

This article was downloaded by: [University of Bath]

On: 13 February 2014, At: 11:03

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tnah20>

Food habits of the threatened bat *Leptonycteris nivalis* (Chiroptera: Phyllostomidae) in a mating roost in Mexico

Ragde Sánchez ^a & Rodrigo A. Medellín ^a

^a Instituto de Ecología , Universidad Nacional Autónoma de México , Ciudad Universitaria, México, D.F., Mexico

Published online: 02 Dec 2010.

To cite this article: Ragde Sánchez & Rodrigo A. Medellín (2007) Food habits of the threatened bat *Leptonycteris nivalis* (Chiroptera: Phyllostomidae) in a mating roost in Mexico, *Journal of Natural History*, 41:25-28, 1753-1764, DOI: [10.1080/00222930701483398](https://doi.org/10.1080/00222930701483398)

To link to this article: <http://dx.doi.org/10.1080/00222930701483398>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

Food habits of the threatened bat *Leptonycteris nivalis* (Chiroptera: Phyllostomidae) in a mating roost in Mexico

RAGDE SÁNCHEZ & RODRIGO A. MEDELLÍN

Instituto de Ecología, Universidad Nacional Autónoma de México, Ciudad Universitaria, México, D.F., Mexico

(Accepted 29 May 2007)

Abstract

The objective of this study was to collect and present data on the food plants that a vulnerable migratory nectarivorous bat, *Leptonycteris nivalis*, used during its seasonal stay at a cave in Tepoztlan, Mexico. This cave is the only mating roost known for this species. Pollen grains from faeces and fur were examined. Little is known about the diet of this bat, especially in the southern half of its distribution. Pollen belonging to 10 plant species was found from five families: Cactaceae (*Stenocereus beneckeii*), Bombacaceae (*Ceiba aesculifolia*, *Pseudobombax ellipticum*), Convolvulaceae (*Ipomoea arborescens*), Fabaceae (*Calliandra houstoniana*, *Bauhinia unguolata*), and Amaryllidaceae (*Agave dasylirioides*, *A. horrida*, *A. inaequidens*, *A. salmiana*). Bats showed the highest dietary diversity in November. There were no significant differences in diet between sexes. Of the four *Agave* species, two have paniculate inflorescences that are commonly attributed to bat pollination, while the other two had spicate inflorescences, which are considered to be primarily insect-pollinated.

Keywords: Chiroptera, conservation, food habits, *Leptonycteris nivalis*, nectarivorous bats

Introduction

Leptonycteris nivalis (Saussure, 1860) is one of the largest nectarivorous bats (Hensley and Wilkins 1988), attaining a body mass of up to 24 g. Its distribution ranges from south New Mexico and west Texas (USA) to south Mexico and Guatemala (Simmons 2005). Although their migration ecology is not well understood, preliminary evidence suggests that females remain in south-central Mexico during the mating season, between September and February (autumn to winter). In early spring (March), pregnant females apparently depart for northern areas to establish maternity roosts; at the end of summer, the young are weaned, maternity roosts disband, and adults and young bats migrate back toward south-central Mexico (Téllez 2001).

Authors have studied certain aspects of the diet of *L. nivalis* mostly in the northern part of its distribution (Álvarez and González 1970; Easterla 1972; Gardner 1977; Hevly 1979; Moreno-Valdez et al. 2004). Also, there is some indirect information on its diet, as a result

of pollination system studies (i.e. Schaffer and Schaffer 1977; Eguiarte et al. 1987; Valiente-Banuet et al. 1997a, 1997b; Arizaga et al. 2000; Slauson 2000). However, in the southern and central part of its distribution there is little information about the diet of *L. nivalis*. There is no information on the diet of bats inhabiting Cueva del Diablo, Morelos, Mexico, which is the only mating roost known for this bat (Téllez 2001). Because the energy requirements of female bats increase during reproduction and lactation periods, it is feasible that their diets may differ from those of males during such periods (Kunz and Nagy 1988; Racey and Entwistle 2000). Indeed, several studies have suggested differences in food requirements between male and female nectarivorous bats (Sánchez-Casas and Álvarez 2000; Riechers et al. 2003; Tschapka 2005). However, actual data about all these topics are scarce for the entire guild.

Leptonycteris nivalis is considered endangered by the IUCN (Chiroptera Specialist Group 2006) and by the US government (US Fish and Wildlife Service 1994). In Mexico *L. nivalis* is categorized as a threatened species (Diario Oficial de la Federación 1991, 2002). The inclusion of this species in endangered species lists is a consequence of recent decreases in abundance that have been mainly attributable to various human-related factors (Wilson et al. 1985; US Fish and Wildlife Service 1994; Medellín 2003). The Mexican long-nosed bat (*Leptonycteris nivalis*) Recovery Plan (US Fish and Wildlife Service 1994) suggests that the two most important steps for the recovery of this bat are: gain more information about roost status (caves) and foraging habitats. The latter is particularly important because very little is known about the composition and distribution of their alimentary resources (US Fish and Wildlife Service 1994).

In order to provide crucial data for conservation and recovery purposes, the goals of our study were: (1) to document the diet of *Leptonycteris nivalis* and its temporal changes during their mating season in the Cueva del Diablo, Morelos, Mexico, and (2) to test whether there are dietary differences between males and females during the mating season.

Methods

Vegetation in the area includes temperate (*Pinus* spp., *Quercus* spp.) and tropical deciduous forests (Hoffmann et al. 1986). The climate is subtropical with most of the rainfall occurring in summer. The climatic pattern following García (1973) is (A)Ca(w₂)(w)(i')g: mean annual temperature 19.9°C, and rainfall is 1463.2 mm (INEGI 2003). The Cueva del Diablo is in the municipality of Tepoztlan, in the state of Morelos, Mexico (18°59'N, 99°03'W), at an elevation of 1883 m a.s.l. The cave has 26 corridors and 11 galleries (Hoffmann et al. 1986). The bat colony in the main gallery was estimated to contain a maximum of about 3000 individuals between October and December of 2001 (Caballero 2004).

At each visit bats were captured inside the cave in a small corridor located 250 m from the entrance, where about 400 individuals typically roosted. A 6 m mist net (Avinet Inc., Dryden, NY, USA) was used. The net was open for 4 h during the period when bats returned to the cave after foraging (between 0:00 and 4:00 h). All captured animals were weighed (precision ±0.5 g); forearm length (caliper, precision: ±0.1 mm), sex, and the reproductive status of females (not reproductive, pregnant or post-lactating) and males (not reproductive or enlarged testicles) was scored.

Pollen was sampled from the fur of captured bats, using gel-safranin squares rolled over the bats' bodies (Medellín et al. 1983). Permanent microscope slides of each sample were prepared, sealing them with transparent nail polish. Faecal samples were obtained by

keeping each captured animal in a clean cloth bag for ca 1–2 h. Each faecal sample was stored in a labelled paper bag. In order to prepare pollen grains for identification the acetolysis standard technique was used (Erdtman 1966), with the modification proposed by Horowitz (1992). This additional step eliminates organic matter present in the faeces (Álvarez and González 1970; Horowitz 1992; Bruch and Pross 1999), with the exception of sporopollenin, chitin or pseudochitin which are the main components of the exine of pollen grains. Slides were prepared by mixing a subsample of the pollen purified in the acetolysis technique with melted glycerine gel (Álvarez and González 1970).

Pollen grains were identified using a light microscope (Olympus, CH30; 40× and 100×) and by comparing the morphological properties and measurements of pollen grains from our samples to reference samples in the Palynological Collection of the Instituto de Geología of the Universidad Nacional Autónoma de México (UNAM) and the Palynological Collection of the MEXU Herbarium (Instituto de Biología, UNAM) as well as with photographs and descriptions from other studies (Palacios 1968, 1970; González 1969; Quiroz et al. 1986). Slides of samples from faeces and fur were deposited in the Palynological Collection of the Instituto de Geología (UNAM).

To determine an individual bat's diet, the presence/absence of pollen species was recorded per sample, following Thomas (1988). Chi-square tests were used with Yates' correction, to determine significant differences in total frequencies of pollen records between paniculate and spicate agaves and in plant use between sexes. Pollen grains from anemophilous plants (like pine and corn) and fungal spores were discarded, because their presence in the samples was considered accidental.

Results

Between September 2001 and February 2002 the Cueva del Diablo was visited approximately every 2 weeks for a total of 11 visits. During our visits a total of 136 individuals (116 males and 20 females) were captured, and 123 fur and 98 faecal samples were collected. Ten food plants were identified: Cactaceae (*Stenocereus beneckeii*), Bombacaceae (*Ceiba aesculifolia*, *Pseudobombax ellipticum*), Convolvulaceae (*Ipomoea arborescens*), Fabaceae (*Calliandra houstoniana*, *Bauhinia unguolata*), and Amaryllidaceae (*Agave dasylirioides*, *A. horrida*, *A. inaequidens*, *A. salmiana*). All 10 species are new records for the diet of *Leptonycteris nivalis*, and two of the genera are also new (*Stenocereus* and *Bauhinia*) (Table I).

Pollen from all plant species was found in both fur and faecal samples, with the exception of *Stenocereus beneckeii*, which was recorded only in the fur samples. Pollen of *Ipomoea arborescens* and *Agave* dominated the faecal samples and were the only two pollen groups present in more than 70% of the faecal samples; all remaining pollens were found in less than 30% of the samples. On fur *Ipomoea arborescens* was most frequently detected (93.49%) and the remaining plants were found at frequencies higher than 50%, with the exception of *Bauhinia unguolata* (4.87%) (Figure 1).

The pollen of four species of *Agave* was identified in faecal samples, but in the fur samples identification of pollen was only possible to the level of genus, primarily due to the abundant debris in each gel-based slide that prevented the observation of species-specific diagnostic characteristics. Combining all four species of *Agave* together, 75% of the faecal samples and 57% of the fur samples showed *Agave* pollen (Figure 1). In faecal samples, *Agave dasylirioides* and *A. horrida* (spicate inflorescences with flowers arranged in rows along the elongated scape) dominate the samples with 54 and 45% respectively; while *A.*

Table I. Species of food plants reported for *Leptonycteris nivalis* including this study and previously published records.

Species plant	Family	Common name	Place	Reference
<i>Agave</i> L.	Amaryllidaceae	–	Mexico	Gardner 1977
<i>Agave chisosensis</i> C. H. Mull., 1939	Amaryllidaceae	Agave or Maguey	Arizona	Easterla 1972
<i>Agave dasylirioides</i> Jacobi and C. D. Bouché, 1865	Amaryllidaceae	Dasylirion Agave	Mexico	This study
<i>Agave havardiana</i> Trel., 1911	Amaryllidaceae	Havard's Century Plant, Chisos Agave	Texas	Kuban 1989
<i>Agave horrida</i> Lem. ex Jacobi, 1864	Amaryllidaceae	Mexcalmetl	Mexico	This study
<i>Agave inaequidens</i> K. Koch, 1860	Amaryllidaceae	Maguey Bruto	Mexico	This study
<i>Agave lecheguilla</i> Torr., 1859	Amaryllidaceae	Shindagger, Maguey lecheguilla	Arizona	Easterla 1972
<i>Agave neomexicana</i> Wootton and Standl.	Amaryllidaceae	New Mexico Century Plant, Mezcal	–	Reid et al. 1985
<i>Agave palmeri</i> Engelm., 1875	Amaryllidaceae	Palmer's Century Plant, Maguey de tlalcoyote	Arizona	See Dobat and Peikert-Holle 1985
<i>Agave parryi</i> Engelm., 1875	Amaryllidaceae	Parry's Agave, Mezcal yapavai	Arizona	See Dobat and Peikert-Holle 1985
<i>Agave salmiana</i> Otto ex Salm-Dyck, 1859	Amaryllidaceae	Ágave ferox, Maguey manso, Tlacamel	Mexico	This study
<i>Agave scabra</i> Ortega, 1797	Amaryllidaceae	Rough Agave, Maguey Cenizo	Arizona	Easterla 1972
<i>Agave schottii</i> Engelm., 1875	Amaryllidaceae	Schott Agave, Maguey puercoespín	Arizona	Cockrum and Hayward 1962, see Geiselman et al. 2006
<i>Bauhinia unguolata</i> L., 1753	Fabaceae	Pata de venado	Mexico	This study
<i>Calliandra</i> Benth.	Fabaceae	–	Mexico	Gardner 1977
<i>Calliandra houstoniana</i> (Mill.) Standl., 1922	Fabaceae	Pambotano	Mexico	This study
<i>Carnegia gigantea</i> (Eng.) Britt. and Rose	Cactaceae	Saguaro	Mexico, USA	Beatty 1955, see Dobat and Peikert-Holle 1985
<i>Ceiba acuminata</i> (S. Watson) Rose, 1905	Bombacaceae	Pochote	Mexico	See Dobat and Peikert-Holle 1985
<i>Ceiba aesculifolia</i> (Kunth) Britten and Baker F., 1896	Bombacaceae	Pochote	Mexico	This study
<i>Ceiba</i> Mill.	Bombacaceae	–	Mexico	Gardner 1977
<i>Ceiba pentandra</i> (L.) Gaertn., 1791	Bombacaceae	Ceiba, Puri	Mexico	See Dobat and Peikert-Holle 1985
<i>Crescentia alata</i> Kunth, 1818 [1819]	Bignoniaceae	Jícara	Mexico	See Dobat and Peikert-Holle 1985
<i>Crescentia cujete</i> L., 1753	Bignoniaceae	Jícara	Mexico	See Dobat and Peikert-Holle 1985
<i>Crescentia</i> L.	Bignoniaceae	–	Mexico	Gardner 1977
<i>Ipomoea arborescens</i> (Humb. and Bonpl. ex Willd.) G. Don, 1838	Convolvulaceae	Morning Glory, Cazahuat	Mexico	This study
<i>Ipomoea</i> L.	Convolvulaceae	–	Mexico	Gardner 1977
<i>Manfreda brachystachya</i> (Cav.) Rose	Amaryllidaceae	Deciduous Agave	–	Cockrum and Hayward 1962, see Geiselman et al. 2006

Table I. Continued.

Species plant	Family	Common name	Place	Reference
<i>Myrtillocactus</i> Console	Cactaceae	–	Mexico	Gardner 1977
<i>Neobuxbaumia macrocephala</i> (F. A. C. Weber ex K. Schum.) E. Y. Dawson, 1952	Cactaceae	Órganos gigantes	Mexico	Valiente-Banuet et al. 1997a
<i>Neobuxbaumia mezcalensis</i> Bravo, 1938	Cactaceae	Columnar cacti	Mexico	Valiente-Banuet et al. 1997a
<i>Neobuxbaumia tetezo</i> (J. M. Coult.) Backeb., 1938	Cactaceae	Tetechos	Mexico	Valiente-Banuet et al. 1997a
<i>Pachycereus weberi</i> (J. M. Coult.) Backeb., 1960	Cactaceae	Cardón Espinoso, Candelabro	Mexico	Valiente-Banuet et al. 1997a
<i>Pilosocereus chrysacanthus</i> F. A. C. Weber ex Schum., 1897	Cactaceae	Golden Old Man, Golden-spined, Cactus Viejita,	Mexico	Valiente-Banuet et al. 1997a
<i>Pseudobombax</i> Dugand	Bombacaceae	–	Mexico	Gardner 1977
<i>Pseudobombax ellipticum</i> (Kunth) Dugand, 1943	Bombacaceae	Clavellina, Pochote	Mexico	This study
<i>Stenocereus beneckeii</i> (Ehrenb.) A. Berger and Buxb., 1961	Cactaceae	Cactus	Mexico	This study
<i>Stenocereus stellatus</i> (Pfeiff.) Riccob.	Cactaceae	Pitaya	–	See Geiselman et al. 2006
<i>Stenocereus thurberi</i> (Engelm.) Buxb., 1961	Cactaceae	Organ Pipe Cactus, Pitaya Dulce	USA	See Geiselman et al. 2006, Dobat and Peikert-Holle 1985
–	Apocynaceae	–	Mexico	Gardner 1977
–	Asteraceae	–	–	See Geiselman et al. 2006
–	Bignoniaceae	–	–	See Geiselman et al. 2006
–	Boraginaceae	–	–	See Geiselman et al. 2006
–	Caesalpiniaceae	–	–	See Geiselman et al. 2006
–	Compositae	–	Mexico	Gardner 1977
–	Convolvulaceae	–	–	See Geiselman et al. 2006
–	Lamiaceae	–	–	See Geiselman et al. 2006
–	Leguminosae	–	Mexico	Gardner 1977
–	Liliaceae	–	Mexico	Gardner 1977
–	Malvaceae	–	Mexico	Gardner 1977

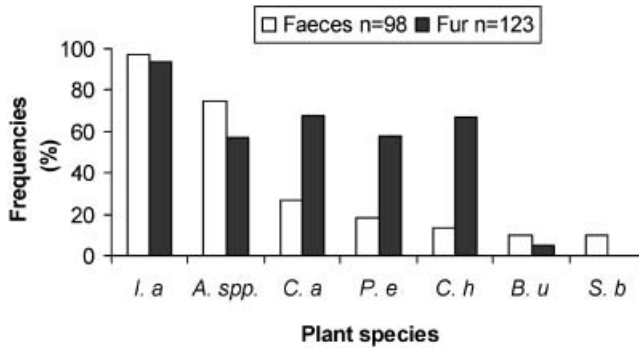


Figure 1. Plant species frequencies (%) in faeces and fur samples of the Cueva del Diablo, Tepoztlan. Species code: I. a, *Ipomoea arborescens*; A. spp., *Agave* spp.; C. a, *Ceiba aesculifolia*; P. e, *Pseudobombax ellipticum*; C. h, *Calliandra houstoniana*; B. u, *Bauhinia unguolata*; S. b, *Stenocereus beneckeii*. Frequency of the four agave species are combined in A. spp., because it was impossible to differentiate in fur samples.

inaequidens and *A. salmiana* (paniculate species characterized by open paniculate inflorescences, with flowers in large umbellate clusters on long lateral peduncles) constituted 39.8 and 19.38%. Frequency of spicate and paniculate species were significantly different ($\chi^2=22.9$, $P<0.001$).

Insect exoskeleton parts were found in 28.57% of the faeces samples and 34.14% in fur samples. Insect parts were too finely chewed to allow identification. Butterfly scales were also found, but not included in the analysis. Flower-visiting insects leave scales and other remains on them, which easily stick to bat fur; but finding them in the faeces does not mean that the bat ate the insects.

The observed monthly frequencies differed between sample types (Figure 2): on fur, the frequencies of many pollen types were high, but in faeces, only *Ipomoea arborescens* had particularly high frequencies in all months (>80% in monthly samples). In both sample types, *Bauhinia unguolata* showed low frequencies and was only found in October and November (Figure 2), which corresponded to months with the highest food species diversity. In December, many species showed a decrease in frequencies and the diet was dominated by *Ipomoea arborescens*.

More samples were obtained from males (107 from pelage, 85 from faeces) than from females (16 and 13, respectively). Therefore, for a comparison of the frequency of occurrence of food items between sexes, 16 and 13 samples from males were randomly selected, in order to have comparable numbers of females and males. In the fur samples, no differences were found for plant species: *Ipomoea* ($\chi^2=0.0370$, $P>0.05$), *Agave*, *Ceiba* and *Calliandra* ($\chi^2=0.0476$, $P>0.05$), *Bauhinia* ($\chi^2=0.0555$, $P>0.05$) or insects ($\chi^2=1.5625$, $P>0.05$). In faeces, samples were abundant enough only for *Ipomoea* ($\chi^2=0.166$, $P>0.05$) and *Agave* ($\chi^2=0.45$, $P>0.05$); no differences were found.

Discussion

There is little information about the dietary habits of *L. nivalis*. Much more is known for the other Mexican species of the genus, *L. curasoe* (Miller, 1900). Apparently, many studies reporting information for *L. nivalis* were actually based on observations on *L. curasoe* (Arita and Humphrey 1988). Because of this confusion, information generated prior to Arita and Humphrey (1988) must be considered carefully. Taking into account

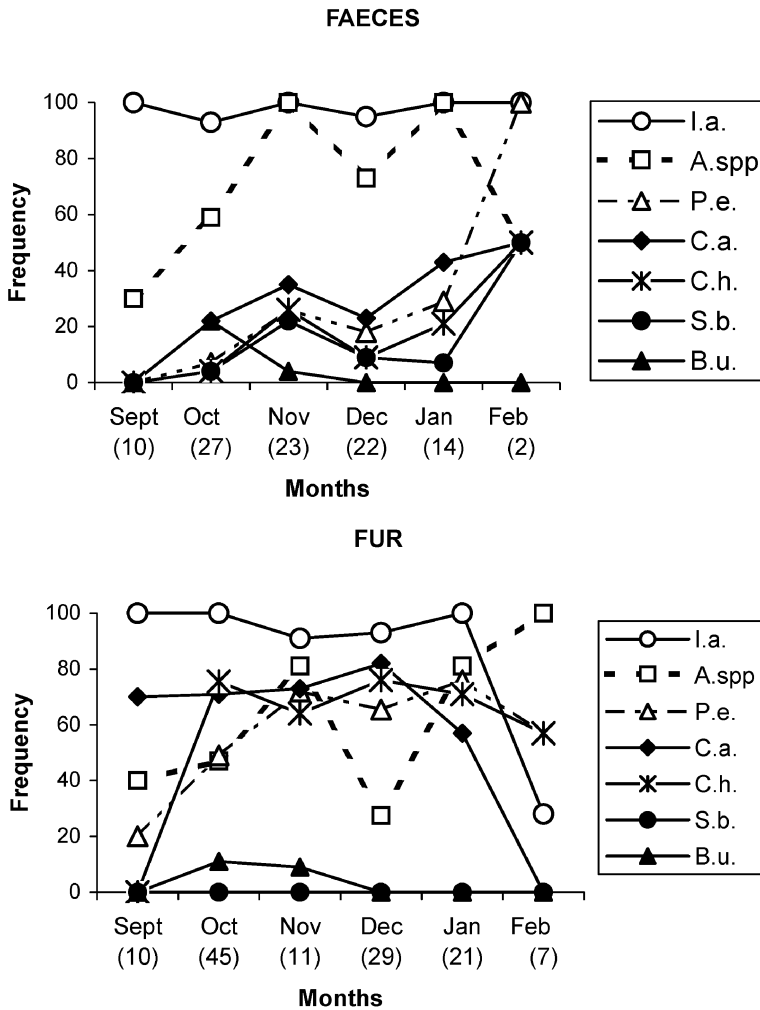


Figure 2. Monthly frequencies (%) of plant species on fur and faeces samples of Cueva del Diablo, Tepoztlan. Species code: I. a, *Ipomoea arborescens*; A. spp., *Agave* spp.; C. a, *Ceiba aesculifolia*; P. e, *Pseudobombax ellipticum*; C. h, *Calliandra houstoniana*; B. u, *Bauhinia unguolata*, S. b, *Stenocereus beneckeii*.

only the published reports that are known to refer to *L. nivalis* with certainty, the number of plants reported in its diet consist of 21 species, 13 genera, and 10 families (Table I).

With the exception of two genera (*Stenocereus* and *Bauhinia*), all plant genera that we report in this paper had been previously reported to be part of the diet of *Leptonycteris nivalis* (Álvarez and González 1970; Gardner 1977; Dobat and Peikert-Holle 1985). However, at a species level, our study adds 10 new food plants to the known diet of this rare, endangered bat.

The diet of *L. nivalis* probably tracks the spatio-temporal availability of local floral resources, while this bat inhabits the Tepoztlan cave. Opportunistic feeding behaviour has been well documented for both species of *Leptonycteris* in the northern parts of their distributions (Bogan et al. 2004; Fleming 2004; Moreno-Valdez et al. 2004). For example, Moreno-Valdez et al. (2004) found that the seasonal presence of a colony of an estimated

4000 *L. nivalis* in northern Mexico from April to October was highly correlated with availability of nearby flowering *Agave*. Although the importance of Bombacaceae and *Ipomoea* as food resources for *L. curasoae* in the southern areas of its distribution has been recognized (Fleming 2004), such a relationship was not previously known for *L. nivalis*.

The Morning Glory tree or cazahuate (*Ipomoea arborescens*) is a dominant plant in the Tepoztlan Mountain range and occurs throughout the tropical deciduous forest regions of Mexico (Ramírez 1944). It is therefore not surprising that this abundant plant dominates the diet of *L. nivalis* in all months. The proposed food shift of *Leptonycteris* between its northern (CAM metabolism plants, like *Agave* and Cactaceae) and south-centre roosts (C₃ metabolism plants, like *Ipomoea*), has been demonstrated by using carbon isotope analysis (Fleming et al. 1993; Téllez 2001). Our results show that in the southern part of the distribution, these bats are feeding on C₃ plants (mostly *Ipomoea*), and also on CAM plants (*Agave*). The difference is that in the north *L. nivalis* apparently only feeds on CAM plants (i.e. Schaffer and Schaffer 1977; Moreno-Valdez et al. 2004), principally *Agave*. In 24 faecal samples and 41 fur samples obtained during two visits (17 July and 2 August) to two maternity colonies in the state of Zacatecas (670.23 km N of El Diablo Cave), only pollen of *Agave* was detected.

Several authors have suggested that paniculate agaves (species with branched scapes and flowers in large umbellate clusters, like *Agave salmiana* and *A. inaequidens*) are pollinated chiefly by bats, while spicate agaves (species with unbranched scapes and with flowers forming directly on the main shoot, like *A. dasylirioides* and *A. horrida*) show pollination syndromes that suggest a predominance of entomophilic mechanisms (Schaffer and Schaffer 1977; Fleming et al. 1993). Thus, we did not expect to find pollen of spicate agaves in our samples from *Leptonycteris nivalis*, much less that the diet of *L. nivalis* in Central Mexico during the winter would be dominated by spicate agaves. However, other authors have also documented the presence of spicate agave pollen in the diet of bats such as *L. curasoae* and *Choeronycteris mexicana* (Tschudi, 1844) in southern USA (Cockrum and Hayward 1962; Schaffer and Schaffer 1977; Hevly 1979).

It has been suggested that spicate species of *Agave* that display certain chiropterophilous characteristics were originally bat pollinated and experienced a recent evolutionary shift towards insect pollination (Schaffer and Schaffer 1977). In temperate zones, this change toward entomophily could be explained by the unpredictable and asynchronous arrival of bats in relation to blooming of *Agave* (Arita and Humphrey 1988; Slauson 2000). Thus, plants may have developed flower characteristics that favour diurnal pollination by insects (Fleming et al. 1996). Although further research is needed, it is possible that this may also have happened with the spicate agave species that *Leptonycteris nivalis* feeds on near Cueva del Diablo. The high abundance of spicate agaves in the Tepoztlan Mountain range makes these plants a very attractive resource for the bats. Furthermore, in the case of *A. dasylirioides*, these plants frequently grow next to paniculate agaves like *Agave inaequidens*, forming dense clusters (A. García, personal communication). These clusters constitute high flower-density patches that might attract bats by maximizing feeding efficiency (Schaffer and Schaffer 1977; Eguiarte 1983) which in turn increases the pollination probability for both species.

The persistence of pollen grains in fur and faeces is influenced by many factors: gut transit time, the position of deposition on the animal's body, length of feeding time, and the amount of pollen grains produced by the flowers as well as timing of open flower and nectar secretion (Howell 1977; Heithaus 1982; Thomas 1988; Herrera and Martínez del Río 1998). These factors could contribute to the differences in plant frequencies between the

two sample types. Therefore both methods should be used simultaneously but should be considered separately when collecting data on the diet of bats. For example, the flowers of *Stenocereus beneckeii* open early in the evening, at approximately 18:30 h (Gentry 1982), so the bats visit them at the beginning of the night. When bats return to the cave groomed, there would be almost no *S. beneckeii* pollen grains in the fur.

Differences in the dominance of certain pollen types in the faeces and fur might be related to the last meal the bats had before heading back to the roost. Both fur and faeces provide diet information, but probably over different time scales. Given the high food intake in nectar-feeding bats (Helvesen and Winter 2003) it is possible that the faeces examined reflect only a rather short period of foraging immediately before the capture (Thomas 1988). Perhaps the most frequently detected type of pollen in the faeces might be the food plant that is most abundant in the area around the cave, and was eaten just before bats returned to the roost. If this is indeed the case, then capturing bats in their feeding grounds, as opposed to in their roost, might yield somewhat different results.

Our diet data did not reveal sexual differences in the diet of *L. nivalis* in Cueva del Diablo. During their stay in Tepoztlan, bats were mating but not forming a maternity colony. Thus, embryo development was only in its earliest stages and the physiological requirements at that time may not vary between the sexes (Kunz and Nagy 1988).

Conservation implications

Since the 1970s many studies have documented severe declines in the population of *L. nivalis* (Easterla 1972). The causes of this decrease have not been completely identified, but are probably related to human activities (Medellín 2003). The recovery plan for this species (US Fish and Wildlife Service 1994) recognizes destruction and modification of foraging and roosting habitat as the greatest threats to the species. For this reason, it was suggested that protection of all known roosts and protection of foraging habitat are the most important aspects to be considered for the recovery of *L. nivalis* (US Fish and Wildlife Service 1994). Our research addresses one of the major points of the Recovery Plan for *Leptonycteris nivalis* (US Fish and Wildlife Service 1994). Before our study, there was no detailed information on this species' diet in the southern parts of the range or during the mating season. According to our data, *Ipomoea arborescens* (Morning Glory tree) is the most important food plant of *L. nivalis* near this critical breeding site in Mexico. At other times of year and in the north of the distribution several species of *Agave* are the main source of food for this species (Fleming 2004; Moreno-Valdez et al. 2004). This information allows us to gain a wider perspective about the relevance of the vegetation types and foraging area that need to be preserved for the purpose of recovery of this species.

Many species of plants seem to rely on *L. nivalis* and other nectar-feeding bats for fruit production (Fleming 2004). Some plant species we found in the diet of this bat are of conservation concern in Mexico. *Agave dasylirioides* is listed as a threatened and endemic plant species (Diario Oficial de la Federación 2002), while *A. inaequidens* and *A. horrida* are endemics to the floristic provinces of Sierra Madre Occidental and Sierra Madre del Sur, respectively (García-Mendoza and Galván 1995). Because of the potential symbiotic relationships between these plants and bats we need to protect both. By doing this, we ensure adequate supplies of food to bats as well as the successful pollination of plants.

Further studies should evaluate the role of bats in the pollination of plants such as the Morning Glory tree (*Ipomoea arborescens*), as well as the spicate and paniculate agaves in Central Mexico.

Acknowledgements

We thank Programa para la Conservación de los Murciélagos Mexicanos (PCMM), BCI, CONACYT, Packard Foundation, NFWF, US Fish and Wildlife Service, INE, SEMARNAT, Fondo Mexicano para la Conservación de la Naturaleza, and Arizona Sonora Desert Museum, for the support of this work; Enrique Martínez for help with pollen identification, and for facilitating the entrance to the Palynological Collection (Instituto de Geología, UNAM); Teresa German for all the facilities in MEXU Herbarium (Instituto de Biología, UNAM); Carlos Nuñez for help with permanent slides; Joaquín Arroyo, Marco Tschapka, Bernal Rodríguez-Herrera, and two reviewers for comments on earlier drafts; and Luis Caballero and Ricardo Rubio for help in the field. We thank Bogan and Hayward for helpful comments. This is Contribution No. 15 of the Wildlife Trust Alliance and BIOCONCIENCIA, A.C.

References

- Álvarez T, González L. 1970. Análisis polínico del contenido gástrico de murciélagos Glossophaginae de México. *Anales de la Escuela Nacional de Ciencias Biológicas* 18:137–165.
- Arita HT, Humphrey SR. 1988. Revisión taxonómica de los murciélagos magueyeros del género *Leptonycteris* (Chiroptera: Phyllostomidae). *Acta Zoológica Mexicana (NS)* 29:1–60.
- Arizaga S, Ezcurra E, Peters E, Ramírez de Arellano F, Vega E. 2000. Pollination ecology of *Agave macroacantha* (Agavaceae) in a Mexican tropical desert II. The role of pollinators. *American Journal of Botany* 87:1011–1017.
- Beatty LD. 1955. Autecology of the Lognose Bat *Leptonycteris nivalis* (Saussure). Master of Science – Thesis, VI + 51S. Univ. Arizona.
- Bogan MA, Sherwin R, Cryan PM, Weise D, Engalnd A, Altenbach JS. 2004. Studies of Long-nosed bats (*Leptonycteris*) in New Mexico [abstract]. 34th Annual North American Symposium on Bat Research; 2004 Oct 27–30; Salt Lake City.
- Bruch AA, Pross J. 1999. Palynomorph extraction from peat, lignite and coal. In: Jones TP, Rowe NP, editors. Fossil plants and spores: modern techniques. London: Geological Society of London. p 26–30.
- Caballero LA. 2004. Observaciones sobre la conducta reproductiva de *Leptonycteris nivalis* (Chiroptera: Phyllostomidae) en Tepoztlán, Morelos, México [dissertation]. Mexico: Universidad Autónoma del Estado de México.
- Chiroptera Specialist Group. 2006. *Leptonycteris nivalis*. In: 2006 IUCN red list of threatened species [online]. www.iucnredlist.org.
- Cockrum EL, Hayward BJ. 1962. Hummingbird bats. *Natural History* 71:39–44.
- Diario Oficial de la Federación. 1991. Protección ambiental—especies nativas de México de flora y fauna silvestres—categorías de riesgo. Secretaría de Ecología, Mexico.
- Diario Oficial de la Federación. 2002. Norma Oficial Mexicana NOM-059-ECOL-2001, Protección ambiental—especies nativas de México de flora y fauna silvestres—categorías de riesgo y especificaciones para su inclusión, exclusión o cambio—lista de especies en riesgo. Segunda Sección. Secretaría de Medio Ambiente y Recursos Naturales, Mexico.
- Dobat K, Peikert-Holle T. 1985. Blüten und Fledermäuse. Frankfurt am Main: Verlag Waldemar Kramer.
- Easterla D. 1972. Status of *Leptonycteris nivalis* (Phyllostomidae) in Big Bend National Park, Texas. *Southwestern Naturalist* 17:287–292.
- Eguiarte LE. 1983. Biología floral de *Manfreda brachystachya* (Cav.) Rose en el Pedregal de San Ángel México, D.F. [dissertation]. Mexico: Universidad Nacional Autónoma de México.
- Eguiarte LE, Martínez del Río C, Arita H. 1987. El néctar y el polen como recursos: el papel ecológico de los visitantes a las flores de *Pseudobombax ellipticum* (H. B. K.) Dugand. *Biotropica* 19:74–82.
- Erdtman G. 1966. Pollen morphology and plant taxonomy: angiosperms. New York: Hafner Publishing Company.
- Fleming TH. 2004. Nectar corridors: migration and the annual cycle of Lesser Long-nosed Bats. In: Nabhan GP, editor. Conserving migratory pollinators and nectar corridors in western North America. Tucson: University of Arizona Press. p 23–42.
- Fleming TH, Nuñez RA, da Silveira L, Sternberg L. 1993. Seasonal changes in the diets of migrant nectarivorous bats as revealed by carbon stable isotope analysis. *Oecologia* 94:72–75.

- Fleming TH, Tuttle MD, Horner MA. 1996. Pollination biology and the relative importance of nocturnal and diurnal pollinators in three species of Sonoran desert columnar cacti. *Southwestern Naturalist* 41:257–269.
- García E. 1973. Modificaciones al sistema de clasificación climática de Köppen, para adaptarlo a las condiciones de la República Mexicana. 2nd ed., Mexico: Universidad Nacional Autónoma de México, Instituto de Geografía. 246 p.
- García-Mendoza A, Galván R. 1995. Riqueza de las familias Agavaceae y Nolinaceae en México. *Boletín de la Sociedad Botánica Mexicana* 56:7–24.
- Gardner AL. 1977. Feeding habits. In: Baker RJ, Jones JK Jr, Carter DC, editors. *Biology of bats of the New World family Phyllostomatidae, part II*. Lubbock: Texas Tech University Museum. p 293–350. (Special publications of the Museum, Texas Tech University).
- Geiselman CK, Mori SA, Blanchard F. 2006. Database of Neotropical bat/plant interactions [online]. New York: New York Botanical Garden. http://www.nybg.org/botany/tlobova/mori/batsplants/database/dbase_frameset.htm.
- Gentry HS. 1982. *Agaves of continental North America*. Tucson: Arizona University Press. 670 p.
- González L. 1969. Morfología polínica: la flora del Valle de Mezquital, Hidalgo. *Paleoecología* 3:1–186.
- Heithaus ER. 1982. Coevolution between bats and plants. In: Kunz T, editor. *Ecology of bats*. New York: Plenum. p 327–367.
- Helversen O, Winter Y. 2003. Glossophagine bats and their flowers: costs and benefits for plants and pollinators. In: Kunz T, Fenton MB, editors. *Bat ecology*. Chicago: University of Chicago Press. p 346–397.
- Hensley AP, Wilkins KT. 1988. *Leptonycteris nivalis*. *Mammalian Species* 307:1–4.
- Herrera LG, Martínez del Río C. 1998. Pollen digestion by new world bats: effects of processing time and feeding habits. *Ecology* 79:2828–2838.
- Hevly RH. 1979. Dietary habits of two nectar and pollen feeding bats in southern Arizona and northern Mexico. *Journal of the Arizona-Nevada Academy of Science* 14:13–18.
- Hoffmann A, Palacios-Vargas JG, Morales-Malacara JB. 1986. Cueva de Oztoyehualco, Morelos. In: Hoffmann A, editor. *Manual de bioespeleología*. Mexico: UNAM. 274 p.
- Horowitz A. 1992. *Palinología of arid lands*. Amsterdam: Elsevier Science.
- Howell DJ. 1977. Time sharing and body partitioning in bat–plant pollination systems. *Nature* 270:509–510.
- INEGI. 2003. Aspectos geográficos de Morelos [online]. Morelos (Mexico): INEGI. <http://mor.inegi.gob.mx>.
- Kunz TH, Nagy NA. 1988. Methods of energy analysis. In: Kunz T, editor. *Ecological and behavioral methods for the study of bats*. Washington: Smithsonian Institution Press. p 277–302.
- Medellín R. 2003. Diversity and conservation of bats in Mexico: research priorities, strategies, and actions. *Wildlife Society Bulletin* 31:87–97.
- Medellín RA, Navarro D, Davis WB, Romero VJ. 1983. Notes on the biology of *Micronycteris brachyotis* (Dobson) (Chiroptera), in southern Veracruz, México. *Brenesia* 21:7–11.
- Miller GS Jr. 1900. Three new bats from the island of Curacao. *Proceedings of the Biological Society of Washington* 13:126.
- Moreno-Valdez A, Honeycutt RL, Grant WE. 2004. Colony dynamics of *Leptonycteris nivalis* (Mexican Long-nosed Bat) related to flowering Agave in Northern Mexico. *Journal of Mammalogy* 85:453–459.
- Palacios R. 1968. Morfología de los granos de árboles del Estado de Morelos. *Anales de la Escuela Nacional de Ciencias Biológicas* 16:41–169.
- Palacios R. 1970. Morfología del polen de las especies mexicanas más comunes del género *Bauhinia* (Leguminosae). *Anales de la Escuela Nacional de Ciencias Biológicas* 18:107–136.
- Quiroz D, Xelhuanzi MS, Zamora MC. 1986. Análisis palinológico del contenido gastrointestinal de murciélagos. Mexico: Instituto Nacional de Antropología e Historia, Colección Científica.
- Racey PA, Entwistle AC. 2000. Life-history and reproductive strategies of bats. In: Crichton EG, Krutzsch PH, editors. *Reproductive biology of bats*. London: Academic Press. p 363–414.
- Ramírez D. 1944. Notas generales sobre la vegetación de la Sierra de Tepoztlán, Morelos [dissertation]. Mexico: Universidad Nacional Autónoma de México.
- Reid WH, Freeman CE, Becvar JE. 1985. Nectar sugar variability in two species of Agave (Agavaceae). *The Southwestern Naturalist* 30(3): 443–445.
- Riechers A, Martínez-Coronel M, Vidal R. 2003. Consumo de polen de una colonia de maternidad de *Leptonycteris curasoae yerbabuena* en Tuxtla Gutiérrez, Chiapas, México. *Anales del Instituto de Biología, Serie Zoología* 74:43–66.
- Sánchez-Casas N, Álvarez T. 2000. Palinofagia de los murciélagos del género *Glossophaga* (Mammalia: Chiroptera) en México. *Acta Zoologica Mexicana* 81:23–62.
- Saussure MH. 1860. Note sur quelques mammifères du Mexique. *Revue et Magasin de Zoologie, Paris, Série 2* 12:479–494.

- Schaffer WM, Schaffer MV. 1977. The reproductive biology of Agavaceae: I. Pollen and nectar production in four Arizona Agaves. *Southwestern Naturalist* 22:157–168.
- Simmons NB. 2005. Order Chiroptera. In: Wilson DE, Reeder DM, editors. *Mammal species of the world*. Baltimore (MD): Johns Hopkins University Press. p 312–529.
- Slauson LA. 2000. Pollination biology of two chiropterophilous agaves in Arizona. *American Journal of Botany* 87:825–836.
- Téllez JG. 2001. Migración de los murciélagos-hocicudos (*Leptonycteris*) en el trópico mexicano [dissertation]. Mexico: Universidad Nacional Autónoma de México.
- Thomas DW. 1988. Analysis of diets of plant-visiting bats. In: Kunz T, editor. *Ecological and behavioral methods for the study of bats*. Washington: Smithsonian Institution Press. p 211–220.
- Tschapka M. 2005. Reproduction of the bat *Glossophaga commissarisi* (Phyllostomidae: Glossophaginae) in the Costa Rican rain forest during frugivorous and nectarivorous periods. *Biotropica* 37(3):409–415.
- Tschudi JJ. 1844–45. Untersuchungen über die Fauna Peruana. Parts 1–6. St Gallen (Switzerland), 262 p.
- US Fish and Wildlife Service. 1994. Plan de Recuperación del Murciélago magueyero (*Leptonycteris nivalis*). Albuquerque (NM): US Fish and Wildlife Service.
- Valiente-Banuet A, Rojas-Martínez A, Arizmendi MC, Dávila P. 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. *American Journal of Botany* 84:452–455.
- Valiente-Banuet A, Rojas-Martínez A, Casas A, Arizmendi MC, Dávila P. 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacan Valley, central México. *Journal of Arid Environment* 37:331–341.
- Wilson DE, Medellín RA, Lanning DV, Arita HT. 1985. Los murciélagos del noreste de México, con una lista de especies. *Acta Zoológica Mexicana* 8:1–26.