DIET AND CRANIAL MORPHOLOGY OF MUSONYCTERIS 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 (Tschanke 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; Tschanke 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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1999) and nothing is known about the ecological significance of the extraordinary cranial morphology.

Extreme morphological adaptations in nectarivores are frequently caused by a tight coevolution with long-tubed flowers. Examples are provided by the long-billed hummingbird Ensiferasensiferathat is the exclusive visitor to some Andean Passiflora species (Lindberg and Olesen 2001) or by the Madagascan sphingid moth genus Xanthophasewith its 25-cm-long proboscis, the sole pollinator of the orchid Angraecum sesquipedale (Nilsson 1998; Wasserthal 1997). The cranial morphology of M. harrisonisuggests that it might depend on certain plant species that require such an elongated rostrum for successful exploitation. Based on this hypothesis, we expected the food spectrum of M. harrisonitobe dominated at least for a part of the year by plants with particularly long-tubed flowers that are not accessible to other nectarivorous bats. The geographical distribution of such plants should also provide an explanation for the unusually small distribution area of the bat. Consequently, our goal was to collect basic morphological data of M. harrisoni, to determine its diet and to provide floral characteristics for the plants visited, and to evaluate the resource situation for the animals over the annual cycle.

**Materials and Methods**

The study site was located in western Mexico, Colima State, near Rancho Callejones (18°48′N, 103°38′W). The climate of the area is characterized by a pronounced dry season between November and May, with a total precipitation of approximately 750 mm. Fieldwork was undertaken between August and October 2002 (wet season), March and April 2003 (dry season), and between January and April 2004 (early dry season). Additionally we used data from 2 short previous visits in March 1996 (2 nights) and July 2001 (2 nights). The natural vegetation at the site is characteristic of a tropical deciduous forest, “selva baja caducifolia” (Rzedowski 1983).

We mistnetted bats mainly in banana plantations in close proximity (less than 700 m) to natural vegetation. The constantly flowering bananas attracted nectar-feeding bats that are not accessible to other nectarivorous bats. The geographical distribution of such plants should also provide an explanation for the unusually small distribution area of the bat. Consequently, our goal was to collect basic morphological data of M. harrisoni, to determine its diet and to provide floral characteristics for the plants visited, and to evaluate the resource situation for the animals over the annual cycle.

For monitoring habitat use we equipped 3 bats with Holohil LB2 radios (weight 0.5 g; Holohil, Inc., Carp, Ontario, Canada), by gluing the radio on the back with acrylate glue. the receiving unit was a Yaesu receiver with a HB9CV antenna (FT-290R II; Wagener Telemetrieanlagen, Cologne, Germany).

For diet analysis, we collected pollen from the bats by rubbing them immediately after capture with small pieces of glycerine gelatin (4 × 4 mm) over the entire body (Beattie 1971). 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:

$$H' = -\sum_{i} p_i \ln p_i,$$

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 (\(\bar{X} = 43.2\) mm, \(SD = 0.70\) mm, \(n = 20\)) and females (\(\bar{X} = 43.1\) mm, \(SD = 0.71\) mm, \(n = 26\); Student’s \(t\)-test; \(t = 0.570, df = 44, P = 0.572\)). Body mass of animals varied significantly between adult males (\(\bar{X} = 12.13\) g, \(SD = 0.88\) g, \(n = 20\)) and nonpregnant females (\(\bar{X} = 11.14\) g, \(SD = 0.84\) g, \(n = 22\); \(t = 3.701, df = 40, P < 0.001\)). 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; \(T = 918.500, df = 48, P < 0.001\); 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; \(t = 7.853, df = 48, P < 0.001\)).

**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; \(T = 563.5, df = 56, P < 0.001\)). There was no difference in plant use between males and females over the entire year (chi-square test: \(\chi^2 = 11.442, df = 13, P = 0.574\)).

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 ascellifolia*), *Crataeva palmeri* and *Cleome spinosa* (Capparaceae), *Helicteres baruensis* (Sterculiaceae), and *Agave colimana* (Agavaceae). All other plants were found only on a few animals and therefore are probably not key parts of the species

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**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 *Bombaceae*) 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* (*Bombaceae*). 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 glosophagine 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 glosophagine 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 syntopic glosophagine species. In contrast to *A. fistulata*, however, *M. harrisoni* seems to follow the correlation between rostrum and tongue length that is typical for glosophagines (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 glosophagine 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 (Sahley 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. curasoae*, 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 glosophagine 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
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-aborigineum*. 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-aborigineum*. 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-Cabrales 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 semiarid 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.*
**RESUMEN**

Estudiamos la morfología y la dieta de *Musonycteris harrisoni*, una especie de murciélago endémico del oeste de México y en peligro de extinción, y exploramos las razones potenciales de las especializaciones craneales de este murciélago 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 polen del pelaje. El análisis de la dieta reveló los géneros *Cleome*, *Pseudobombax*, *Crataeva*, *Agave*, *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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**LITERATURE CITED**


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