DIET AND CRANIAL MORPHOLOGY OF MUSONYCERYS HARRISONI, A HIGHLY SPECIALIZED NECTAR-FEEDING BAT IN WESTERN MEXICO

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We studied the morphology and diet of Musonycteris harrisoni, an endangered nectar-feeding bat endemic to western Mexico, and explored potential reasons for the cranial specialization of this extraordinarily long-snouted bat. We achieved 28 captures in the wet season and 30 in the dry season, which represents the largest data set in existence for this rare species. We took morphological data and collected pollen from the bats’ pelage. Diet analysis revealed the genera Cleome, Pseudobombax, Crataeva, Agave, Helicteres, and the columnar cactus Pachycereus pecten-aboriginum as main food plants. We found no indication for a tight relationship between M. harrisoni and long-tubed flowers that would obligatorily require a long rostrum for exploitation, with the possible exception of the columnar cactus. However, because cacti are common food plants for many less-specialized nectar-feeding bats, the extraordinarily long rostrum might permit M. harrisoni to use the same abundant plant species as larger species while maintaining a smaller body size, therefore having lower absolute energy requirements. This in turn could facilitate a resident lifestyle in a habitat with annual resource bottlenecks. Males have significantly longer snouts (approximately 9%) than females, suggesting that rostrum length also might be influenced by intraspecific interactions or restrictions. Our favored explanation is that the rostrum length of females may be limited by stability issues, because calcium mobilization during pregnancy and lactation can considerably weaken bone structure.

Key words: Cactaceae, Colima, conservation, dry forest, endangered bats, evolution, pollination, sexual dimorphism, tongue length

The neotropical nectar-feeding bats (Phyllostomidae: Glossophaginae) comprise approximately 40 species that differ widely in their dependence on a diet of nectar. Several species within this subfamily do not feed exclusively on nectar and there are even reports that treat some glossophagine species as frugivorous or insectivorous (Gardner 1977; Sazima 1976; Willig 1983). However, the main autapomorphic adaptations of the group clearly point to a diet of nectar: the bats visit flowers in a specialized hovering flight, and their long tongue, which may exceed two-thirds of the body length, allows extracting nectar from flowers (Tschapka and Dressler 2002; Winter and von Helversen 2003). The dentition is partially reduced, and particularly in the higher specialized species the lower incisors are missing, allowing improved movement of the tongue (Freeman 1995). However, the most obvious morphological character is an elongated rostrum that varies from moderate elongation in the generalist Glossophaga species to extreme elongation in specialists (Freeman 1995), for example, in Platalina genovensium from the Peruvian deserts or in the morphologically most specialized glossophagine Musonycteris harrisoni (Schaldach and McLaughlin 1960) from the tropical dry forests of Mexico.

Musonycteris harrisoni is endemic to western Mexico with a main distribution in the states of Colima, Michoacán, and Guerrero, and is one of the phyllostomid bats with the smallest distribution areas of all, covering only approximately 20,000 km². The species is characterized by an extremely long rostrum, as is adequately reflected in its common name, murciélago trompudo (Schaldach and McLaughlin 1960; Villa-R. 1967). Although other nectar-feeding bats may shift their main diet from nectar to fruits or insects for part of the year (Gardner 1977; Howell and Burch 1974; Tschapka 2004), the long jaws largely exclude M. harrisoni from the use of nonliquid food resources such as fruits and insects for leverage reasons (Aguirre et al. 2003; Freeman 1995). Very few data are available on the food plants of M. harrisoni (Tellez and Ortega

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were interested in the diet of *M. harrisoni* on bat activity. Occasional mistnetting at cactus flowers was only moderate amounts of insecticides and fertilizers. They were nonindustrialized, small-scale family businesses that used the area is characteristic of a tropical deciduous forest, *baja caducifolia* (Rzedowski 1983). In the laboratory, the gelatin was melted with a cover slip on a glass slide and analyzed under a light microscope using a magnification of 40–400×. Pollen was identified using a reference collection from the area as well as samples taken from herbarium specimens from the National Herbarium, Mexico City. Pollen identification was aided by taking into account plants found flowering during our fieldwork, as well as by a literature review from related study sites (Alvarez and Sanchez-Casas 1997; Chávez 1975; Stoner et al. 2003). Pollen was recorded on a presence–absence scale, but only when 5 or more pollen grains of the same species were found in a sample. Diet diversity between the dry season and the wet season was compared using the Shannon–Wiener diversity index:

\[
H' = -\sum p_i \ln p_i,
\]

with \(p_i\) being the proportion of the examined individual samples containing plant species \(i\) in the pollen records for a season. In addition, we collected fecal samples opportunistically from captured individuals and examined them under the microscope for plant and animal material.

**RESULTS**

**Capture results.**—During the main study period we accumulated data on 563 captures of nectar-feeding bats over 76 nights, including 53 captures of *M. harrisoni*. The entire guild of nectarivorous bats present at the study site included *Glossophaga soricina*, *Leptonycteris curasoae*, and *Anoura geoffroyi*. Because large numbers of *G. soricina* and *L. curasoae* were frequently captured in our nets, we were unable to process all individuals of these 2 species within a reasonable amount of time. The total number of captured bats was therefore much higher than the 563 captures noted above, and consequently our 53 captures of *M. harrisoni* overestimate the relative abundance of the species within the local guild. Five earlier captures from March 1996 and July 2001 were added to the main data set, so we had a total of 58 captures (27 females and 31 males) that provided data for the diet analysis. Because 6 individuals (1 female and 5 males) were recaptured at least once, including 2 males that were captured 3 times each, the total number of individuals was 50 (26 females and 24 males). Recaptures were always less than 1 km apart; most were within 100 m of the initial capture.

Capture success for *M. harrisoni* in the banana plantations varied distinctly between field seasons. Although we caught an average of about 1 bat per night in both wet season (26 *M. harrisoni*/25 nights) and dry season (23 *M. harrisoni*/23 nights), captures were extremely low in the early dry season.
During that time, only 1 M. harrisoni was captured at our usual capture locations within the banana plantations, whereas the remaining 3 bats were caught on 2 evenings using an elevated mist net in front of a flowering cactus (Pachycereus pecten-aboriginum). On 1 of these evenings we also videotaped another M. harrisoni visiting the flowers of P. pecten-aboriginum.

Eight lactating females were caught in the dry season between mid-March and mid-April. Females caught between July and September showed no signs of advanced pregnancy or lactation, so M. harrisoni seems to reproduce during the dry season and only once a year. One adult, non-reproductive female was captured in August 2002 and subsequently lactating when recaptured in March 2003.

Morphology.—Forearm length did not differ between adult males (X = 43.2 mm, SD = 0.70 mm, n = 20) and females (X = 43.1 mm, SD = 0.71 mm, n = 26; Student’s t-test; t = 0.570, d.f. = 44, P = 0.572). Body mass of animals varied significantly between adult males (X = 12.13 g, SD = 0.88 g, n = 20) and nonpregnant females (X = 11.14 g, SD = 0.84 g, n = 22; t = 3.701, d.f. = 40, P < 0.001). Rostrum length varied significantly between males (median = 20 mm, range 19–21 mm, n = 24) and females (median = 18.5 mm, range 17–19.5 mm, n = 26; Mann–Whitney rank sum test; T = 918.500, d.f. = 48, P < 0.001; Fig. 1). Even after standardization for body size by dividing by the cubic root of the respective body mass (Winter and von Helversen 2003), males had significantly longer rostra than females (Student’s t-test; t = 7.853, d.f. = 48, P < 0.001).

Diet.—Based on 84 pollen findings, we deduced that M. harrisoni visited at least 14 pollen-producing plant species during the annual cycle. Additionally, these bats were using the cultivated bananas (Musa) that did not produce any pollen (Fig. 2). Bats used 9 plant species during the dry season, and 6 species during the rainy season. Only Cleome spinosa (Capparaceae) was visited during both seasons. Diversity of the diet of M. harrisoni as measured by the Shannon–Wiener diversity index was 1.76 during the dry season and 1.38 during the rainy season. An individual M. harrisoni in the dry season had visited an average of 2.03 (SD = 1.07, n = 30) plant species before capture, whereas during the rainy season this value dropped significantly to 0.82 (SD = 0.72, n = 28; Mann–Whitney rank sum test; T = 563.5, d.f. = 56, P < 0.001). There was no difference in plant use between males and females over the entire year (chi-square test: χ² = 11.442, d.f. = 13, P = 0.574).

The 6 most important food plants (86% of all pollen findings) were a cactus (judging from the local abundance and flowering time this was probably P. pecten-aboriginum), a group of Bombacaceae (including mainly Pseudobombax ellipticum, and probably Bombax palmeri and Ceiba asclepiadifolia), Crataeva palmeri and Cleome spinosa (Capparaceae), Helicteres baruensis (Sterculiaceae), and Agave colima (Agavaceae). All other plants were found only on a few animals and therefore are probably not key parts of the species diet.

**Fig. 1.—** Rostrum length in males of Musonycteris harrisoni is significantly longer than in females (Mann–Whitney rank sum test; P < 0.001). Data from 24 male and 26 female bats.

**Fig. 2.—** Diet of Musonycteris harrisoni from pollen found in the pelage. Data are from 30 captures from the dry season and 28 captures from the rainy season. 100% refers to the total number of bats captured in dry and rainy season, respectively.
diet. Only 6 M. harrisoni produced fecal samples. All of the fecal samples contained pollen and 2 of these samples (1 from a male and 1 from a female) also contained a modest amount of insect parts, probably from small Lepidoptera. We did not find any indication of fruit consumption.

Food plant morphology.—Most of the main food plants used by M. harrisoni had brush-type flowers (Capparaceae and Bombacaceae) that presented nectar openly to approaching visitors (Figs. 3a, 3c, and Fig. 4). Helicteres baruensis (Fig. 3b) had a 3.5-cm-deep calyx, and the almost 4-cm protruding complex of stamens and stigma made this plant’s morphology similar to that of the brush type. Agave colimana showed a comparable morphology with an approximately 4-cm floral tube and stamens exceeding the corolla up to 5 cm. Only the early-dry-season–flowering columnar cactus P. pecten-aboriginum had a long corolla tube of 7–9 cm (Fig. 3d).

Habitat use.—Because of difficult terrain, we were not able to follow the 3 radioequipped animals continuously during the night. However, all animals were observed to move back and forth between the banana groves and the adjacent natural selva baja vegetation, thus further confirming a diet that included both forest and cultivated plant species.

**DISCUSSION**

Diet and cranial morphology.—Before our study, only 4 native plant species were known to be used as food by M. harrisoni: pollen from Cordia alliodora, Ceiba pentandra, and Ipomoea were found on the pelage and in stomachs of 5 individuals (Alvarez and Sanchez-Casas 1997), and Stoner et al. (2002) videotaped the species visiting Ceiba grandiflora (Bombacaceae). Our study adds at least 12 new native plants to the known diet of the species. We found no pronounced use of particularly long-tubed flowers; on the contrary, several of the important food plants have very short corollas and offer the nectar openly (Figs. 3a and 3c). The flowers of Helicteres baruensis (Sterculiaceae; Fig. 3b) are short and are visited by unspecialized glossophagine bats in Costa Rica and Brazil (Sazima and Sazima 1988; von Helversen and Voigt 2002). The columnar cactus P. pecten-aboriginum (Fig. 3d) was a noteworthy example of a large-flowered exception. However, flowers of columnar cacti also are frequently visited by other bats with shorter rostra than Musonycteris, such as Leptonycteris, Choeronycteris mexicana, and even the unspecialized Glossophaga (Arizmendi et al. 2002; Dobat and Peikert-Holle 1985; Petit 1997; Petit and Pors 1996).

Because our sampling covered only January–April and July–October, a hypothetical long-tubed flower could still represent a critical resource for M. harrisoni for a short period of the year, either in May–June or November–December. In order to exert significant selective pressure on the bat, such a plant would need to be rather common and monopolizable, so that its use would gain Musonycteris a distinct advantage over the coexisting glossophagine species. However, for evolutionary reasons, this is rather unlikely. For the plant, dependence on a single, rare bat species would be a rather unstable strategy evolutionarily, especially when coupled with a short flowering period. Furthermore, exploitation of long-tubed flowers seems to be
more expensive than exploitation of shorter flowers. Lapping frequency of *Glossophaga* is 12 Hz when feeding on a pipette next to the snout but it drops to 4–5 Hz when reaching with the tongue 35 mm into a tube (von Helversen and von Helversen 1975; Winter 1998; Winter and von Helversen 2003). Assuming nectar uptake is a direct function of lapping frequency, this translates into longer hovering times in front of long-tubed flowers for extracting the same amount of nectar than from a shorter flower. Given the cost-efficiency found in many aspects of glossophagine behavior and choice of food plant (Tschapka 2004; von Helversen and Winter 2003), such flowers would be less attractive in the presence of alternative food plants, thus selecting against a tight coevolution. For the same reason, pollinator-mediated intraspecific selection should strongly favor individual plants with more easily accessible shorter flowers, thus further selecting against a one-to-one coevolution between long-tubed flowers and a long-snouted bat species.

Muchhala (2006) suggests that the recently described extremely long-tongued glossophagine bat, *Anoura fistulata*, from Ecuador (Muchhala et al. 2005) has coevolved with particularly long-tubed flowers. Because of a unique anatomical storage solution, the length of the tongue of *A. fistulata* almost doubles that of all sympatric glossophagine species. In contrast to *A. fistulata*, however, *M. harrisoni* seems to follow the correlation between rostrum and tongue length that is typical for glossophagines (Gonzalez et al. 2007; Winter and von Helversen 2003), thus the difference in tongue reach compared to the coexisting species is much smaller. Selection on a plant to coevolve exclusively with *Musonycteris* for pollination should therefore be much weaker than in *A. fistulata*.

Perhaps the main reason for the cranial specializations of *M. harrisoni* is not long-tubed flowers, but the necessity for an efficient use of all available chiropterophilous flowers in western Mexican ecosystems. Examination of our data confirms the prediction from Simmons and Wetterer (2002) that *M. harrisoni* frequently visits the large flowers of columnar cacti. It is noteworthy that some of the most specialized glossophagine bats are associated with cacti. For example, in addition to the North American *M. harrisoni* and *C. mexicana*, the South American species *Platalina genovensium* also is associated with cacti (Shahley and Baraybar 1996; Simmons and Wetterer 2002). The “oversized” rostrum and the associated long tongue (Winter and von Helversen 2003) might allow the small *M. harrisoni* to extract nectar even from large cactus flowers, in similar fashion to larger nectar-feeding bat species such as *L. curasoeae*, while at the same time retaining a small body size, thus requiring less food per unit time (von Helversen and Winter 2003). By using a broad spectrum of plants, the rare *M. harrisoni* may persist at low population densities during nectar bottleneck periods without the necessity to switch their main diet seasonally like *Glossophaga* (Tschapka 2004) or migrating such as *Leptonycteris*. A comparable situation was found in the rare Central American rain-forest bat *Hylonycteris underwoodi*, which also has the longest rostrum of all sympatric glossophagine species and lives year-round on nectar (Tschapka 2004). Therefore, morphological adaptations and the low abundance of such rare, nectar-specialized bats might be attributable to a life history adapted to surviving low availability of nectar resources in bottleneck situations during the annual cycle. Additionally, the long rostrum and the associated long tongue (Freeman 1995; Winter and von Helversen 2003) might give *M. harrisoni* an advantage at deeper flowers by being able to extract even small amounts of nectar that are beyond the reach of the other species. Such

**Fig. 4.**—Female *Musonycteris harrisoni* with inflorescence of *Cleome spinosa* (Capparaceae). Photo from flightcage, April 2006, Callejones, Mexico.
a competitive advantage, however small, might further aid the species to lead a resident lifestyle, rather than being forced to undergo seasonal migrations. Comparative experiments on the nectar extraction capabilities of coexisting glossophagine species might help to understand the actual performance differences between the sympatric species.

Seasonal resource landscape.—Several data sets indicate that nectar availability in the natural vegetation varied distinctly over the year. First, our extremely low capture rate during the early dry season coincided with the flowering of the abundant, bat-pollinated columnar cactus _P. pecten-aboriginum_. Mist-net captures as well as video observations at cactus flowers at that time confirmed that _Musonycteris_ regularly visited _Pachycerus_. Although banana inflorescences may produce several milliliters of nectar per night (Liu et al. 2002), many cultivated varieties lack pollen, which especially for highly specialized glossophagines is an important source of proteins (Herrera and Martínez del Río 1998). The low capture rates at the plantations during the early dry season suggest an increased seasonal abundance of higher-quality resources in the natural vegetation, probably due to _P. pecten-aboriginum_. Second, an average of 0.82 plant species visited per bat before capture in the rainy season, compared to 2.03 plant species in the dry season, confirms the change in natural flower availability and indicates that some bats even used the pollenless bananas as their main food source in the rainy season. It is possible that we owe our high capture success of the rare _M. harrisoni_ (up to 1 animal per night) to the nonindustrialized banana plantations buffering periods of low nectar availability, thus permitting a relatively high local population density.

In spite of an obviously variable floral resource environment, _M. harrisoni_ was a year-round resident in the study area, which might be also related to its body size. Migrations following regional nectar availability (Fleming et al. 1993) are known so far only from larger glossophagine species such as _Leptonycteris, C. mexicana_, and to a lesser extent, _A. Geoffroyi_ (Arroyo-Cabral et al. 1987; Fleming et al. 1993; Galindo-Galindo et al. 2000; Ramírez-Pulido et al. 2001). A key factor for migration in glossophagines over larger distances seems to be a large body size that permits storing energy for traveling over areas without available food (von Helversen and Winter 2003). Following this idea, _C. mexicana_ might be the larger, migrating version of the small, resident sister taxon _M. harrisoni_ (Carstens et al. 2002). Resident species (compared to a migrating species) may know their relatively small home ranges on a fine-grained level, including also locations of less-profitable food plant species. Migrating species, on the other hand, tend to focus on predictably flowering, high-quality resources (von Helversen and Winter 2003).

_Musonycteris harrisoni_ occurs only in the subtropical semi-arid lowlands on the west coast of Mexico and does not extend farther north than the state of Jalisco (Tellez and Ortega 1999). Our data show that dependence on a long-flowered food plant species does not appear to be among the factors determining this geographical distribution. Instead, limiting factors may include thermoregulation, with the small body size of _Musonycteris_ not permitting ventures into cooler areas of the higher Sierras, as well as the necessity for year-round nectar availability. In the northern deserts of Mexico, columnar cacti and _Agave_ only provide a seasonal supply of nectar. These plants are visited by seasonally migrating bats such as _L. curasoeae_ and _C. mexicana_ or by diet-switching species such as _Glossophaga_ that may also use alternative types of food at other times of the year. Nectar availability and night temperatures during the winter months might be simply too low in the northern deserts (Fleming et al. 2001; Scott 2004) to allow a continuous presence of the nonmigratory, strictly nectarivorous _M. harrisoni_.

Sexual dimorphism of the rostrum.—The difference in rostrum length between males and females (Fig. 1) is obvious when seeing both sexes at the same time. We detected no significant difference between the diets of males and females, so it is unlikely that resource partitioning between the sexes (Selander 1966; Temeles et al. 2000) is the cause for this sexual dimorphism.

A 2nd possibility is that snout morphology of males plays an ornamental role for mate choice by females or is used in antagonistic interactions between competing males. However, no indications of such a direct role of rostrum morphology in mating behavior have been reported for microchiropterans. In a more indirect way, glossophagines frequently vocalize in a social context, and although no specific mating calls are known for glossophagines, rostrum morphology may shape frequency response of the vocal apparatus, which in turn might influence mate choice by females.

We favor a 3rd possibility. The delicate rostrum of the species, together with the lightweight bone architecture in bats (Neuweiler 2000), might be pushing the stability limit of mammalian bone structures. Because of its size and uniquely elongated rostrum, _M. harrisoni_ is among the mammals with the most delicate skull structures. Stability issues could become critical in females during reproduction, especially because calcium has been suspected to be a limiting factor in bat reproduction (Barclay 1994, 2002). Following this idea, the considerable calcium mobilization from the skeleton during pregnancy and lactation (Kwiecinski et al. 1987; Wysolmerski 2002) would restrict the females to a shorter and therefore more robust rostrum. Given the increased nutritional requirements of reproducing females, a more robust skull certainly would also be advantageous for consuming insects, fruit, or both.

Conservation aspects.—We found no indication for dependence on a particular species of food plant whose protection would be crucial for the survival of the species. Some of the main food plants such as columnar cacti, _Agaves_, and species of Bombacaceae are common members of the Mexican Pacific dry forest, the sole habitat of _M. harrisoni_. However, dry forests are among the most endangered habitats in Mexico, because of increasing human population pressures (Bullock et al. 1995; Janzen 1988). This aspect, combined with the natural rarity of the species, poses a significant potential danger for the species and consequently the Mexican government categorized it as “threatened” (Secretaría de Medio Ambiente y Recursos Naturales 2002), and the International Union for the Conservation of Nature and Natural Resources lists it at “vulnerable” (Tellez and Ortega 1999). Other researchers have found _M._
columnar Pseudobombax podríana requerir un rostro largo para su explotación, con la M. harrisoni relaciones cercanas entre pelaje. El análisis de la dieta reveló los géneros especie. Tomamos datos morfológicos y colectamos pollen del representa la base de datos más grande en existencia de esta capturas en la temporada de lluvias y 30 en secas, lo que largo del rostro extraordinariamente alargado. Obtuvimos 28 posible excepción del cacto columnar. Sin embargo, dado que especies de murciélagos nectarívoros menos especializados, el los cactos son fuentes comunes de alimento para muchas ecología son urgentemente necesitadas para designar un programa hospitalidad y el kind permission to work on their property. Crucial durante el initial phase of the project came from H. Arita from support during the initial phase of the project came from H. Martínez- Hernandez (National Herbarium, Mexico City) and H. Behling (University of Götingen). It was a pleasure to share the fieldwork con E. Kalko, L. B. Vazquez, S. Gallo, R. Sanchez, Y. Rodriguez, V. Rosa, C. Rothenwöhler, and N. Becker. The picante de Doña Rosa, who cooked for us in Callejones, deserves an honorable mention. Financial support for the project came first from a grant of the National Geographic Society, from the Programa para la Conservación de los Murciélagos de México, and the Wildlife Trust Alliance. Scientific collecting permits were kindly provided by Secretaría de Medio Ambiente y Recursos Naturales (FAUT DGVS-0001) and Consejo Nacional de Ciencia y Tecnología.

**LITERATURE CITED**


**RESUMEN**

Estudiamos la morfología y la dieta de Musonycteris harrisoni, una especie de murciélagos endémico del oeste de México y en peligro de extinción, y exploramos las razones potenciales de las especializaciones craneales de este murciélagos de rostro extraordinariamente alargado. Obtuvimos 28 capturas en la temporada de lluvias y 30 en secas, lo que representa la base de datos más grande en existencia de esta especie. Tomamos datos morfológicos y colectamos pollen del pelaje. El análisis de la dieta reveló los géneros Cleome, Pseudobombax, Crataeva y Helicteres y el cacto columnar Pachycereus pectin-aboriginum como las plantas principales de alimentación. No encontramos evidencia de relaciones cercanas entre M. harrisoni y flores tubulares que podrían requerir un rostro largo para su explotación, con la posible excepción del cacto columnar. Sin embargo, dado que los cactos son fuentes comunes de alimento para muchas especies de murciélagos nectarívoros menos especializados, el rostro extraordinariamente largo de M. harrisoni le permitiría usar las mismas plantas abundantes que otras especies de mayor tamaño, pero manteniendo un tamaño corporal menor, teniendo así requerimientos energéticos absolutos menores. Esto a su vez podría facilitar un estilo de vida residente en un hábitat que tiene cuellos de botella en los recursos anuales. Los machos tienen rostros significativamente más largos (aproximadamente 9%) que las hembras, lo que sugiere que la longitud del rostro puede estar influenciada también por interacciones o restricciones intraespecíficas. Nuestra explicación preferida es que la longitud del rostro de las hembras puede estar limitada por factores de estabilidad, tales como la movilización del calcio durante el embarazo y la lactancia, lo que podría debilitar considerablemente la estructura ósea del rostro.

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