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Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: does a generalized migration pattern really exist?

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Abstract

Aim This paper examines the migration of the tropical nectarivorous bat *Leptonycteris curasoae* considered as a latitudinal migrant that breeds in south-west United States and northern Mexico in spring and migrates southward during fall. We tested the hypothesis that the latitudinal migration occurs only locally given by the local availability of bat resources, leading to migratory movements in zones with seasonal scarcity of resources and to resident bat populations where resources are available throughout the year.

Localization We analysed the presence of *L. curasoae* along its distribution range in North America (between 14°N and 33°N). Study cases were also conducted in three Mexican localities: the Tehuacán Valley (17°48′–18°58′N and 96°48′–97°43′W), Sonoran Desert (28°41′N and 110°15′W), and the coast of Jalisco (19°32′N and 105°07′W).

Methods Geographic evidence for latitudinal migration of *L. curasoae* was analysed using 94-year capture records housed in twenty-two collections of North America. Records were analysed using a Geographical Information System (GIS), in which floral resources and capture records were integrated. Monthly captures in the Tehuacán Valley were conducted during three years and bats abundance and reproductive status were correlated with the phenology of bat resources. Bat captures were also conducted during two consecutive years in an extratropical desert during winter and spring, and during one spring in the coast of Jalisco.

Results The latitudinal migration of *L. curasoae* in North America only occurs at latitudes near 30°N, whereas bats may be residents at latitudes lower than 21°N. Captures were associated always to the availability of floral resources in both geographical and local scales.

Main conclusions The existence of resident populations in the tropics with two reproductive events support the hypothesis that migration only occurs in the northern distribution limit of this nectar-feeding bat.

Keywords
Floral-bat resources, *Leptonycteris curasoae*, migration, reproduction, México.

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Resumen

Objetivo Este trabajo examina la migración del murciélago nectarívoro *Leptonycteris curasoae*, considerado como un migratorio latitudinal que se reproduce durante la primavera y el verano en el SW de los Estados Unidos y el norte de México, y que regresa hacia el sur durante el invierno. Nosotros analizamos la hipótesis de que la migración latitudinal ocurre sólo localmente, debido a la disponibilidad diferencial de los recursos florales a lo largo de su área de distribución. Esto provoca movimientos migratorios en zonas templadas con escasez estacional de recursos y la existencia de poblaciones residentes en lugares donde los recursos florales están disponibles todo el año.

Localización En este trabajo analizamos la presencia estacional de *Leptonycteris curasoae* a lo largo de su distribución geográfica en Norte América (entre los 14°N y 33°N). Además realizamos estudios de caso en tres localidades mexicanas: en el Valle de Tehuacán (17°48′–18°58′N y 96°48′–97°43′ W), en el desierto de Sonora (28°41′N y 110°15′ W), y en la costa de Jalisco (19°32′ N y 105°07′ W).

Método Las evidencias geográficas sobre la migración latitudinal de *Leptonycteris curasoae* fueron analizadas utilizando 94 años de registros de captura acumulados en 22 colecciones de Norte América. Los registros fueron analizados utilizando un Sistema de Información Geográfica (SIG), en el cual los recursos florales y los registros de captura fueron integrados. En el Valle de Tehuacán realizamos capturas mensuales durante tres años en los cuales registramos la abundancia y la condición reproductiva de los murciélagos, datos que fueron relacionados con la fenología de los recursos florales quiropterófilos. Además llevamos a cabo capturas durante dos años consecutivos en un desierto extratropical durante el invierno y la primavera, y durante la primavera en la costa de Jalisco.

Resultados La migración latitudinal de *L. curasoae* en Norte América sólo ocurre en latitudes cercanas a los 30°N, mientras que los murciélagos son residentes en latitudes menores a los 21°N. Las capturas de este murciélago están asociadas siempre a la existencia de recursos florales tanto a nivel geográfico como local.

Conclusiones principales La existencia de poblaciones residentes en el trópico donde existen dos periodos de reproducción, apoyan la hipótesis de que la migración sólo ocurre en los límites norteños de la distribución de este murciélago nectarívoro.

Palabras clave
Leptonycteris curasoae, migración, murciélago nectarívoro, reproducción, recursos quiropterófilos, México.

INTRODUCTION

Migration is a term used to describe movements and defined as the changes in habitat, periodically recurring and alternating in direction, which tend to secure optimal environmental conditions at all times (Thomson, 1926). In North America many animals, such as birds, butterflies and bats, migrate from their northern breeding grounds on summer, southwards to feeding wintering grounds in tropical America. Explanations to this behaviour have been related to several nonindependent factors, such as the length of the day, seasonal changes in the availability of food resources and the presence of adverse climate (Dingle, 1996). In all the cases the residence status of any species is related to its presence and its breeding behaviour.

The tropical long-nosed bat *Leptonycteris curasoae* Martínez & Villa, is considered an endangered species (USFWS, 1986; SEDESOL, 1994), highly specialized in feeding on floral resources in arid and semiarid environments of North America (Alvarez & González, 1970; Fenton & Kunz, 1977; Humphrey & Bonaccorso, 1979; Koopman, 1981; Heithaus, 1982). Nectar and pollen of columnar cacti, and plants of the genus *Agave* constitute its principal feeding resources (Alvarez & González, 1970; Arita, 1991; Valiente-Banuet *et al.*, 1996, 1997a,b; Arizmendi *et al.* unpublished data). This bat has been considered as a generalized latitudinal migrant, this is, it moves throughout all its distribution range in North America (Humphrey & Bonaccorso, 1979; Arita, 1991; Valiente-Banuet *et al.*, 1996; Koopman, 1981; Cockrum, 1991; Fleming *et al.*, 1993). The literature on *L. curasoae* indicates that migration of this bat may be explained by three main postulates. (1) Bats are forced to migrate during spring to higher latitudes, as far north as the SW of the United States and during fall to lower latitudes in tropical regions of Mexico, in order to find food resources and suitable environmental conditions (Cockrum, 1991; Fleming *et al*., 1993). (2) The migration then is possible because a latitudinal sequential bat-blooming resources occurs along North America (Gentry, 1982; Cockrum, 1991; Fleming *et al*., 1993), and (3) as a consequence of migration, a spring and summer reproduction only occurs in the Sonoran Desert (Howell & Roth, 1981; Cockrum, 1991; Ceballos *et al*., 1997).

Since migration of *L. curasoae* was proposed in 1954 (Cockrum, 1991), it has been widely accepted as a fundamental ecological feature of the species. However, most of the studies have been conducted in the northern regions of its range and little is known about the ecology of the species in tropical Mexico, where the most extensive distributional area occur (Villa, 1967; Hall, 1981; Koopman, 1981; Valiente-Banuet *et al*., 1996) and where floral food resources are abundant throughout the year (Rojas-Martínez, 1996; Valiente-Banuet *et al*., 1996; 1997b).

Evidence of the possible resident status of this bat species in Mexico, has been provided for Sierra de la Laguna, Baja California Sur (Woloszyn & Woloszyn, 1982), and for South-Central Mexico (Valiente-Banuet *et al*., 1996; 1997b). However, these studies have not addressed the magnitude of resident bat populations and its ecological significance in a geographical perspective, as in other bat species (Mccracken *et al*., 1994). Residence might be based in the seasonal availability of food resources promoting local movements among different vegetation units. For example, at the Sierra de la Laguna in Baja California, vegetation is characterized by presenting a mosaic of plant communities including xerophytic shrublands, tropical deciduous forests, and pine-oak forests, which provide food to the bats in different seasons of the year (Rzedowski, 1978; Valiente-Banuet *et al*., 1996), whereas in south-central Mexico, including the Balsas River Basin and the Tehuacán Valley, besides the presence of fifteen vegetation types with abundant chiropterophyllous resources, this zone is considered as a centre of diversification of giant columnar cacti (tribes Pachycereeae and Cereeae) and paniculated agaves (Gentry, 1982; Valiente-Banuet *et al*., 1996; Valiente-Banuet & Arizmendi, 1998).

The purpose of this work is to test the hypothesis that the latitudinal migration of this nectarivorous bat is conditioned by the changes in the seasonal availability of floral resources. If this hypothesis is true, the latitudinal migration can not be regarded as a generalized phenomenon throughout the distribution range of the species, but in terms of the local conditions generated by the resource availability throughout the year producing changes in the biology of each population. We studied (i) the seasonal presence and reproductive condition of *L. curasoae,* at different North American latitudes analysing 94-years of capture records contained in museums (ii) the seasonal availability of bat-floral resources along the distribution of *L. curasoae* and as case studies (iii) the abundance and reproduction of the bats inhabiting a tropical desert in Mexico correlated with the phenology of the plant species used by them, and (iv) the abundance of this bat in an extratropical locality in the Sonoran desert, Mexico during winter and spring, and in a tropical region located in the Pacific coast of Mexico during spring.

METHODS

Geographical analysis

To analyse the distribution for *L. curasoae* in its North American range, we used the data base of Arita & Humphrey (1988) which contains records for a total of twenty-two North American mammal collections (Appendix 1). This data base was complemented with recent information from the Mexican collections: Escuela Nacional de Ciencias Biológicas, IPN (ENCB), Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México (FCUNAM), Instituto de Biología, UNAM (IBUNAM) and Universidad Autónoma Metropolitana, Ixtapalapa (UAM-I). The data analysed represent a 94-years sample, in which species identity has been rigorously revised by Arita & Humphrey (1988) and in Mexico by the authors. Data consisted of capture localities with dates, and reproductive condition considering information on young bats and pregnant or lactating females. Reproduction data were complemented with information obtained from Cockrum (1991) and Rojas-Martínez (1996). Each capture locality was geopositioned using a topographic map 1:1,000,000 (SPP, 1980).

In order to have a geographical pattern of capture records with respect to time of the year, the latitudinal records were plotted against seasons. The purpose was to examine firstly if the latitudinal clustering of capture records have a distributional presence according to the migration hypothesis (i.e. spring and summer presence in the North and absence in the South, and fall-winter presence in the South and absence in the North).

A Geographic Information System IDRISI-Windows V.2. (Eastman, 1997; Jones, 1997) was used to create a 'raster image' with the areas covered with the vegetation types which provide resources for *Leptonycteris curasoae* in North America. These vegetation areas were selected according to the vegetation map of Mexico and south-west U.S.A. (Rzedowski, 1978; Brown, 1982) always with respect to the distribution range of *L. curasoae* (Gentry, 1982; Gibson & Nobel, 1986; Arita, 1991; Valiente-Banuet *et al*., 1996). These vegetation areas included tropical deciduous forests and xerophytic shrublands and their areas were calculated in km^2.

Also we calculated the total surface of the contour of Mexico added with the area of bat resources in the SW of the United States (Howell & Roth, 1981; Gentry, 1982; Gibson & Nobel, 1986; Cockrum, 1991).

Phenological information (time of flowering and fruiting) of the chiropterophyllous plant species of families Agavaceae, Bombacaceae, Bignoniaceae, Cactaceae (tribes Pachycereeae and Cereeae), Convolvulaceae and Leguminosae was obtained from different studies (Rzedowski, 1978; Gentry, 1982; Quiroz *et al*., 1986; Lott, 1993; Valiente-Banuet *et al*., 1996; 1997a; b; Arizmendi *et al*. unpublished data; Appendix 2). Accordingly, phenological information was grouped in spring-summer and fall-winter seasons of blooming to be analysed in a geographical and temporal context.

The temporal presence of bats in North America was analysed making two maps of captures in spring and summer and during fall and winter. The seasonal periods were defined as follows: spring-summer (21 March to 20 September), and fall-winter period with the rest of the year. Localities of capture were rasterized localizing and counting them over vegetation maps.

In order to relate captures along the range of distribution of *L. curasoae* with annual floral resources, a binomial test normal approximation (Fleiss, 1981) was used to compare the observed frequency of bat capture records over area of vegetation that offer floral resources, with a null distribution based on the proportion of captures expected from a random distribution over the territory covered by the vegetation considered. The captures were split into two groups, those which coincided with the area of the vegetation and those which did not. Deviation from the null distribution would suggest a non random distribution of *Leptonycteris curasoae* in terms of vegetation area offering resources.

Considering that *L. curasoae* depends exclusively on floral resources for feeding (Alvarez & González, 1970) we defined three latitudinal ranges in order to represent floral offer conditions according to Rzedowski (1978). First, the extratropical range was located at latitudes higher than 29°N where only spring and summer resources exist (Cockrum, 1991; Fleming *et al.*, 1993). A transitional range including the Northern boundary of the tropical vegetation located between 29° and 21°N, where food availability might be continuous. A third tropical range was located at latitudes lower than 21°N, where floral offer is year-round continuous (Rojas-Martínez, 1996; Valiente-Banuet *et al.*, 1996; 1997b). Each latitudinal area was measured in km^2.

To test if the seasonal captures are associated with the area occupied by the vegetation offering abundant floral resources for bats in each latitude, we applied a χ^2 test. We calculated the expected number of captures in the area of each one of the geographical regions previously defined, by multiplying the proportion that occupies the area of each latitudinal zone (of the total surface that offer resources), by the total seasonal capture dividing by 100. Null hypothesis considered that if a random capture exists, seasonal presence of bats along the distribution should be proportional to the magnitude of the latitudinal area. Standardized residuals were used to analyse the differences between the seasonal captures to each latitudinal region (Greig-Smith, 1983).

Study cases

To verify the capture records at different latitudes, field studies were conducted in the Tehuacán Valley, one locality in the Sonoran desert, and in the Chamela region (Fig. 1).

The Tehuacán Valley is located in South-Central Mexico at 17°48′–18°58′ N and 96°48′–97°43′ W at elevations ranging between 1000 and 1500 m a.s.l. It has been considered to be an important region for conservation of nectar feeding-bats (Rojas-Martínez & Valiente-Banuet, 1996; Valiente-Banuet *et al.*, 1996). The Valley is an isolated arid-semiarid region (10,000 km^2) located in the south-east boundary of the state of Puebla and north-east of the state of Oaxaca. It is considered to be the most tropical arid zone of North America (Rzedowski, 1978).

This region owes its aridity to the rain shadow produced by the eastern Sierra Madre (Smith, 1965). Average rainfall is 495 mm per year, and annual mean temperature of 21 °C, with very rare frosts (García, 1978). The Valley flora is constituted by about 2750 plant species, 30% of them being endemic to the area (Dávila *et al.*, 1993). In the Tehuacán Valley and the Balsas River Basin a total of forty-five columnar cacti species have been reported, and more than the 50% of them show a chiropterophyllous syndrome (Valiente-Banuet *et al.*, 1996). In the northern part of the Valley, columnar cacti produce flowers between spring and summer (Valiente-Banuet *et al.*, 1996). These plants constitutes cacti forests with densities as high as 1800 individuals/ha (Valiente-Banuet *et al.*, 1997a). In the southern part of the Valley, tropical deciduous forests are the most common vegetation type with a significant number of species blooming between fall and winter.

The study site in the Sonoran Desert is located at Rancho San Francisco situated 80 km SE of Hermosillo (28°41′ N and 110°15′ W), at 450 m a.s.l. The vegetation in the site is a thorn scrub dominated by the columnar cacti *Stenocereus thurberi* (Engelm.) Bux., *Pachycereus pecten-aboriginum* Britt. & Rose and *Carnegia gigantea* (Engelm.) Britt. & Rose. Average rainfall is 346 mm per year, and annual mean temperature of 23.3 °C (García, 1978).

The study site in the Chamela Region is located at Isla Pajarera, located in the Chamela Bay at (19°32′N, 105°07′W) at elevations of less of 150 m. The mean annual rainfall in the Estación de Biología, Chamela is 748 mm with 80% falling from July to October, and annual mean temperature of 24.9 °C (Bullock & Solís-Magallanes, 1990). The vegetation in the island is a tropical deciduous forest in which *Pachycereus pecten-aboriginum, Crataeva tapia* (L.) Gaertn., and *Cordia eleagnoides* DC., are the dominant species.

Bat captures in the Tehuacán Valley

We conducted monthly captures of *Leptonycteris curasoae* in five different localities during three years (1994–96) in columnar cacti forests and tropical deciduous forests. Three nets (3 m high, 20 m length) distributed in one ha were opened during all night (1900 to 600 h), by two consecutive nights. To reduce net-avoidance by bats, netting sites were changed each night.

The columnar cacti forests were sampled in two localities of the state of Puebla (1.8 km E Zapotitlán Salinas and 2 km SW San Juan Raya), at altitudes ranging between 1500 and 1700 m a.s.l. The total sampling effort in these sites was of 1812 h-night-net in the spring-summer period and of 648 h-night-net in autumn-winter. Tropical deciduous forest was sampled in three localities San Rafael and Barranca Seca (35 km SE of Tehuacan city) in the state of Puebla and in Chinango, in the state of Oaxaca, at altitudes between 900 and 1100 m a.s.l. The total capture effort was of 576 h-night-net in spring-summer and of 576 h-night-net in autumn-winter.

Bat captures were pooled in two seasonal periods (spring-summer and fall-winter) and the relation bat/(h*night-net)*100 was employed to compare the annual bat permanence in the Tehuacán area. Bats captured were also examined in order to determine their reproductive condition, considering testis

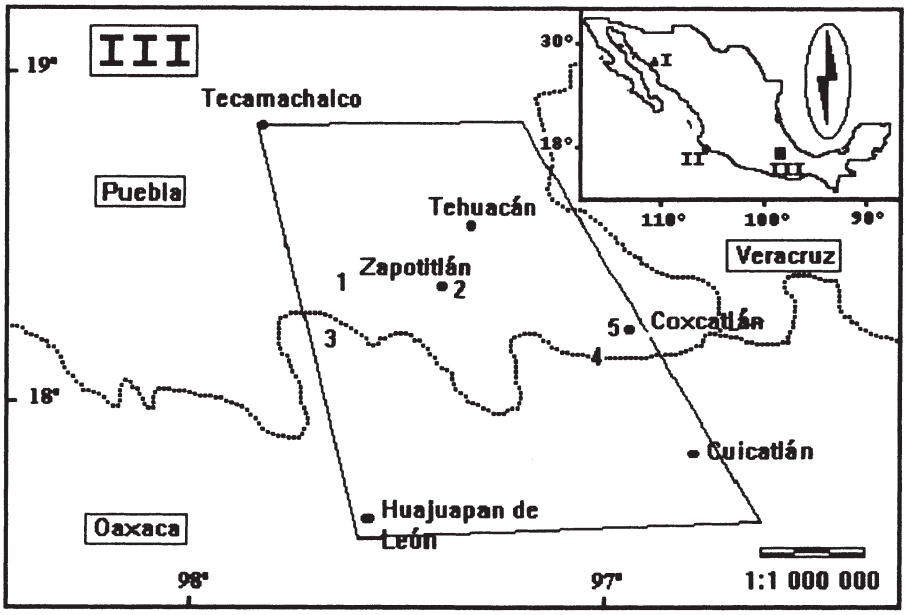

Figure 1 Study site locations. I. – Rancho San Francisco, 80 km SE Hermosillo, Sonora. II. – Isla Pajarera, Chamela, Jalisco. III. – The area of the Tehuacan Valley is delimited by the polygon. The dotted line represent the state boundary between Puebla and Oaxaca. Localities: (1) 2 km SW San Juan Raya. Puebla (2) 1.8 km E Zapotitlán Salinas. Puebla (3) Chinango. Oaxaca (4), Barranca Seca. Puebla (35 Km SE de Tehuacan) (5) San Rafael. Puebla.

position for males and pregnant or lactating conditions for females.

Localities of bat capture were surveyed every month during three years to identify plant species with chiropterophyllous and chiropterocoric syndromes (Faegri & Van der Pijl, 1979; Soriano *et al.*, 1991; Valiente-Banuet *et al.*, 1997b). Presence or absence of flowers and fruits were recorded. Information from the literature (Quiroz *et al.*, 1986; Lott, 1993) was also considered for chiropterophyllous plants present in the Tehuacán and the Balsas River Basin.

Bat captures in the Sonoran Desert

Two capture periods were conducted at this locality. The first sampling was in spring (from 21 to 24 March 1996), during the flowering of *S. thurberi* and *P. pecten-aboriginum*. We used four nets whole night (3 m high, 20 m long), during four nights. Total capture effort was of 192 h/night-nets. A second sampling was conducted in winter (from 3 to 6 February 1998). Five nets were used for the whole night (3 m high, 20 m long) during four nights in the flowering time of *P. pecten-aboriginum*. Capture effort was of 240 h/night-net.

Bat captures in the Chamela region

One sampling period was conducted at the beginning of the spring season (from 20 to 22 March 1998) during the flowering time of *Pachycereus pecten-aboriginum*. A total of five nets were used for the whole night (3 m high, 20 m long), during three nights. Capture effort was of 165 h/night-net.

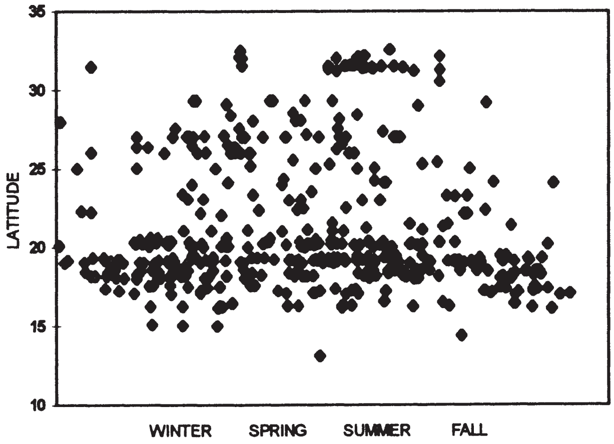

Figure 2 Location of 94-years capture records of *Leptonycteris curasoae*, with respect to latitude and season of the year obtained from twenty-two North American collections ($N = 1881$ capture records). Spring–summer period embraces between 21 March and 20 September and fall–winter period embraces the rest of the year.

RESULTS

Geographical analysis

Geographic captures of *L. curasoae* along its range of distribution (Fig. 2), showed a spring-summer bat presence in latitudes above 29°N and scarce records during fall and winter; an almost continuous capture pattern in the transitional region

Table 1 Seasonal capture localities of *Leptonycteris curasoae* in three latitudinal regions that offer floral resources. Data obtained from twenty-two North American collections ($N=319$ capture localities). Upper left numbers are observed localities, numbers in parenthesis are expected localities. Numbers in italics are standardized residuals. *Standardized residuals>1.9 are significant, $\chi^2=262.76$, d.f. $=5$, $P<0.001$.

Region	Fall–Winter	Spring–Summer
Extratropical (> 29°N)	1 (33.02)	10 (60.19)
264637.16 km^2	*−5.63**	*−4.53**
Transitional (21° to 29°N)	18 (44.6)	63 (81.31)
357457.63 km^2	*−1.94**	*−3.17**
Tropical (< 21°N)	94 (35.38)	133 (64.5)
283581.30 km^2	*+10.64**	*+9.30**

Table 2 Numbers of female reproductive records along the range of distribution of *Leptonycteris curasoae* obtained from twenty-two North American collections ($N=1801$ records) and literature review. Information in parenthesis indicates the number of localities (see Appendix 3).

Latitudinal region	Reproduction signs	Season	
		Fall–Winter	Spring–Summer
Extratropical	Pregnant	–	8 (4)
	Lactating	–	5 (4)
(> 29°N)	Young	1 (1)	22 (14)
Transitional	Pregnant	2 (2)	22 (7)
	Lactating	–	5 (2)
(21°N to 29°N)	Young	–	27 (8)
Tropical	Pregnant	10 (8)	11 (8)
	Lactating	3 (2)	–
(< 21°N)	Young	12 (4)	6 (4)

(between 21°N and 29°N) and a year-round presence in regions below 21°N. Therefore, the number of captures is differentially distributed throughout the year and with respect to the latitude ($x^2=262.76$, d.f. $=5$, $P<0.001$; Table 1). Standardized residuals were significant in the three zones, being the tropical (below 21°N), the area containing a higher annual proportion of captures than expected, and the two other regions with lower number of captures than expected by random.

We identified a total of eighty-four plant species offering floral resources to *L. curasoae* along its range of distribution in North America (Table 3; Appendix 2). The geographical captures of *L. curasoae* are positively associated with the geographical area of the vegetation that offers floral resources (binomial test $Z=337.79$, $P<0.001$, $n=460$). Therefore, captures of *L. curasoae* during spring-summer coincide with all the known area of its distribution in North America (Fig. 3). In these seasons columnar cacti (tribes Pachyceereae and Cereeae) and agaves provide floral resources to the bats. During the fall-winter period, capture area is reduced and is practically restricted to the Mexican territory (Fig. 4). Geographically the records are grouped mainly to the Pacific Slope of Mexico and the Balsas River Basin that coincide with the area of distribution of the tropical deciduous forests in Mexico.

Pregnant and lactating female records were found in the three latitudinal regions analysed. However in the tropics, two reproductive events were detected during spring-summer and fall-winter seasons (Table 2; Appendix 3).

Study cases

In the Tehuacán Valley and the Balsas River Basin, thirty-four chiropterophyllous plant species can offer floral food resources throughout the year (thirteen offer only flowers, four only fruits and seventeen both flower and fruits) (Table 3). Twenty-two plant species are cited by first time as chiropterophyllous plants, seventeen of them are columnar cacti and five are agaves.

Most species offer food resources for bats between March and August. In this period seventeen types of flowers and fourteen fruit species may be simultaneously offered to the bats. Low resource offer occurs during fall-winter.

Leptonycteris curasoae was captured year-round in the Tehuacán Valley (Table 4), being more abundant during the months of spring–summer. During winter, the species is scarce in the cacti areas, but in the tropical deciduous forest bats showed an annual continuous presence. A total of ninety-nine males and forty-six females were caught (Table 5). Females were not captured during fall. Evidence of reproduction was observed in males and females between March and June. A second period was represented only by males with scrotal testis in the fall.

Bat captures conducted in the Sonoran Desert, confirmed a low presence of *L. curasoae* in early February in high latitudes *c*. 29°N (one female, 0.41 bats/(h* night-net)*100). Late march captures were low with three females (1.56 bats/(h* night-net)*100), two of them pregnant.

Bat captures in the Chamela region indicated an abundant presence of *L. curasoae* within the tropics with 47.88 bats/(h*night-net)*100 during spring. One pregnant, four inactive females and seventy-four males were captured.

DISCUSSION

A complete generalized latitudinal migration of *Leptonycteris curasoae*, has been extensively accepted without knowing the magnitude of geographical migration, and assuming a seasonal bat permanence in tropical Mexico (Cockrum, 1991; Fleming *et al*., 1993; Wilkinson & Fleming, 1996). The analysis of 94 years of capture records questions the existence of a generalized bat migratory behaviour in North America. Rather, the results suggest a seasonal extra-tropical region with migratory bat populations at latitudes above 29°N, and one intertropical region with annual continuous bat-presence at latitudes below 21°N. Although the fall-winter absence of *L. curasoae* in high latitudes can be related to differences in the capture effort throughout its distribution, Cockrum (1991) have documented the seasonally absence of *L. curasoae* in the north-western part of its distribution (Arizona, Nuevo Mexico, Sonora, and Chihuahua). According to an exhaustive revision

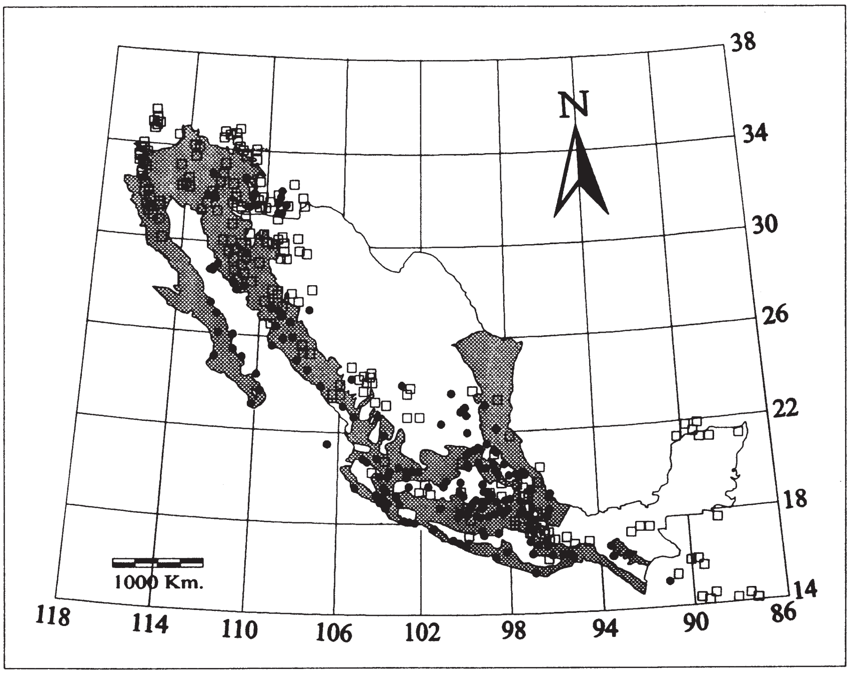

Figure 3 Capture records of *Leptonycteris curasoae* in Mexico and SW United States during spring and summer over 94 years. The dashed area corresponds to the distribution of chiropterophyllous columnar cacti. Squares indicate the distribution of agave species blooming during spring and summer (*Agave angustifolia, A. applanata, A. chrysantha, A. deserti, A. durangensis, A. flexispina, A. fortiflora, A. karwinskii, A. kerchovei, A. macroacanta, A. palmeri*).

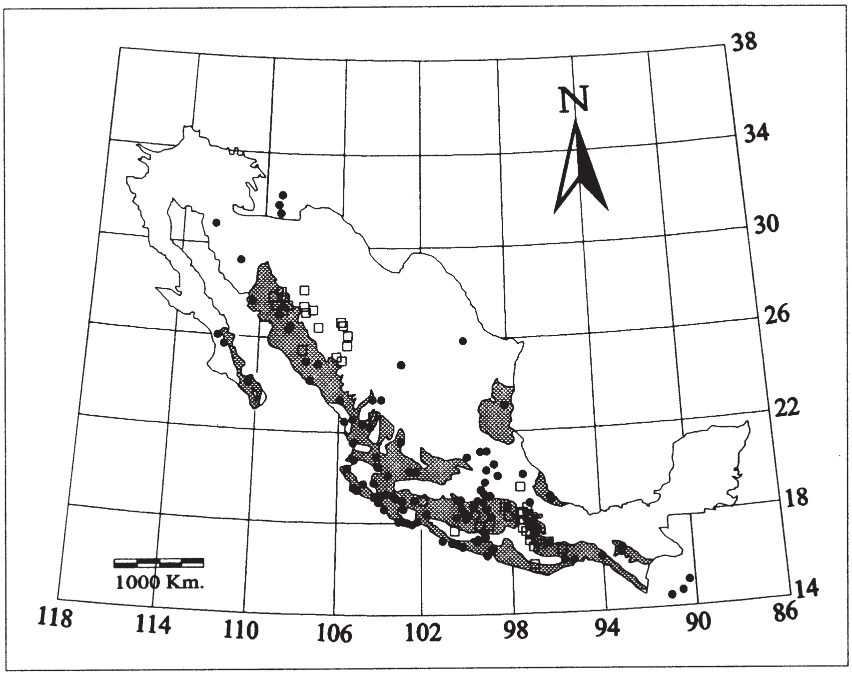

Figure 4 Capture records of *Leptonycteris curasoae* in Mexico and SW United Sates during fall and winter. The dashed area corresponds to the tropical deciduous forest distribution in Mexico with floral resources available in this period, and squares indicate the distribution of agave species flowering during fall and winter (*Agave colorata, A. marmorata, A. peacookii, A. potatorum, A. wocomahi*).

Table 3 Flower and fruiting phenology of thirty-four bat plants in the South Central Mexico. Flowers are indicated by thin lines, fruits are indicated by bold lines.

Plant species	J	F	M	A	M	J	J	A	S	O	N	D
Agave macroacanta Zucc.					—	—	—	—				
Agave marmorata Roezl.		—	—	—								
Agave karwinskii Zucc.						—	—	—	—			
Agave kerchovei Lem.								—	—	—	—	—
Agave peacocki Croucher.		—	—									
Agave potatorum Zucc.	—	—										
Ceiba aesculifolia (Kunth) Britt. & Baker	—	—	—	—	—						—	
Ceiba parvifolia Rose	—	—									—	—
Cephalocereus columna-trajani (Weber) Schuman				—	— ━	— ━	━					
Cephalocereus purpusii Britt. & Rose			—	—	—	— ━	— ━	— ━	— ━			
Escontria chiotilla (F.A.C. Weber) Rose				━	━	━	━	━				
Hylocereus undatus (Haw.) Britt. & Rose						—	— ━	— ━	━			
Ipomoea arborescens G. Don.	—	—								—	—	
Myrtillocactus geometrizans (C. Martius) Console	—	— ━	— ━	— ━	— ━	— ━	— ━	━				
Neobuxbaumia macrocephala (Weber) Dawson					━	━	━	━				
Neobuxbaumia mezcalaensis (Bravo) Backeb.				—	— ━	— ━						
Neobuxbaumia tetetzo (Weber) Backeb.				—	— ━	— ━						
Pachycereus fulviceps (Weber) Backeb.					—	— ━	— ━	— ━				
Pachycereus hollianus (Weber) Buxb.			—	—	— ━	— ━	— ━	— ━	— ━	— ━	—	—
Pachycereus pecten-aboriginum Britt. & Rose		—	—	—								
Pachycereus weberi (Coulter) Backeb.	— ━	— ━	— ━	— ━	— ━						—	— ━
Parmentiera edulis D. C.			—	—	—	—	—	—	—	—	—	—
Pilosocereus chrysacantus (Web) Britt. & Rose	—	—	—	— ━	— ━	━						
Polaskia chende (Gosselin) A. Gibson & K. Horak					━	━						
Polaskia chichipe (Gosselin) Backeb.					━	━	━					
Pseudobombax ellipticum H. B. K.	—	—	—	—							—	—
Stenocereus chrysocarpus Sanchez-Mejorada						—	— ━	━				
Stenocereus dumortieri (Scheidw.) Buxb.		—	—	— ━	— ━	━						
Stenocereus fricii Sanchez-Mejorada						—	—	━				
Stenocereus marginatus (D.C.) Berger & Buxb.			━	━	━							
Stenocereus pruinosus (Otto) Buxb.	— ━	— ━	— ━	— ━	— ━					—	— ━	— ━
Stenocereus standleyi (Gonzalez-Ortega) F. Buxb.						—	— ━	— ━	— ━			
Stenocereus stellatus (Pfeiffer) Riccob.				—	—	— ━	— ━	— ━	— ━	━		
Total Flowers	9	11	13	16	16	15	13	10	7	5	8	9
Total Fruits	2	3	4	8	14	13	12	2	5	2	1	2

Table 4 Seasonal captures of *Leptonycteris curasoae* in the cacti forests and in the tropical deciduous forests in the Tehuacán Valley, Mexico (1994–96. $N = 145$).

Vegetation	Fall–Winter	Spring–Summer
Cacti forest	1	93
Bat/(h*night-net) * 100 index	0.15	5.13
Tropical deciduous forest	16	35
Bat/(h*night-net) * 100 index	2.77	6.07

Table 5 Reproductive condition of *Leptonycterus curasoae* in the Tehuacán Valley (1994–96, $N = 145$).

Reproductive signs	Winter	Spring	Summer	Fall
Males				
Abdominal testis	1	36	12	3
Testis in scrotum	1	33	7	6
Females				
Inactive	4	21	9	0
Pregnant	2	9	0	0
Lactating	0	1	0	0
Total	8	100	28	9

conducted by him, embracing a 58-years period of published and unpublished data, as well as field notes including information about the seasonal occupation in caves, availability of floral resources, and collectors, he concluded that *L. curasoae* is absent during winter at these latitudes. Our results obtained by the samplings accomplished by us in the Sonoran Desert, the Chamela region and in the South Central Mexico, support a seasonal bat presence and a latitudinal migration only in the northern limit of the distribution of this nectarivorous bat.

At the same time, sequential blooming that may provide a space-temporal predictable nectar corridor, proposed to explain the mechanisms that may be used by bats to move throughout

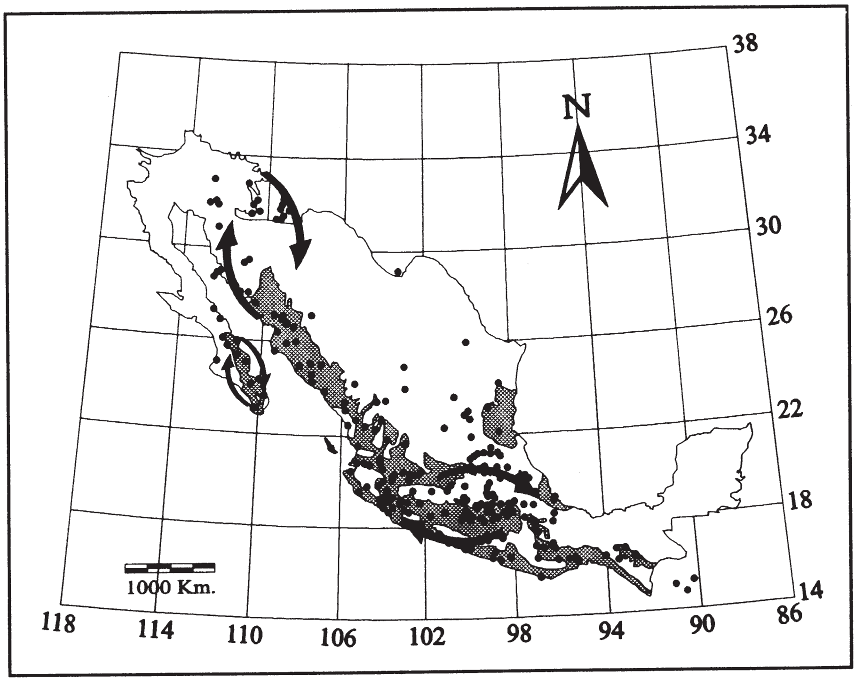

Figure 5 North American distribution of *Leptonycteris curasoae* capture records (dots; $N = 1881$ records in 460 localities). The dashed area corresponds to vegetation zones with chiropterophyllous floral resources available throughout the year. Arrows indicate the geographical movements proposed in this study and by Fleming *et al.* (1993) for Baja California.

their latitudinal distribution is not clear when the total phenological information is analysed (Valiente-Banuet *et al.*, 1996; this study). Columnar cacti and agave blooming has been proposed as a principal element of this process (Howell, 1974; Gentry, 1982; Arita, 1991; Fleming *et al.*, 1993; Fleming *et al.*, 1996), however, the geographical examination of columnar cacti that bloom in North America, does not support the notion of a sequential latitudinal phenology for these plants, because they bloom almost synchronically in spring along the bat distributional range (Valiente-Banuet *et al.*, 1996).

The presence of *Leptonycteris curasoae* during spring and summer corresponds with the totality of the distributional area known for this bat in North America, which also is closely related to the geographical area of blooming columnar cacti and twelve *Agave* species, extensively distributed in Mexico (Rzedowski, 1978; Gentry, 1982; Valiente-Banuet *et al.*, 1996). During fall and winter, columnar cacti, high density of different species of the genus *Agave* and many species of trees in the tropical deciduous forests offer food resources to the bats (Alvarez & González, 1970; Hevly, 1979; Quiroz *et al.*, 1986; Fleming *et al.*, 1993). In this part of the year bat captures in North America are restricted to the areas of distribution of the tropical deciduous forests in the Pacific coast of Mexico and Central Mexico including the Balsas River Basin and the Tehuacán Valley.

In the Tehuacán Valley, year-round capture of bats was observed. Here, columnar cacti, agaves and species of the tropical deciduous forest have a continuous distribution and offer continuous annual food resources for bats (Rojas-Martínez, 1996; Valiente-Banuet *et al.*, 1996). Under these conditions, altitudinal bat movements ranging from 900 to 1700 m a.s.l., rather than latitudinal migration may be enough to find floral food resources throughout the year (Valiente-Banuet *et al.*, 1996; Herrera, 1997). Therefore we propose that the contiguous position of xerophytic shrublands dominated by columnar cacti and agaves, as well as tropical deciduous forests, is the condition to maintain *L. curasoae* populations throughout the year (Fig. 5). This condition occurs also for the Sierra de La Laguna in Baja California Sur where *L. curasoae* has been reported as resident (Woloszyn & Woloszyn, 1982).

Additional evidence of year round bat presence in the Tehuacán Valley, is supplied by pollination studies of columnar cacti species which indicate that bats are the sole pollinators of the densest columnar cacti that bloom during spring-summer such as *Neobuxbaumia tetetzo, N. macrocephala* and *N. mezcalaensis* (Valiente-Banuet *et al.* 1996, 1997a) or during Fall–Winter; *Pachycereus weberi* and *Pilosocereus chrysacanthus*. (Valiente-Banuet *et al.*, 1997b). The high specialization to bat pollination observed in most of the tropical columnar cacti in Mexico and Venezuela (Valiente-Banuet *et al.*, 1996; 1997b; Nasar *et al.*, 1997) might be a plant response to a stable and continuous pollinator coexistence in the arid tropics, which only may occur if the patterns of this mutualistic relationship are predictable through time as a condition to ensure mutual beneficial relationship (Wolf & Stiles, 1989).

The high fruit set shown by these cacti species, the continuous captures of *L. curasoae* and the cacti pollen loads obtained from the bodies (Arizmendi; unpublished data), are all evidences that this bat is consuming the pollen of local species allowing its permanence throughout the year in South Central Mexico (Valiente-Banuet *et al*., 1996; Valiente-Banuet *et al*., 1997a,b). Also, a total of thirty-four plant species were identified as chiropterophyllous, offering flowers and fruits sequentially in space and time to *L. curasoae*. This bat species can be considered as a sequential specialist that moves altitudinally to obtain food (Howell, 1974; Heithaus, 1982; Cockrum, 1991; Sosa & Soriano, 1993). Considering its high capacity of long-distance flight (Sahley *et al*., 1993) these movements are possible. By analysing faeces of the long-nosed bat in the Tehuacan Valley (Rojas-Martínez *et al*. unpublished data), the seeds of seventeen species of columnar cacti fruits consumed by this bat were identified indicating that the fruits of these cacti are important food resources for *L. curasoae* in dry Central Mexico. Fruit as a food has been commonly considered to be of low importance for Glossophaginae bats (Howell, 1974; Gardner, 1977); however, different studies have reported that cactus fruits are crucial seasonal resources for *Glossophaga longirostris* and *Leptonycteris curasoae* (Soriano *et al*., 1991; Sosa & Soriano, 1993; Fleming & Sosa, 1994).

According with the results of this study, latitudinal migration of *L. curasoae* appears to occur only in the northern region out of the limit of the tropical deciduous forest, and where resources are not produced throughout the year. Considering this, we propose that probably bat populations migrate only from the xerophytic shrublands of Arizona and New Mexico (USA) to the tropical deciduous forest of Sinaloa, Mexico (Fig. 5), as it has been proposed by Arita & Martínez del Río (1990). In this context, a low gene flow may occur between extratropical and intertropical regions as has been observed by Wilkinson & Fleming (1996), who detected two geographical clades in levels of mtDNA of *L. curasoae*, with a high 3% sequence divergence between bats of Northern and Southern roost sites in North America.

L. curasoae is considered to be an endangered species in North America, due to the decreasing numbers observed in populations of the south-west of the United States and the lack of knowledge of this bat in Mexico (SEDESOL, 1994; USFWS, 1986). However, environmental conditions observed in South Central Mexico do not support this status, because it was assigned only with information from the Northern part of the distribution of the species, and not considering the tropics (Cockrum & Petryzyn, 1991; Hoyt *et al*., 1994).

In short, our results strongly suggest that only a partial view of the biology of *L. curasoae* has been considered to propose a generalized migration pattern. If the residence status of a migratory species implies breeding behaviour, the occurrence of two reproductive events of *L. curasoae* in South-Central Mexico as well as its year round presence, we argue that there are not insights of a generalized latitudinal migratory pattern of this bat species in North America.

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Appendix 1. Mammal collections consulted to obtain *Leptonycteris curasoae* información.

American Museum of Natural History (AMNH); Escuela Nacional de Ciencias Biológicas, IPN, México (ENCB); Museo de Zoología, Facultad de Ciencias, UNAM (FCUNAM); Field Museum of Natural History (FMNH); Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM); Museum of Natural History, University of Kansas (KU); Natural History Museum of Los Angeles County (LACM); Louisiana State University Museum of Zoology (LSUMZ); Museum of Comparative Zoology, Harvard University (MCZ); Museum of the High Plains, Fort Hays State University (MHP); Museum of South-western Biology, University of New Mexico (MSB); The Museum, Michigan State University (MSU); Midwestern State University (MWSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Stovall Museum, University of Oklahoma (OU); Texas Cooperative Wildlife Collection, Texas A & M University (TCWC); The Museum, Texas Tech University (TTU); Department of Ecology and Evolutionary Biology, University of Arizona (UA); Universidad Autónoma Metropolitana, Iztapalapa, México (UAM-I); Northern, Bird and Mammal Collection, University of California, Los Angeles (UCLA); Museum of Zoology, University of Michigan (UMMZ); United States National Museum, Washington (USNM).

Appendix 2. List of chiropterophyllous plants that offer floral and fruit resources to *Leptonycteris curasoae* in North America.

Spring–summer blooming: (Howell, 1979; Howell & Roth, 1981; Gentry, 1982; Quiroz *et al*., 1986; Martínez del Río & Eguiarte, 1987; Cockrum, 1991; Fleming *et al*., 1993; Lott, 1993; Valiente-Banuet *et al*., 1996; 1997a,b)

Agavaceae: *Agave applanata* Koch ex Jacobi, *A. colourata* Gentry, *A. chrysantha* Pebles, *A. desertii* Engelm, *A. flexispina* Trel., *A. fortidens*, *A. fortiflora* Gentry, *A. karwinskii* Zucc., *A. macroacanta* Zucc., *A. marmorata* Roezl., *A. parryi* Engelm, *A. salmiana* Otto & Salm-Dyck, *A. schottii* Engelm. Bombacaceae: *Crecentia alata*. Cactaceae: *Carnegiea gigantea* (Engelm.) Britt. & Rose, *Neobuxbaumia mezcalaensis* (Haworth) Buxb., *N. macrocephala* (Web.) Dawson, *N. mezcalaensis* (Bravo) Backeb., *N. sanchez-mejorada*, *N. scoparia* (Poselberg) Backeb., *N. tetetzo* (Web.) Backeb., *Pachycereus fulviceps* (Web.) Backeb., *P. hollianus* (Web.) Buxb., *P. pringlei* (Watson) Britt. & Rose, *Polaskia chende* (Gosselin) Gibson & Horak, *P. chichipe* (Gosseline) Backeb., *Stenocereus chrysocarpus* Sánchez-Mejorada, *S. fricii* Sánchez-Mejorada, *S. griseus* (Haw.) Buxb., *S. gumosus* (Engelm) Gibson & Horak, *S. montanus* (Britt. & Rose) Buxb., *S. standleyi* (González-Ortega) Buxb., *S. stellatus* (Pfeiffer) Riccob, *S. thurberi* (Engelm) Buxb., *S. treleasi* (Vaupel) Backeb.

Fall–winter-blooming: (Alvarez & González, 1970; Gentry, 1982; Heithaus, 1982; Quiroz *et al*., 1986; Eguiarte & Búrquez, 1987; Fleming *et al*., 1993; Valiente-Banuet *et al*., 1996).

Agavaceae: *Agave angustifolia* Haw, *A. durangensis* Gentry, *A. kerchovei* Lem, *A. peacokii* Lem, *A. peacokii* Croucher, *A. potatorum* Zucc., *A. shrevei* Gentry, *A. tequilana* Web., *A. wocomahi* Gentry, *Manfreda brachistachya*. Bignoniaceae: *Parmentieria edulis* D.C. Bombacaceae: *Pseudobombax ellipticum* H.B.K., *Ceiba aesculifolia* (H.B.K.) Britt. & Rose, *C. parvifolia* Rose, *C. pentandra* (L.) Gaertner, *C. acuminata* (Watson) Rose. Cactaceae: *Backebergia militaris* (Audot) Bravo & Sánchez-Mejorada, *Myrtillocactus cochal* (Orcutt) Britt. & Rose, *M. geometrizans* Console, *Neobuxbaumia polylopha* (DeCandolle) Backeb., *Pachycereus grandis* Rose, *P. pecten-aboriginum* Britt. & Rose, *P. weberi* (Coulter) Backeb., *Pilosocereus auricetus*, *P. brasilensis*, *P. chrysacantus* (Web.) Britt. & Rose, *Pterocereus foetidus* McDougall & Miranda, *Rathbumia alamosensis* (Coulter) Gibson & Horak, *Stenocereus benekei* (Enrbr.) Buxb., *S. dumortieri* (Scheidw.) Buxb., *S. eichlamii* (Britt. & Rose) Buxb., *S. marginatus* Berger & Buxb., *S. pruinosus* (Otto) Buxb., *S. queretaroensis* (Web.) Buxb. *S. quevedonis* Convolvulaceae: *Ipomoea arborescens* G. Don. Leguminoseae: *Bauhinia ungulata*

Appendix 3. Localities of reproductive records, housed in twenty-two North American mammal collections.

Extratropical region. WINTER. Arizona: Cochise Co., Bucklew Cave, 13 mi N Portal, 1 young, 25-Jan-72 (MMSU). SPRING. Arizona: Pinal Co., Organ Pipe National Monument, 1 pregnant female, 24-Apr-82 (UA), 1 young, 28-Jun-79 (UA). Pinal Co., Picacho Peak, 45 mi N Tucson, 1 lactating females, 13-May-60, (UA). Pinal Co., Saguaro National Monument, 1 pregnant female, 12-May-67 (UA). Sonora: Cueva del Tigre, 14.9 mi SE Carbo, 2 pregnant females, 11-Apr-58 (UA). Tesia between Navojoa and Camoa, 4 pregnant females, 17-Apr-56 (AMNH). Minas Nuevas, 4 mi NW Alamos, 2 lactating females, 29-May-81 (TTU). SUMMER. Arizona: Pima Co., Colosal Cave, 30 mi SE Tucson, 1 lactating female, 3-Jun-1966 (UA). Pima Co. Alamo Canyon, 1 young, 10-Jul-79 (OPCNM). Cochise Co., Bucklew Cave, 13 mi N Portal, 2 young, 28–8–68 (UA). Cochise Co., 1 mi N Paradize, 5200 ft, 6 youngs, 14-Aug-55 (UA). Cochise Co., 17 mi S San Simón, Bucklew Cave, 1 young, 6-Aug-57 (UA). Pinal Co., Picacho Peak, 45 mi N Tucson, 1 young, 25-Aug-55 (UA). Pinal Co., Saguaro National Monument, 1 young, 24-Aug-60 (UA). Maricopa Co., Phoenix, 1 young, 30-Aug-63 (UA). Graham Co., Gillespine Was, 25 mi N Higway 266 (Stockton Pass Road), 1 young, 20-Sep-86 (UA). Nuevo Mexico: Co., Guadalupe Canyon Peloncillo Mountais, 1 young, 11-Aug-62 (MHP). Hidalgo Co., creek in Clenton Canyon. T325, R21W, s 17, 1 young, 11-Aug-62 (MSB). Sonora: Cueva del Tigre, 14.9 mi SE Carbo, 1 lactating female, 19-Jul-60 (UA). Minas Armolillo, 6 mi NW Alamos, 1 young, 24-Jul-71 (MVZ). El Tigre Mountains, Santa Maria mine, 3 youngs, 6-Aug-35 (UMMZ). 25 mi N Hermosillo, 1 young, 8-Aug-60 (TCWC).

Transitional region. WINTER. Sinaloa: 20 km W pericos, 1 gestant female, 27-Feb-60 (LACM). SRING. Baja California Sur: 1.3.mi SW Comondu, 1 gestant female, 18-apr-79 (USNM). 1 mi E San Antonio, 8 youngs, 20-May-48 (MVZ). — mi S Mulege, 4 gestant females, 4-May-48 (MVZ). Cerro del Elote, 4 youngs, 7-Jun-48 (MVZ). Sinaloa: 1 mi N, 5 mi E San Miguel, 1 young, 20-Jun-55 (KU). Sonora: Bahia San Carlos, N Guaymas, 1 gestant female 27-Mar-59 (UA). La Aduana, 1 gestant female, 9-Apr-58 (LACM). 11 mi NNE San Jose de Guaymas, 100 ft., 4 lactating females, 22-May-51 (AMNH). Isla Tiburon, Tecomate, 2 young, 20-Jun-80 (MSB). SUMMER: Baja California Sur: 2 mi W Santa Rosalia, 7 youngs, 30-Jun-48 (MVZ). 3 mi W Santa Rosalia, 1 lactating female, 30-Jun-48 (MVZ). San Luis Potosi: 2 km E El Custodio, 1100 m, 1 young, 23-Aug-71 (ENCB). Puebla: Cueva de Las Vegas, 1 gestant female, Sep-86 (Medellín y López 1986). Sinaloa: 6 km SW San Blas, 30 ft., 4-Aug-62, 1 young, Sep-86 (KU). Sonora: Bahia de San Carlos, N of Guaymas, 1 gestant female, 23-Jun-60 (LACM). 1 mi S, 7.6 mi E Vicam, 2 youngs, 25-Aug-63 (UA). Tamaulipas: 6.5 mi N, 13 mi W Jimenez, 1250 m, 13 gestant females, 27-Aug-61 (KU). FALL. Sinaloa: El Dorado, 1 gestant female, 13-Nov-57 (KU).

Tropical region. WINTER. Estado de México: Zacazonapan, 2 youngs, 20-Jan-68 (IBUNAM). 15 km S, 10 km E Amatepec, 860 m, 2 youngs, 6-Feb-80 (ENCB). Guerrero: Mexicapan, 4.3 km N Teloloapan, 7 youngs, 27-Feb-65 (IBUNAM). Jalisco: Francisco Villa, 1 gestant female, 3-Feb-73 (IBUNAM). Michoacán: km 258 carretera Uruapan-Playa Azul, 1 gestant female, Feb-82 (Rojas-Martínez, personal observation). Oaxaca: Tequisistlán, 1 young, 9-Mar-69 (MVZ). SPRING. Guerrero: 8 km SW Teloloapán, 1 young, 23-Mar-70 (IBUNAM). Cueva de la Cruz, 2 youngs, 24-Mar-70 (IBUNAM). Oaxaca: 6 mi NW Mixtequilla, 1 young, 6-May-60 (TCWC). SUMMER. Distrito Federal: Cerro Tehutli, 2.8 mi NNW Milpa Alta, 2600 m, 3 gestant females, 19-Aug-57 (MCZ). Estado de México: Tultitlán, 1 gestant females, 14-Aug-69 (IBUNAM). Guerrero: 10 km S Mezcala, 2 youngs, 2-Aug-69 (KU). Gruta de Juxtlahuaca, 4 mi E Colotlipa, 3200 ft, 1 gestant female, 27-Aug-82 (IBUNAM). Michoacán: Lake Patzcuaro, Island of Janitzio, 2 gestant females, 26-Aug-57 (MCZ). Querétaro: 2.5 km N, 5.7 km E Tequisquiapan, 1 gestant female, 14-Aug-83 (ENCB). Morelos: 3.4 km S Tequesquitengo, 1 gestant female, Sep-66 (Villa, 1967). Tequesquitengo, 1 gestant female, Sep-66 (Villa, 1967). Cueva del Cerro, 1 km S, Lago de Tequesquitengo, 1 gestant female, 7-Sep-66 (IBUNAM). FALL. Estado de México: Puerta de Santiago, 1 gestant female, Nov-66. (Villa, 1967). 3 km S Puerta de Santiago, 1 gestant female, Dec-66 (Villa, 1967). Guerrero: Arroyo Alcholoya, 7 km N Teloloapan, 1 gestant female, 7-Nov-59 (IBUNAM). 58 km NW de Tecpan, 1 gestant and 2 lactating female, Dec-86 (Quiroz *et al*., 1986). Palo Blanco, 3 gestant females, Dec-82 (Rojas-Martínez, personal observation). 4 km N, 8 km e Petacalco, 1 lactating female, 15-Dec-79 (ENCB). Veracruz: 3 km W Boca del Rio, 25 ft., 1 gestant female, 4-Nov-62 (IBUNAM).

BIOSKETCHES

This study constitutes part of the PhD thesis work of **Alberto Rojas-Martínez** who has been analysing the biology of the nectar-feeding bat *Leptonycteris curasoae* for six years in dry-tropical Mexico. The ecology of this bat and its role on the pollination and seed dispersal of giant columnar cacti in Mexico, constitute one of the research programs of the Community Ecology Laboratory at the Instituto de Ecología, UNAM, which is currently directed by **Alfonso Valiente-Banuet**. **Ariel Alacantara** is a PhD student working with Geographical Information Systems in the same laboratory. **María del Coro Arizmendi** is a research ecologist at UBIPRO, ENEP-Iztacala, UNAM working with birds and bats feeding interactions in central Mexico, and **Héctor Arita** is a mammalogist working at the Instituto de Ecología, UNAM, interested in the ecology and biogeography of bats.