

# Frugivory diet of the lesser long-nosed bat (*Leptonycteris yerbabuenae*), in the Tehuacán Valley of central Mexico

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## Abstract

The lesser long nosed bat *Leptonycteris yerbabuenae* (Phyllostomidae: Glossophaginae), is a migratory species highly specialized for nectar and pollen consumption. Although they can consume fruits of columnar cactus (Family Cactaceae, tribes Pachicereae and Cereeae), this habit has not been studied sufficiently to know the importance of this frugivory. Available information shows that this bat can consume actively fruit of columnar cactus, and indeed seven of these fruits have been cited as part of their diet in North America. Nevertheless, it is unknown whether other cactus fruits are edible for them. In Tehuacán Valley, located in south central México *L. yerbabuenae* co-occur with 21 species of cactus that produce sweet, juicy and soft fruits, with small seeds appropriate to be eaten by the long-nosed bat. We conducted one study to determine the identity of cacti fruits eaten by *L. yerbabuenae*, through the identification of seeds deposited as guano and obtained in the Obispo cave (municipality of Santiago Chazumba, Oaxaca). Seeds of all species of cactus that inhabit Tehuacan Valley were identified in guano. We recollected 31,895 seeds inside the cave, but more than the 84% corresponded to four species of cacti seeds: *Isolatocereus dumortieri*, *Stenocereus pruinosus*, *Stenocereus stellatus* and *Neobuxbaumia macrocephala*. The species *Escontria chiotilla*, *Pachocereus hollianus*, *Hilocereus undatus*, *Pachocereus fulviceps* and *Stenocereus treleasei*, were rare and they had less than 20 seeds in the sample. So results obtained suggest that *L. yerbabuenae*, may eat fruits as an important part of its diet, and probably serves as an important disperser of columnar cactus in dry environments of South Central Mexico.

**Key words:** Obispo cave, cactus fruits, *Leptonycteris yerbabuenae*, cactus fruit resources

## Resumen

El murciélago de hocico largo menor *Leptonycteris yerbabuenae* (Phyllostomidae: Glossophaginae), es una especie migratoria altamente especializada en el consumo de néctar y polen. Aunque se conoce que pueden consumir frutas de cactáceas

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columnares (Familia Cactaceae, tribus Pachicereus y Cerrae), este hábito no ha sido estudiado apropiadamente para conocer la importancia de la fruta en su alimentación. La información disponible muestra que siete frutos de cactáceas han sido citadas como parte de su dieta en Norte América, sin embargo, se desconoce si pueden consumir otras.

En el valle de Tehuacán, localizado en la parte sur-central de México, *L. yerbabuena* coexiste con 21 especies de cactus columnares que producen frutos dulces, jugosos y blandos, con pequeñas semillas que son apropiadas para su alimentación. En esta zona determinamos la identidad de los frutos de cactáceas columnares que son consumidos por *L. yerbabuena*, por medio de la identificación de las semillas depositadas como guano en la cueva del Obispo (municipio de Santiago Chazumba, Oaxaca). Todas las semillas de los cactus que habitan en el valle de Tehuacán fueron encontradas en ella. De 31,895 semillas recolectadas, más del 84% pertenecieron a cuatro especies: *Isolatocereus dumortieri*, *Stenocereus pruinosus*, *Stenocereus stellatus* y *Neobuxbaumia macrocephala*. Por el contrario *Escontria chiotilla*, *Pachicereus hollianus*, *Hilocereus undatus*, *Pachicereus fulviceps* y *Stenocereus treleasi*, fueron raras con menos de 20 semillas en la muestra. Los resultados sugieren que *L. yerbabuena*, consume frutas como parte importante de su dieta y probablemente es un importante dispersor de las semillas en los ambientes secos de la parte sur y central de México.

**Palabras clave:** Cueva del Obispo, frutas de cactus, *Leptonycteris yerbabuena*, recursos frutales de cactus.

## Introducción

The lesser long nosed bat *Leptonycteris yerbabuena* Martínez and Villa (Phyllostomidae: Glossophaginae), is considered a migratory species threatened with extinction (Cockrum 1991). It is highly specialized for nectar and pollen consumption of plants belonging to the families Cactaceae, Agavaceae and Bombacaceae, among others (Alvarez and González 1970; Gardner 1977). Although they can consume fruits of columnar cactus (Family Cactaceae, tribes Pachicereae and Cereeae), this habit has not been studied appropriately. Available information shows that this bat can consume some fruit of columnar cactus in South America (Sosa and Soriano 1993), and some authors have observed as well a significant consumption of cactus fruits by bats in North America (Fleming and Sosa 1994; Godínez-Alvarez and Valiente-Banuet 2000; Castillo 2011).

Seventy species of columnar cactus that inhabit Mexico produce fleshy fruit probably edible by bats (Rojas-Martínez 2001). Indeed seven of these fruits have been cited as part of their diet in North America (*Carnegiea gigantea* (Engelm.) Britt. and Rose, *Neobuxbaumia mezcalaensis* (Bravo) Backeberg, *Neobuxbaumia tetetzo* (Web.) Backeb., *Pachycereus pringlei* (Watson) Britt. and Rose, *Stenocereus pecten-aboriginum*, *Stenocereus stellatus* (Pfeiffer) Riccob., and *Stenocereus thurbery* (Engelm.) Buxb. (Dalquest 1953; Villa 1967; Gardner 1977; Fleming and Sosa 1994; Valiente-Banuet et al. 1996; Castillo 2011).

Nevertheless, it is unknown whether long nosed bats consume other cactus fruits.

The Tehuacan Valley is located in the south-east limit of the state of Puebla and the adjacent region of Oaxaca in south-central Mexico. Here *L. yerbabuena* co-occurs with 19 species of sylvan columnar cacti (Hall 1981; Rojas-Martínez and Valiente-Banuet

1996; Valiente-Banuet *et al.* 1996), and with *Acanthocereus subinermis* Britt. and Rose (used locally as an ornamental cactus) and *Hylocereus undatus* (Haw.) Britt. and Rose (a climber cultivated cactus; Dávila *et al.* 1993; Valiente-Banuet *et al.* 1996). All these cacti produce sweet, juicy and soft fruits with small seeds appropriate to be eaten by the long nosed bat (Faegri and Van der Pijl 1979; Rojas-Martínez 2001). Fruit produced by these plants may represent a food source, not considered up to now, to explain the ecology of this migratory bat. On the other hand, columnar cactus can receive additional benefits from this nectar-feeding bat, because in addition to pollinating flowers, they may act as dispersers of their seeds (Valiente-Banuet *et al.* 1996; 1997a, 1997b; Godínez-Alvarez and Valiente-Banuet 2000; Godínez-Alvarez, Valiente-Banuet and Rojas-Martínez 2002; Castillo 2011).

The Tehuacan Valley is situated in a tropical environment with a high diversity of columnar cacti. This study was designed to determine the identity of cactus fruits eaten by *L. yerbabuena*, through the identification and quantification of seeds deposited as guano, inside one roost inhabited permanently by these long-nosed bats. With this information we discuss the importance of bats as potential seed dispersers in dry environments and some implications of the fruit resources for the ecology of the lesser long-nosed bat.

## Material y Methods

The study was conducted in a semi-arid region of the Tehuacan Valley (17° 48' to 18° 58' N and -96°48' to -97° 43' W) located in southern Puebla and northern Oaxaca, Mexico (Fig. 1). Mean annual rainfall is ca. 400 mm with an average temperature of 21° C (García 1973). The region has a high number of columnar cacti species, containing 19 of the 45 reported for south-central Mexico (Valiente-Banuet *et al.* 1996). Columnar cacti form the dominant elements of several different vegetation types (Rzedowski 1978). In this region the densest columnar cacti forests have been reported as ranging between 1,200 to 1,800 plants ha<sup>-1</sup> (Valiente-Banuet *et al.* 1997a; 2000), and *L. yerbabuena* has been reported as a resident and abundant species in this area (Rojas-Martínez *et al.* 1999; Rojas-Martínez 2001).

**Bat-roost.** One permanent lesser long-nosed bat roost, located in Oaxaca state (San Juan Nochixtlan, municipality of Santiago Chazumba; 18° 03' N and -97° 40' W), that houses a colony of 100,000 bats, was visited every three months between January 1998 and June 1999. We installed 10 guano traps (53 x 42 cm) inside the cave, just below the long-nosed bat colony for collecting guano. The content of guano traps was collected and traps were newly installed on each visit.

Collected faeces were placed in paper bags recording the date, and stored in a dry place until seed identification.

**Seed identification.** Fruits of 19 sylvan columnar cactus species that live in Tehuacán Valley and fruit of *Acanthocereus subinermis*, and *Hylocereus undatus*, were collected and identified during two years (1998-1999). Seeds were extracted and stored in a dry place for use as a reference collection. Seeds defecated by bats were obtained by guano dissection, using a stereoscopic microscope and were identified by comparing them with the cactus seeds reference collection, and consulting specialized literature (Barthlott and Hunt 2000).

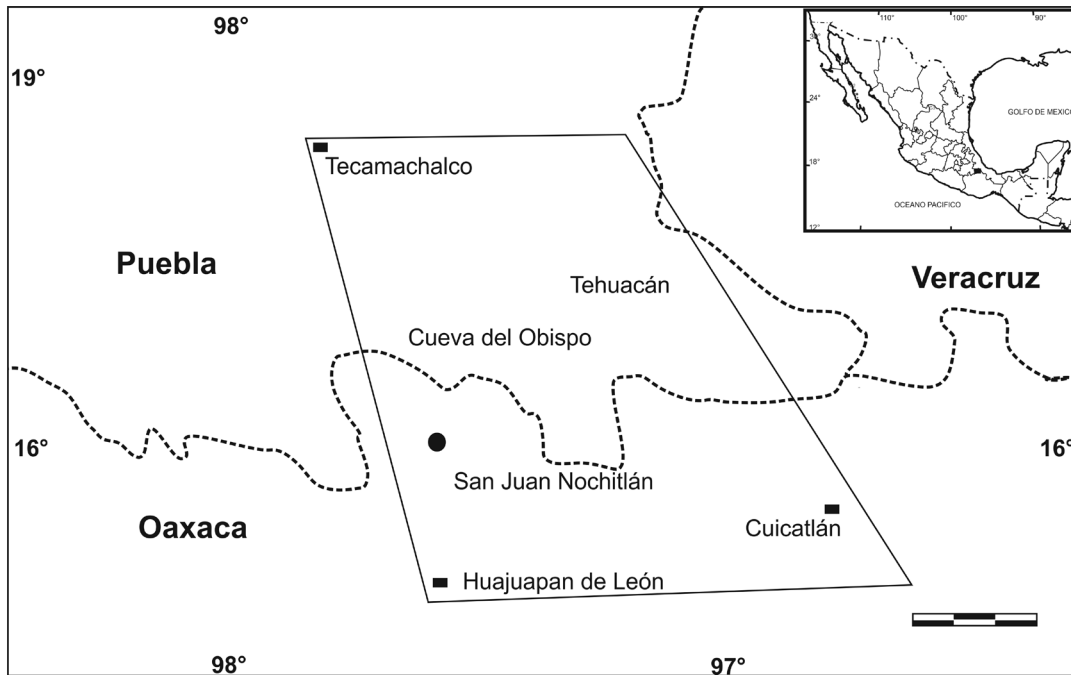


Figure 1. Location Map

## Results

Obispo cave roost was inhabited all year by *L. yerbabuena*, and was shared with insectivorous bats such as *Mormoops megalophylla* (Peters), *Pteronotus parnellii* (Gray) and *Tadarida brasiliensis* (L. Geoffroy). Seeds of all 19 species of columnar cactus inhabiting the Tehuacan Valley were found in the roosts as well as those of Eighteen of these species represent the first report of these fruits as food for bats (*Acanthocereus subinermis* Britton & Rose, *Cephalocereus columna-trajani* (Weber) Schuman, *Escontria chiotilla* (F. A. C. Weber) Rose, *Hylocereus undatus* (Haw.) Britt. and Rose, *Marginatocereus marginatus* (D. C.) Berger and Buxb., *Myrtillocactus geometrizans* (C. Martius) Console, *Myrtillocactus schenkii* (J. A. Purpus) Britt. and Rose, *Neobuxbaumia macrocephala* (Weber) Dawson, *Pachycereus fulviceps* (Weber) Backeb., *P. hollianus* (Weber) Buxb., *P. weberi* (Coulter) Backeb., *Pilosocereus chrysacanthus* (Web) Britt. and Rose, *Polaskia chende* (Gosselin) A. Gibson and K. Horak, *P. chichi* (Gosselin) Backeb., *Isolatocereus dumortieri* (Scheidw.) Buxb., *S. griseus* (Haw.) Buxb., *S. pruinosus* (Otto) Buxb., and *S. treleasei* (Rose) Backeb.).

*Escontria chiotilla*, *S. stellatus*, *S. pruinosus* and *Hilocereus undatus* (climber cultivated cacti), produce edible fruit used by people and include both wild and cultivated populations in the Tehuacan Valley. *Neobuxbaumia tetetzo* and *S. stellatus* fruits have been cited previously as part of the *Leptonycteris* diet.

We recollected 31,895 seeds inside the cave. More than 84% corresponded to four species of cacti each represented by more than two thousand seeds: *I. dumortieri*, *S. pruinosus*, *S. stellatus*, and *Neobuxbaumia macrocephala*. There were 17 species represented by less than one thousand seeds each. Five species, *E. chiotilla*, *P. hollianus*, *H. undatus*, *P. fulviceps* and *S. treleasei*, were rare with less than 20 seeds in the sample (Table 1). The deposition of seeds in the cave was continuous during the year. However in the entire sample [?], the fruits of two species that were available during the winter were the most abundant (64.5%; *I. dumortieri*, *S. pruinosus*).

## Discussion

Differences in the number of seeds observed inside roosts probably are related to species diversity of columnar cacti around the roost and with food preferences of the bats. However, an unbiased and specific methodology is required to determine the effects of abundance, distance and palatability of cactus fruit as food for these long-nosed bats.

**Table 1.** Species number and percent of seeds obtained in the Obispo Cave.

CACTUS FRUIT SPECIES	SEEDS NUMBER	%
<i>Isolatocereus dumortieri</i>	12,231	38.3
<i>Stenocereus pruinosus</i>	8,361	26.2
<i>Stenocereus stellatus</i>	3,793	11.8
<i>Neobuxbaumia macrocephala</i>	2,562	8.03
<i>Neobuxbaumia mezcalaensis</i>	771	2.41
<i>Polaskia chichipe</i>	742	2.32
<i>Stenocereus marginatus</i>	615	1.92
<i>Myrtillocactus shenkii</i>	521	1.63
<i>Stenocereus griseus</i>	519	1.62
<i>Pachocereus weberi</i>	400	1.25
<i>Cephalocereus columna-trajani</i>	380	1.19
<i>Myrtillocactus geometrizans</i>	367	1.15
<i>Neobuxbaumia tetetzo</i>	268	0.84
<i>Polaskia chende</i>	164	0.51
<i>Escontria chiotilla</i>	89	0.27
<i>Pachocereus hollianus</i>	71	0.22
<i>Hylocereus undatus</i>	46	0.14
<i>Pachocereus fulviceps</i>	47	0.14
<i>Pilosocereus chrysacanthus</i>	28	0.08
<i>Acanthocereus subinermis</i>	14	0.04
<i>Stenocereus treleasi</i>	5	0.01
<b>Total</b>	<b>31,895</b>	<b>100</b>

In spite of these possible biases, three fruit species represented 70% of seeds recovered inside the cave, and likely this high frequency is robust. *S. stellatus* and *S. pruinosus* are cultivated cactus that seasonally have abundant fruit next the cave, but *I. dumortieri* is a rare columnar cacti in the Tehuacan valley, and this suggests that *L. yerbabuenae* may has preferences for this species of fruit and therefore searches actively for it. In the Tehuacan Valley, the long nosed bats are able to consume fruits of all the columnar cactus species that inhabit this semiarid zone, in spite of the common statement that they occasionally feed on fruits (Villa 1967; Gardner 1977; Howell 1980; Sánchez 1984; Cockrum 1991; Fleming and Sosa 1994; Valiente-Banuet *et al.* 1996). The present study supports the suggestion that these bats are important consumers of fruit and possible dispersers of seeds in dry environments (Sosa and Soriano 1993; Fleming and Sosa 1994; Ruiz *et al.* 1997; Godínez-Álvarez and Valiente-Banuet 2000; Godínez-Álvarez *et al.* 2002). The great diversity of seeds found in the guano of *L. yerbabuenae* suggests that the fruits are a common food for this nectar-feeding bat in central Mexico. The importance of this food habit has not been recognized before, although since 1970, detailed studies of the lesser

long-nosed bat diet have been undertaken (Alvarez and González, 1970; Hevly 1979; Arizmendi *et al.* 2002). The importance of frugivory has been probably underestimated due to three causes: 1) the brief retention time of the food in the bat gut (*ca.* 20 min according to Howell 1974; Godínez-Alvarez and Valiente-Banuet, 2000), 2) bats spit out the seeds while consuming the pulp of the fruits (Godínez-Alvarez and Valiente-Banuet 2000), and 3) many bats frequently defecate when being caught in mist-nets (Thomas 1988). The great diversity of seeds detected inside the roost shows the importance of frugivory for these nectar-feeding bats and shows the need to complement studies of bat diet with the analysis of the food remains accumulated in their roosts (Thomas 1988). Seeds carried inside caves represent the last part of the nocturnal feeding activity of the bats, because to survive on floral products, these bats must alternate feeding episodes periods with rest and defecation periods, about 12 times each night (Howell 1974; Godínez-Alvarez and Valiente-Banuet 2000). If these estimates are correct, seeds placed inside the caves are approximately 8.3% of the seeds dispersed each night in the field.

The importance of frugivorous bats (Stenodermatinae: Phyllostomidae) as seed dispersers in the humid tropics of the New World are well known (Gardner 1977; Heithaus 1982; Muscarella and Fleming 2007). In moist environments of the New World, fruit-feeding bats are high-quality dispersal agents, capable of dispersing thousands of seeds to potential safe sites each night (Heithaus 1982; Bonaccorso and Humphrey 1984; Fleming 1988; Muscarella and Fleming 2007). Seeds swallowed by bats, not only evade seed predators that are concentrated near the fruiting plants (Godínez-Alvarez *et al.* 2002), but may be released from inhibitors of germination through the bat's digestive enzymes, accelerating their germination. In this way, bats contribute to the regeneration of the disturbed environments and to maintenance of vegetative cover in humid tropical regions (Heithaus 1982).

In arid and semiarid environments, the idea that this process is nonexistent prevails because juicy fruit has been considered scarce (Silvius 1995) and frugivorous bats uncommon (Arita 1993). Previous affirmation ignores the existence of columnar cacti, which are very abundant and diverse in dry tropical environments of the south-central and Pacific Coast region of Mexico (Valiente-Banuet *et al.* 1996; Rojas-Martínez *et al.* 1999). In these rich columnar cactus communities, juicy fruits are seasonally abundant and seasonally complementary. For example in the Tehuacan Valley, columnar cactus forests can produce 815 kg ha<sup>-1</sup> of fruit during the spring and the summer, while in the fall and winter, in tropical deciduous forests, cactus fruit production has been estimated at 1,100 kg ha<sup>-1</sup> (Rojas-Martínez 2001). Seed dispersal in dry environments is undoubtedly an essential mechanism for maintenance of vegetation, because places that favor seedling survival are scarce and discrete in dry environments (Drezner and Lazarus 2008) where the lack of water strongly limits the establishment of the plants (Godínez-Alvarez *et al.* 2002). For example in deserts, the successful establishment of columnar cacti occurs only in suitable sites beneath the canopies of perennial nurse plants, which ameliorate environmental conditions, enhancing seed germination, and seedling survivorship (Valiente-Banuet and Ezcurra 1991; Drezner and Lazarus 2008). In deserts, bats are able to act as effective dispersers by depositing seeds under the shade of nurse plants, while resting among branches of the shrubs (Howell 1974; Godínez-Alvarez and Valiente-Banuet 2000; Godínez-Alvarez *et al.* 2002; Castillo 2011).

This process can be intense because, under experimental conditions, *L. yerbabuenae* removes 75% of the pulp and seeds from fruits of the columnar cactus, *Neobuxbaumia tetetzo*, in the Tehuacan Valley (Godínez-Alvarez and Valiente-Banuet 2000), and 10 to 80% in the Sonoran Desert for *Carnegiea gigantea*, *Pachycereus pringlei*, and *S. thurbery* (Fleming and Sosa 1994). Considering that some fruits of *N. tetetzo* can contain more than 700 seeds (Godínez-Alvarez and Valiente-Banuet 2000), and that Obispo Cave can house more than 100,000 bats (Rojas-Martínez, unpubl. data), each night hundreds of thousands of seeds may be dispersed in the Tehuacan Valley.

We can conclude that mutualistic interactions between long nosed-bats and columnar cacti are more complex than have been considered previously. Columnar cacti take advantage of the nectar-feeding bats as pollinators and dispersers. In turn, bats complement their nectar and pollen diet, significantly consuming fruit at times when flowers are scarce (winter fruiting species). They therefore obtain nourishment when others foods are scarce (Rojas-Martínez 2001). Moreover, the hypothesis of seasonal migration of this bat (Fleming *et al.* 1993) needs to be reconsidered. Although evidence suggests that these bats are important for recruitment of columnar cacti in dry environments, their relative role as seed dispersers remains as an open question for future investigation. So far, little research has been conducted on this topic (Godínez-Alvarez and Valiente-Banuet 2000; Godínez-Alvarez *et al.* 2002; Castillo 2011).

Considering information found in the literature about the feeding habits of phyllostomid bats as well as the results of our study, it is possible to hypothesize that the lesser long-nosed bat should play a key role in the maintenance of biodiversity in dry environments, because they can feed on 21 different species of columnar cacti in south-central Mexico, and four other species in northwestern Mexico (Dalquest 1953; Villa 1967; Fleming and Sosa 1994; Gardner 1977). Therefore, *L. yerbabuenae* may consume the fruits of 25 different species of cacti in the Americas, 18 of which are reported here for the first time. In conclusion, results obtained from seeds found in long-nosed bat guano obtained from one roosts localized in the Tehuacan Valley, suggest that *L. yerbabuenae*, a bat species considered highly specialized to consume nectar and pollen, has an important function as a fruit-feeder and seed disperser of columnar cactus. The magnitude of this process may be similar to that previously reported for bats in the humid neotropical forest. These bats may be a key component in maintaining the plant structure of the tropical dry ecosystems dominated by columnar cactus. Future, well-designed studies of the magnitude and spatial extent of the dispersal process are required to evaluate the importance of bat-cactus interaction in the Tehuacán Valley, Mexico, and to inform efforts for conservation of this highly biodiverse dry community.

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## References

- Álvarez, T., and Q. L. González.** 1970. Análisis polínico del contenido gástrico de murciélagos Glossophaginae de México. *Anales de la Escuela Nacional de Ciencias Biológicas* 18:137-165.
- Arita, H. T.** 1993. Riqueza de especies en la mastofauna de México. Pp. 109-128 in *Avances en el estudio de los mamíferos de México* (Medellín, R. A., and G. Ceballos, eds.). Publicaciones especiales 1, Asociación Mexicana de Mastozoología A. C. México.
- Arizmendi, Ma. del C., A. Valiente-Banuet, A. Rojas-Martínez, and P. Dávila-Aranda.** 2002. Columnar cacti and the diets of nectar-feeding bats. Pp. 264-282 in *Columnar cacti and their mutualists: Evolution, ecology, and conservation* (Fleming T. H., and A. Valiente-Banuet, eds.). The University of Arizona Press. Tucson, USA.
- Barthlott, W., and D. Hunt.** 2000. Seed-diversity in the Cactaceae, subfamily Cactoideae. *Succulent plant research*. Vol.5. David Hunt, United Kingdom.
- Bonaccorso, F. J., and S. R. Humphrey.** 1984. Fruit bat niche dynamics: their role in maintaining tropical forest diversity. Pp. 169-183 in *Tropical-rain forest: The Leeds Symposium* (Chadwick A. C., and S. L. Sutton, eds.). Philosophical and Literary Society, United Kingdom.
- Castillo, L. J. P.** 2011. Dispersión biótica de semillas de la cactácea columnar *Neobuxbaumia mezcalaensis* (Bravo) Backeberg en el valle de Tehuacán, Puebla. Ph. D. Thesis. Instituto de Ecología. Universidad Nacional Autónoma de México. Mexico city, Mexico.
- Cockrum, E. L.** 1991. Seasonal distribution of northwestern populations of the nosed bats, family Phyllostomidae. *Anales del Instituto de Biología. Serie Zoología* 62:181-202.
- Dalquest, W. W.** 1953. Mammals of the Mexican state of San Luis Potosi. *Louisiana State University Studies, Biological Scientist Series* 1:1-229.
- Dávila, A. P., J. L. Villaseñor, L. R. Medina, R. A. Ramírez, T. A. Salinas, J. Sánchez-Ken, and L. P. Tenorio.** 1993. Flora del Valle de Tehuacán-Cuicatlán. Listados florísticos de México X. Instituto de Biología, Universidad Nacional Autónoma de México. Mexico city, Mexico.
- Drezner, T. D., and B. L. Lazarus.** 2008. The population dynamics of columnar and other cacti: A review. *Geography Compass* 2:1-29.
- Faegri, K., and L. Van der Pijl.** 1979. *The principles of pollination ecology*. Third edition. Pergamon Press. Oxford, United Kingdom.
- Fleming, T. H.** 1988. *The short-tailed fruit bat*. University of Chicago Press. Chicago, USA.
- Fleming, T. H., and V. Sosa J.** 1994. Effects of nectarivorous and frugivorous mammals on reproductive success of plants. *Journal of Mammalogy* 75:845-851.
- Fleming, T. H., R. A. Nuñez, and L. S. Sternberg.** 1993. Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. *Oecologia* 94:72-75.
- García, E.** 1973. Modificaciones al sistema de clasificación climática de Köppen. Instituto de Geografía, Universidad Nacional Autónoma de México. Mexico city, Mexico.



- Gardner, A. L.** 1977. Feeding habits. Pp. 239-350 in Biology of bats of the new world family Phyllostomidae (Baker, R. J., J. K. Jones, and D. C. Carter, eds.). Part II. Special Publications Museum 13. Texas Tech University. Lubbock, USA.
- Godínez-Alvarez, H., and A. Valiente-Banuet.** 2000. Fruit-feeding behavior of the *Leptonycteris curasoae* and *Choeronycteris mexicana* in flight cage experiments: consequences for dispersal of columnar cactus seeds. *Biotropica* 32:552-556.
- Godínez-Álvarez, H., A. Valiente-Banuet, and A. Rojas-Martínez.** 2002. The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology* 83:2617-2629.
- Hall, E. R.** 1981. The mammals of North America. John Wiley and Sons. New York, USA.
- Heithaus, R. H.** 1982. Coevolution between bats and plants. Pp. 327-361 in Ecology of bats. (Kunz T. H., ed.). Plenum Press. New York, USA.
- Hevly, R. H.** 1979. Dietary habits of two nectar and pollen feeding bats in Arizona and Northern Mexico. *Journal of Arizona-Nevada Academic Science* 14:13-18.
- Howell, D. J.** 1974. Bats and pollen: physiological aspects of the syndrome of chiropterophily. *Comparative Biochemistry and Physiology* 48:263-276.
- Howell, D. J.** 1980. Adaptative variation in diets of desert bats has implications for evolution of feeding strategies. *Journal of Mammalogist* 61:730-733.
- Muscarella, R., and T. H. Fleming.** 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews* 82:573-590.
- Rojas-Martínez, A.** 2001. Determinación de los movimientos altitudinales estacionales de tres especies de murciélagos nectarívoros (Phyllostomidae: Glossophaginae) en el Valle de Tehuacán y la cuenca del Balsas, México. Ph. D. Thesis. Facultad de Ciencias. Universidad Nacional Autónoma de México. Mexico city, Mexico.
- Rojas-Martínez, A. E., and A. Valiente-Banuet.** 1996. Análisis comparativo de la quiropterofauna del Valle de Tehuacán-Cuicatlán con respecto a las zonas áridas y dos localidades tropicales costeras de Norte América. *Acta Zoológica Mexicana* (n. s.) 67:1-22.
- Rojas-Martínez, A., A. Valiente-Banuet, Ma. del C. Arizmendi, A. Alcantara-Eguren, and H. T. Arita.** 1999. Seasonal distribution of the long-nosed bat (*Leptonycteris curasoae*) in North America: does a generalized migration pattern really exist? *Journal of Biogeography* 26:1065-1077.
- Rzedowski, J.** 1978. *Vegetación de México*. LIMUSA. Ciudad de México, México.
- Ruíz, A., M. Santos, J. P. Soriano, and A. Cadena.** 1997. Relaciones mutualistas entre el murciélago *Glossophaga longirostris* y las cactáceas columnares en la zona árida de la tatacoa, Colombia. *Biotrópica* 29:469-479.
- Silvius, K. M.** 1995. Avian consumers of cardón fruits (*Stenocereus griseus*: Cactaceae) on Margarita Island, Venezuela. *Biotrópica* 27:96-105.
- Sosa, M. and P. J. Soriano.** 1993. Solapamiento de dieta entre *Leptonycteris curasoae* y *Glossophaga longirostris* (Mammalia: Chiroptera). *Revista de Biología Tropical* 41:529-532.
- Thomas, D. W.** 1988. Analysis of diets of plant-visiting bats. Pp. 211-220 in Ecological and behavioral methods for the study of bats (Kunz T. H., ed.). Smithsonian Institution Press. Washington, USA.

- Valiente-Banuet, A., M. del C. Arizmendi, A. Rojas-Martínez, and L. Domínguez-Canseco.** 1996. Ecological relationships between columnar cacti and nectar-feeding bats in Mexico. *Journal of Tropical Ecology* 12:103-119.
- Valiente-Banuet, A., Casas A., A. Alcántara, P. Dávila, N. Flóres-Hernández, M. C. Arizmendi, J. L. Villaseñor, and J. Ortega.** 2000. La vegetación del Valle de Tehuacan-Cuicatlán. *Boletín de la Sociedad Botánica de México* 67:24-74.
- Valiente-Banuet, A., and E. Ezcurra.** 1991. Shade as a cause of the association between cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, Mexico. *Journal of Ecology* 79:961-971.
- Valiente-Banuet, A., A. Rojas-Martínez, M. del C. Arizmendi, and P. Dávila.** 1997a. Pollination biology of two columnar cacti (*Neobuxbaumia mezcalaensis* and *Neobuxbaumia macrocephala*) in the Tehuacan Valley, central Mexico. *American Journal of Botany* 84:452-455.
- Valiente-Banuet, A., A. Rojas-Martínez, A. Casas, M. del C. Arizmendi, and P. Dávila.** 1997b. Pollination biology of two winter-blooming giant columnar cacti in the Tehuacan Valley, central Mexico. *Journal of Arid Environmet* 37:331-341.
- Villa, R. B.** 1967. Los murciélagos de México. Instituto de Biología. Universidad Nacional Autónoma de México. Mexico city, Mexico.

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