eastern part of the Mexican State of Querétaro. In this mountain range, the orographic rain phenomenon produces wet environment in the eastern slope, facing the Gulf of Mexico, whereas dry areas constitute the occidental slope towards the Mexican Plateau (Mosiño and García, 1974).

Collecting sites in the dry part include Peña Miller, Camargo and Maguey Verde. The humid face was represented by Pinal de Amoles, Ahuacatlán and Jalpan. A locality (Santa Inés) in a contiguous mountain was selected for comparison. An extensive description of the study area was presented elsewhere (León, 1986), and a brief description of the sites, using Holdridge's life zones, is as follows:

Peña Miller (21° 10' Lat. N, 99° 05' Long. W; 1,400 m) is located in the arid Mexican Plateau, with 22°C in mean annual temperature and 482 mm as mean annual rainfall. The scrubby vegetation is classified as a Tropical Premontane Thorn Woodland with *Morkillia mexicana* and *Acacia sororia*. Tracts of microphyll scrub are found in some areas, with *Acacia vernicosa* and *Fouquieria splendens*. The only trees in the area are located along a branch of the nearby Extorax river.

Camargo (21° 06' Lat. N, 99° 43' Long. W; 1,850 m) is characterized by a Tropical Premontane Thorn Forest, with *Neopringlea integrifolia* and *Mimosa* as dominant plants. Trees were virtually absent. The mean annual temperature is 22.3°C and no data is available on rainfall.

Maguey Verde (21° 07' Lat. N, 99° 41' Long. W; 2,290 m) is a vegetation transition zone. A patchy forest of *Pinus cembroides* (pinyon) and *Juniperus flaccida* in the lower limit of this forest intermingles with a thorn forest. Mean annual temperature is 17°C. Deep canyons and abandoned mercury mines are characteristic of the site. Mean annual rainfall is 600 mm.

Pinal de Amoles (21° 07' Lat. N, 99° 37' Long. W; 2,650 m) is the highest locality in the transect, characterized by a Lower Montane Moist Forest, with abundance of pines (*Pinus patula*, *P. teocote*, *P. montezumae* and *P. pseudostrobus*). In the lower stratum of the forest, scrub species such as *Baccharis lancifolia*, *Senecio hartwegi* and *Cestrum flavescens* are found. The pine forest presents an upper canopy of 25 m. An oak forest is found nearby.

Ahuacatlán (21° 14' Lat. N, 99° 34' Long. W; 1,140 m) is located in the eastern slope of the range. Mean annual temperature and rainfall are of 22.3°C and 964 mm, respectively. A Tropical Premontane Dry Forest, conspicuously taller than the vegetation found in the western slope, is the dominant vegetation type. Common species are *Lysiloma divaricata*, *Bursera simaruba*, *Diospyros palmeri*, *Pseudobombax ellipticum*, *Capparis incana*, and *Pithecellobium dulce*. Along streams, trees such as *Platanus mexicanus*, *Vitex mollis*, and *Populus* form a gallery forest.

Jalpan (21° 14' Lat. N, 99° 30' Long. W; 840 m) is located at the lower part of the eastern slope, and the vegetation type is a Tropical Very Dry Forest. Mean annual temperature is 26°C and annual rainfall is 880.7 mm. Vegetation elements are deciduous and reach a medium height of 10 to 12 m, and include *Lysiloma divaricata*, *Pseudobombax ellipticum,* and *Erythrina flabelliformis*.

Santa Inés (21° 10' Lat. N, 99° 05' Long. W; 1,420 m) is characterized by a Tropical Dry *Quercus* (oak) Forest. Mean annual temperature is 25.3°C and mean annual rainfall reaches 1,379 mm. Common plant species include several species of oaks (*Quercus*), and plants such as *Brahea dulcis*, *Dioon edule*, *Hicoria pecan*, *Cercis canadensis*, *Litsea glaucescens*, *Ungandia speciosa*, *Juniperus flaccida*, *Pistacia mexicana,* and *Arbutus xalapensis*.

RESULTS

Species Richness

A total of 413 bats, belonging to 4 families, 19 genera and 29 species were collected in a total of 1,064 m of mist net. Table 1 lists the species following Hall (1981) and Wilson and Reeder (1993). A detailed account for every species was presented elsewhere (León, 1986).

Several species were found in only one locality, including *Pteronotus dayvii* in Ahuacatlán, *Lasiurus ega* and *Molossus rufus* in Jalpan, *Anoura geoffroyi* and *Plecotus mexicanus* in Pinal de Amoles, *Myotis thysanodes* in Camargo and *Antrozous pallidus*, *Macrotus waterhousii* and *Nyctinomops macrotis* in Peña Miller. Other bat species such as *Euderma maculatum* in Peña Miller, *Pteronotus personatus* in Camargo, *Myotis velifer* in Ahuacatlán, and *Diphylla ecaudata* in Santa Inés, were not included in this analysis because they were not caught the year considered in this study (León, 1986).

No significant differences were found for the number of species trapped in each side of the mountain ($X^2 = 0.43$, $P > 0.1$). Twenty one species were found in the eastern (humid) slope, whereas 18 were caught in the western (dry) slope; 13 species were common to both sides of the mountain range.

Species richness decreased with increasing altitude ($F = 11.672$, $P < 0.02$, $r = -0.863$); Jalpan and Maguey Verde showed the highest and lowest species richness values, respectively (Fig. 1). The locality of Santa Inés, in a mid-elevation position, with an oak (*Quercus*) forest, showed unexpected low species richness.

The number of species captured per linear meter of net was not significantly correlated with altitude ($F = 0.302$, $P > 0.6$, $r = -0.264$) and the highest value was found in the dry part, Camargo, roughly doubling the lowest value found in Pinal de Amoles.

The number of species as function of time showed a larger number for the localities in the more humid slope of the mountain and a larger species richness for the warm months of the dry season (Fig. 2). The months with the highest and lowest number of species for the humid slope were April and January, respectively. In contrasts, in the dry region of the transect, the highest number of species was found in May, and the lowest in February.

Density

The number of individuals captured per linear meter of mist net was negatively correlated to altitude ($P < 0.026$, $r = -0.863$) and the locality with the highest density was Ahuacatlán, whereas the minimum was located in the top of the mountain (Fig. 3). Bat density was higher in the localities found in the humid slope.

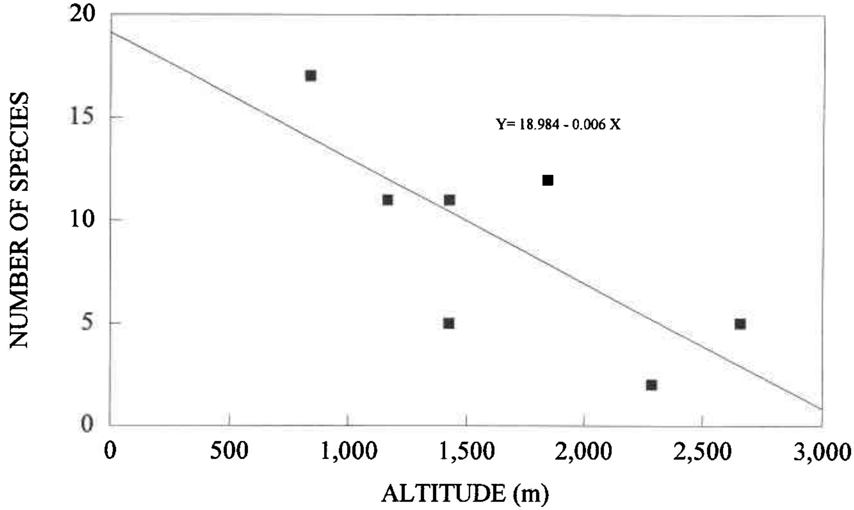

Figure 1. Changes in species richness of bats as a function of altitude.

The number of individuals captured (Table 1) was strongly biased towards two species: *Tadarida brasiliensis* and *Sturnira lilium*, which accounted for 29% and 20% of the total captures, respectively. A seasonal variation of the number of *Tadarida* individuals per mist net was observed, with a maximum of 0.358 ind/mn in January, declining drastically towards July (0.049 ind/mn) and the following months (0 ind/mn), until it began to appear again in December (0.030 ind/mn). The variation in *Sturnira lilium* was also seasonal, but the observed maximum was located in the warm months of April to July, declining towards October.

Density was separately computed for the frugivorous and insectivorous bats. A significant negative correlation between the frugivorous bats and elevation was found ($P < 0.005$, $r = -0.940$); such correlation was not significant for the insectivorous species ($P > 0.2$, $r = -0.543$). The density of insectivorous bats outnumbered the frugivorous species in localities found at higher altitudes.

Two peaks in density of frugivorous bats were found, one in April for the humid side of the mountain and another in August for the dry slope. This can probably be explained by the high number of species found in the warm months of April, but there is not a similar increase noted for the dry slope of the mountain.

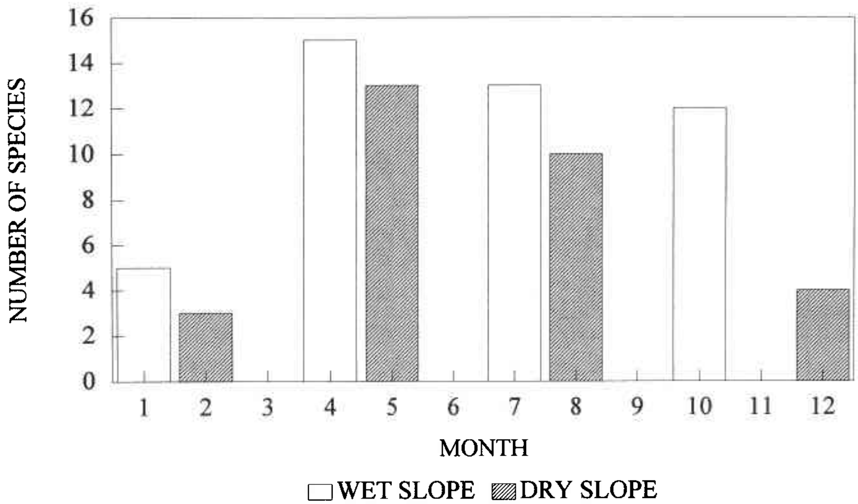

Figure 2. Changes in species richness through time, for the two slopes of the mountain range.

The fluctuations in the density of insectivorous bats were not parallel for each side of the mountain; when the maximum density for insectivorous bats was observed for the humid side in January (0.555 ind/mn), a low value was noted for February in the dry slope (0.068 ind/mn).

Biomass

The biomass was considered to evaluate the impact of the two abundant species (*Tadarida brasiliensis* and *Sturnira lilium*) and other species which may be less abundant but with a massive weight. The bat biomass was negatively correlated to altitude ($P < 0.005$, $r = -0.927$), with the lowlands accounting for the highest values (Fig. 4).

The total biomass for the bats during the study was of 8,964.6 g. A very large proportion (6,858.7 g; 76.5%) was, however, found in the humid slope. The highest biomass contribution by a single species was for *Artibeus lituratus* (2,259 g). The

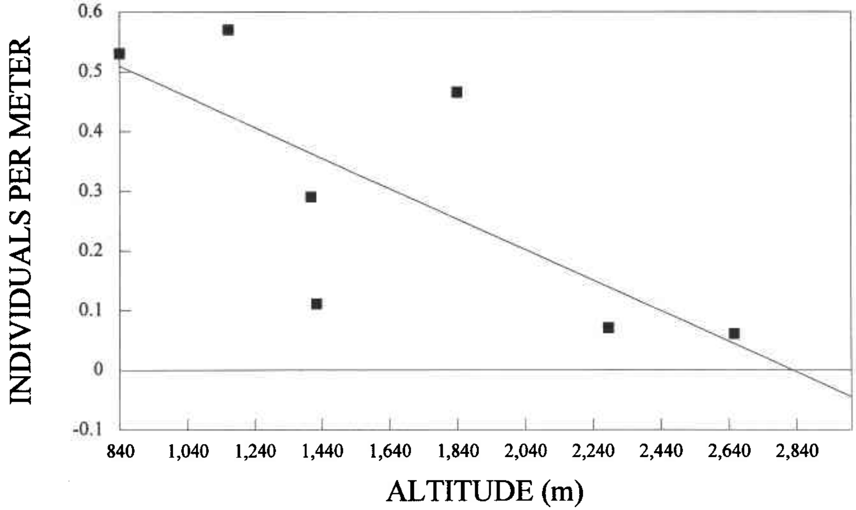

Figure 3. Changes of bat density as a function altitude. Note the low value for the Santa Ines locality, at 1,420 m.

contribution of the two common species was most conspicuous in the humid slope, where 88.9% (1,102.4 g) of the *Tadarida* and 95.2% (1,582.8 g) of *Sturnira* biomass was recorded.

The most important frugivores, in terms of biomass, were *Artibeus lituratus* and *Sturnira ludovici* in the humid and dry slopes, respectively. The insectivorous species with the highest biomass was *Tadarida brasiliensis* in the humid slope and *Eptesicus fuscus* in the dry slope (317.9 g; 85.2%).

The biomass of fruit-eating bats was negatively correlated with altitude ($P < 0.05$, $r = -0.874$), with higher values in the lowlands. No similar results were found for the insectivorous bats, and the correlation with altitude was not significant ($P > 0.2$, $r = -0.599$). The highest biomass for the insectivorous bats was represented in mid-elevation localities of Peña Miller and Camargo, with 4.284 g/mn and 4.746 g/mn, respectively.

Frugivore species show a seasonal variation in biomass; in the humid slope, there were low values from January to March, increasing towards April (11.490 g/m) and sharply decreasing until the end of the year, reaching a value similar to the January biomass (6.325 g/m and 5.611 g/m, respectively). The situation in the dry slope was

Table 1.- A list of the bat species found in the altitudinal gradient in the Mexican State of Querétaro. Species common to the humid (east) and dry (west) slopes are marked with an asterisk.

Scientific Name	N	Mean Body Weight (g)	Biomass (g)
Pteronotus parnellii	2	17.0	34.0
Pteronotus davyi	1	10.0	10.0
*Mormoops megalophylla**	10	15.8	158.0
Macrotus waterhousii	1	15.0	15.0
*Glossophaga soricina**	7	10.7	74.9
Anoura geoffroyi	1	18.0	18.0
*Choeronycteris mexicana**	2	15.5	31.0
*Leptonycteris curasoae**	28	28.7	804.0
*Sturnira lilium**	86	19.3	1661.3
*Sturnira ludovici**	11	23.4	257.0
Artibeus jamaicensis	16	42.6	681.0
Artibeus lituratus	36	62.8	2259.3
*Dermanura azteca**	15	20.3	305.0
Dermanura tolteca	8	18.4	147.0
*Desmodus rotundus**	7	35.1	246.0
Myotis californica	2	4.5	9.0
Myotis thysanodes	1	7.0	7.0
*Pipistrellus hesperus**	9	4.9	44.0
*Eptesicus fuscus**	22	16.6	364.9
Lasiurus ega	1	14.0	14.0
Lasiurus borealis	1	8.3	8.3
*Lasiurus cinereus**	10	24.3	243.0
Idionycteris phyllotis	8	11.2	90.0
Plecotus towsendii	1	9.0	9.0
Antrozous pallidus	1	22.0	22.0
*Tadarida brasiliensis**	120	10.2	1240.2
Nyctinomops macrotis	1	28.0	28.0
*Molossus rufus**	5	40.8	204.0

somewhat opposite, with no frugivore bats in February and a biomass of 0.423 g/m in May, which was extremely low biomass when compared with the April value for the humid slope.

The pattern observed for the insectivorous bats is similar to the one for the fruit-eating bats. High values in the January and April samples for the humid slope and low values thereafter. The insectivore biomass in the submontane forest of the dry slope was

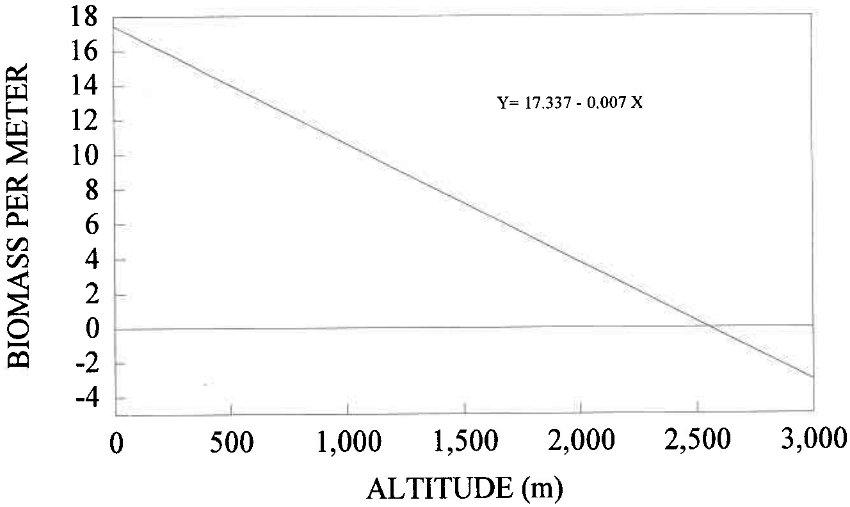

Figure 4. Changes of biomass as a function of altitude. Note that the value of the slope is very similar to the value found for the slope of the number of species against altitude.

low during the warm months of the year, increasing towards August-September. The nectarivore bats produced a biomass of 927 g, and *Leptonycteris curasoae*, which was found in the dry slope, accounted for 86.6%.

The vampire bat, *Desmodus rotundus*, was found in the lowlands of the humid slope, with a contribution of 246 g.

DISCUSSION

We have shown that elevation alone can explain as much as 90% of the variability in several variables included in this analysis, such as the overall species richness, species density and species biomass. It is clear that the changes in species richness are correlated with altitude; the data for Querétaro show a decrease of about eight bat species for every 1,000 m of increase in elevation, which looks very conservative when contrasted to Graham (1983) data for the Peruvian Andes. Graham (1983) reports a lose of 29 species for the 1,000 to 2,000 m elevational range and an additional 12 species for the 2,000 to 3,000 m altitudinal range.

There is no other available data on bat density and biomass related to altitude, which could be used also for comparison; so, additional studies on bat community are needed (see Humphrey and Bonaccorso, 1979). However, we can contrast our results and discern several explanations for the observed patterns in this study, based on studies done in other groups, mainly birds. There are at least three lines for explanation of the observed results that can be summarized as follows:

Food Resources

Food availability is a strong alternative explanation for the abundance of frugivores in lowlands, and a lack of members of this trophic guild at higher elevations, as had been previously suggested by Graham (1983). Pratt and Stiles (1985) demonstrated that fruit size and structure influence the composition of assemblages of birds. Food availability has been suggested as an important factor for other organisms as well, including small rodents (Brown, 1973) and squirrels (Emmons, 1980). At higher elevations, the plant components of the pine forest found in the highlands produce types of fruits not edible for bats. Pines produce a type of fruit which can be classified as structurally protected (Janson, 1983), and bats are very unlike to exploit this type of resource.

The lack of adequate food supply can be also a factor in Santa Inés, with an oak forest containing half of the number of species found in the xerophyll scrub of Peña Miller located on the dry slope of the mountain. The bat density and biomass were also low in the oak forest site.

The nectarivore bat species increased in biomass in May, during the dry season, which might be associated with a massive bloom of flowers, as observed in birds (Wolf, et al., 1976; Bell, 1982); however, little data is available.

The seasonality in the climate provokes a differential response in the bat insectivore fauna, which translates also in the non-linear altitudinal patterns observed in this study. Insectivore bats are apparently more seasonal and this is possibly a pattern more generalized, as reported by Karr (1976) for insectivorous birds, and Pizzimenti and De Salle (1981) for rodents, probably related to insect density (Janzen and Schoener, 1968). A higher density and biomass was observed at mid-elevation sites, which is probably explained by an increase in insect density at these altitudes. There is no available data to support this observation, but the few studies on insect productivity in other tropical areas suggest an increase of insect density and biomass at intermediate elevation sites (Janzen, 1973).

Thermoregulatory Abilities of Bats

The lower temperatures correlated with increasing elevation may affect the pattern and timing of food production, as seen in the previous paragraphs. The environmental changes associated with elevation, however, also involve the physiological abilities of bats to tolerate colder conditions. Several studies have indicated that bat species can enter into torpor as a response to low ambient temperatures and that most of the tropical bats are poor thermoregulators (McNab, 1969, 1973, 1974; McManus, 1977; Studier and Wilson, 1970). We found torpid individuals of *Dermanura azteca* in several caves inspected in the high site of Pinal de Amoles, suggesting that the reduction in biomass observed can be explained by either individuals entering into torpor, or species avoiding high elevation sites through altitudinal or latitudinal migration.

One of the species which accounted for the changes in density and biomass of insectivorous bats is the molossid *Tadarida brasiliensis*. This species was present in massive numbers in the January and April samples of the wet slope of the mountain. In Querétaro, this species was extremely important in terms of high population density (second to none) and biomass (second only to *Artibeus lituratus*). Seasonality in *Tadarida* from Querétaro very likely is linked to the latitudinal migratory pattern reported for the species (Svoboda et al., 1985).

We did not find evidence for altitudinal migration from bats occupying the habitats in higher elevations during more favorable periods of the year, although this remains a probability. One factor related to environmental constrains is the availability (of roosting sites as suggested by Humphrey, 1975); however, there were apparently enough roosting sites available for bats. The Maguey Verde and Pinal de Amoles are areas rich in caves and abandoned mines wich we found empty during our survey.

Habitat Complexity

MacArthur and MacArthur (1961) found that a measure of habitat complexity in the form of foliage height density was a good predictor of bird species density. This result was analyzed by Rotenberry (1978), who found that spatial heterogeneity was a key factor determining bird community structure in unstable environments. Graham (1983) considered the habitat complexity as a factor acting against inmigration of tropical bat species into highlands.

We failed to find evidence of habitat complexity as an important factor influencing bat species richness in Querétaro. This statement is based on two observations: i) despite the conspicuous differences in habitat complexity, the number of species in both sides of the mountain range is similar, and ii) the Pinal de Amoles and Santa Inés localities are heterogeneous from a vegetational standpoint; however, species richness was higher in the dry part of the range, where the virtual absence of trees creates a simple landscape. The role of habitat complexity might be important for the determination of bat density and biomass, and additional studies are needed.

In conclusion, The Sierra de Pinal de Amoles constitutes a formidable barrier preventing the homogeneous distribution of bats, using the habitats according to its availability, and imposing strong environmental constraints which are reflected in the observed changes in density and biomass.

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