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Repartición de recursos y patrones de alimentación en murciélagos nectarívoros del Bosque tropical seco de México

TESIS

Que presenta:

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*El amor por todas las criaturas
vivientes es el más noble atributo
del hombre.*

Charles Darwin

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RESUMEN

La repartición de nicho permite la coexistencia entre especies simpátricas y reduce competencia por recursos. La selección del alimento en murciélagos nectarívoros, puede estar influenciada por las interacciones bióticas entre polinizadores, así como por las variaciones en la disponibilidad y calidad del alimento. Los murciélagos nectarívoros *Leptonycteris yerbabuenae* y *Glossophaga soricina* son simpátricos en gran parte de su distribución y presentan requerimientos similares. En este trabajo, evaluamos la repartición de nicho entre estas especies durante el tiempo que coexisten en el bosque seco del centro de México y analizamos los patrones de alimentación de estas especies en condiciones de cautiverio. Se capturaron murciélagos en el bosque seco de Lázaro Cárdenas, Michoacán, se colectaron muestras de polen del pelaje y heces fecales para determinar la dieta, y se analizaron los patrones de actividad diaria. Posteriormente, realizamos experimentos en cautiverio removiendo las interacciones, controlando el tipo de recurso y su disponibilidad. Como resultado observamos la mayor abundancia de murciélagos durante la temporada seca, lo cual coincide con una mayor disponibilidad de recursos florales en el área. Tanto en campo como en cautiverio, se observaron diferencias en la dieta y en los patrones de actividad diaria de ambas especies, además las especies modificaron el patrón de actividad cuando existía gran densidad de individuos. Debido a las diferencias observadas entre *G. soricina* y *L. yerbabuenae*, creemos que las especies no deberían de competir entre ellas cuando coexisten en el bosque seco de México, y que la selección del recurso podría estar más relacionada con la disponibilidad y calidad de alimento que con la presencia de otras especies nectarívoras.

Palabras clave: Competencia, comportamiento de forrajeo, *Leptonycteris yerbabuenae***,** *Glossophaga soricina, Dieta.*

ABSTRACT

Niche partitioning is a strategy that favors the coexistence of sympatric species, and reduces competition for resources. Biotic interactions among pollinators, as well as variations in the availability and quality of resources, are important factors that determine food selection in bats. Since *Leptonycteris yerbabuenae* and *Glossophaga soricina* are sympatric species in much of their distribution and have similar requirements, we evaluate if species present niche partitioning during its coexisting time in the tropical dry forest of western México, and analyzed feeding patterns in these bat species under captive conditions. We conduct the study in Lázaro Cárdenas, Michoacán. Diet determination was made by taking pollen samples from bats fur and feces, and patterns of daily activity were also analyzed. Then, we conduct experiments in which we control for resource type and availability by offering the bats different artificial nectar solutions while we further removed interspecific interactions. We found more abundance of bats during November to January which corresponds to the dry season. This may be associated with a greater availability of floral resources in the study area. We did not found evidence that species diets may be changing in relation to the presence of potential competitors. However, we found niche partitioning in daily activity patterns related to high density of *L. yerbabuenae.* Our data on food selection and feeding patterns in captivity suggests differences in resource use between these bat species in time as well as in diet selection. Therefore, we think that species should not compete when coexisting, and that resource selection in these bat species is more related to food characteristics than to the presence of other nectarivorous bat species.

Key words: Competition, foraging behavior, *Leptonycteris yerbabuenae***,** *Glossophaga soricina, Diet.*

INTRODUCCIÓN GENERAL

La segregación de nicho es una de las principales estrategias que permiten la coexistencia de especies con requerimientos similares (Schoener 1974). Generalmente, estas especies reducen la competencia al diferir en sus patrones de explotación de recursos; siendo comunes las diferencias en patrones de actividad diaria y dieta (Griffin y Silliman 2011; Denzinger y Schnitzler 2013; Salinas-Ramos et al. 2015)

En los murciélagos la dieta puede ser considerada una de las principales causas de competencia entre especies (Tschapka 2004), especialmente los murciélagos que se alimentan de néctar, requieren de una gran cantidad de energía para cubrir las demandas energéticas del vuelo; por lo tanto, dependen totalmente de las características del alimento (Winter y Helversen 1998; Hainsworth y Wolf 1972). En estos murciélagos el comportamiento de alimentación puede estar influenciado por diversos factores relacionados con las características de las especies y de los recursos disponibles. Estos factores determinan la dieta de los organismos (Freeman 1995; Nicolson y Thornburg 2007; Ayala-Berdon et al. 2011; González-Terrazas et al. 2012), y limitan la competencia por los recursos (Tschapka 2004; Briffa y Sneddon 2010; Griffin y Silliman 2011). Se ha observado que las especies coexistentes presentan adaptaciones morfológicas y fisiológicas que les permiten explotar los recursos de diferentes maneras. Por ejemplo, la morfología del aparato bucal puede determinar la eficiencia de extracción de néctar en murciélagos nectarívoros (González-Terrazas et al. 2012), ocasionando que especies más grandes prefieran flores más grandes cuando coexisten con especies más pequeñas (Fischer 1992). Lo anterior sugiere que el tamaño podría ser uno de los factores que regulan la segregación de nicho. Además, las diferencias en los horarios de alimentación también son comunes cuando las especies se alimentan de recursos similares (Griffin y Silliman 2011). La segregación de nicho en la actividad diaria se ha estudiado en varios grupos de mamíferos, como ungulados, felinos y roedores (Basurto 2016; Bu et al. 2016). Sin embargo, se sabe poco sobre el traslape de alimentación en murciélagos que coexisten (Ramírez-Pulido y Armella 1987).

Los murciélagos nectarívoros *Leptonycteris yerbabuenae* y *Glossophaga soricina* son especies que difieren en características morfológicas asociadas a la forma de alimentarse. Además, algunas poblaciones de *L. yerbabuenae* son migratorias (Howell 1979; Cole y Wilson 2006), mientras que *G. soricina* mantiene poblaciones residentes a lo largo de todo su rango de distribución (Gardner 1977; Álvarez et al. 1991; Herrera 1999). Esto ocasiona que las dos especies normalmente no coexistan durante la mayor parte del año en el bosque seco del oeste de México, donde *L. yerbabuenae* y *G. soricina* sólo co-ocurren durante el invierno (Sandoval-Soto 2013; obs. pers.), temporada en la cual podrían competir por recursos.

La llegada de especies migratorias puede generar competencia temporal entre los individuos migrantes y los residentes, provocando que las especies deban adoptar estrategias alternativas en los periodos de coexistencia para limitar la competencia. La repartición de nicho entre migrantes y residentes ha sido estudiada principalmente en aves, estos estudios han reportado diferencias en el comportamiento de alimentación entre ambas especies (Salewski et al. 2003). Sin embargo, para el grupo de los murciélagos sigue siendo en gran medida desconocido el efecto que tiene la llegada de una especie migratoria en la explotación de los recursos de la especie residente. Investigar los patrones de alimentación y la repartición de recursos entre especies es importante especialmente en hábitats con gran variación en la disponibilidad de alimento, como es el bosque tropical seco. La llegada temporal de una especie nectarívora altamente especializada en el consumo de néctar, podría generar cambios en los patrones de tiempo y el uso de los recursos de la especie residente. Por lo tanto, el objetivo de este estudio fue evaluar la repartición de nicho en tiempo y dieta entre los murciélagos nectarívoros *Leptonycteris yerbabuenae* y *Glossophaga soricina* en el bosque tropical seco de México y contrastarlo con lo observado en condiciones de cautiverio. Esperando que las especies residentes exhiban un cambio en los patrones de uso de los recursos y la actividad diaria.

OBJETIVOS

Evaluar la repartición de nicho entre los murciélagos nectarívoros *Leptonycteris yerbabuenae* y *Glossophaga soricina.*

- Objetivos particulares: Capítulo 1

1. Evaluar si existe repartición de nicho entre *Leptonycteris yerbabuenae* y *Glossophaga soricina* en el bosque seco de México.
2. Caracterizar la dieta, evaluar amplitud y el traslape de nicho entre ambas especies en una zona de simpatría dentro del BTS del oeste de México.
3. Evaluar los patrones de actividad diaria de estas especies en el BTS del oeste de México

- Objetivos particulares: Capítulo 2

1. Evaluar la repartición de nicho en *Leptonycteris yerbabuenae* y *Glossophaga soricina* en condiciones de cautiverio y bajo escenarios no competitivos.
2. Evaluar la selección de recurso entre las dos especies en condiciones de cautiverio y bajo escenarios no competitivos.
3. Evaluar los patrones de alimentación de las dos especies en condiciones de cautiverio y bajo escenarios no competitivos.

HIPÓTESIS

Los murciélagos presentarán preferencia por aquellas especies de plantas con características quiropterofílicas. Por otro lado, debido a que *L. yerbabuenae* es migratorio, altamente especializado en el consumo de néctar y presenta características morfológicas diferentes a las de *G. soricina* (asociadas al tamaño del organismo), el uso de los recursos será diferente. Se espera que *L. yerbabuenae* presente mayor especialización hacia el recurso en comparación con *G. soricina*. Además, La llegada temporal de una especie migratoria como *L. yerbabuenae* generará cambios en los patrones de actividad diaria y el uso de los recursos en la especie residente, como una posible estrategia para evitar la competencia.

Por otro lado, una vez que se eliminemos la competencia, se espera que los patrones de uso de recursos y actividad diaria observados en condiciones naturales sean similares a los observados en cautiverio. Por lo que podríamos sugerir que la competencia no es el principal factor influenciando la segregación de estas especies y que el comportamiento de alimentación puede estar relacionado con la calidad y disponibilidad de los recursos.

CAPÍTULO 1

Does degree of foraging specialization and activity patterns enable niche partitioning in two nectarivorous bats?

FORMATO DE LA REVISTA: OECOLOGIA

Does degree of foraging specialization and activity patterns enable niche partitioning in two nectarivorous bats?

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[1]Author Contributions: ASM and YHD performed the experimental design and improved the manuscript; ACE performed the experimental design, fieldwork, analyzed the data and wrote the manuscript.

ABSTRACT

Niche partitioning is a strategy that favors the coexistence of sympatric species, and reduces competition for resources. Usually, resource partitioning occurs in time and space axis, as well as in the niche breath. The lesser long nosed bat (*Leptonycteris yerbabuenae*) and the Pallas's long-tongued bat (*Glossophaga soricina*) are sympatric in much of their distribution. Both can be found in the Mexican tropical dry forest and species co-occur during the winter in the pacific coast of Michoacán. These bats have similar requirements but differ in morphological characteristics associated with the way of obtaining the food. Therefore, we evaluate if species present niche partitioning during its coexisting time. For bat sampling mist-nets were set up at ground level from 7:00pm to 3:00am in Lázaro Cárdenas, Michoacán. Diet determination was made by taking pollen samples from bats fur and feces. Patterns of daily activity were also analyzed. We found more abundance of bats during November to January which corresponds to the dry season. This may be associated with a greater availability of floral resources in the study area. Bats fed on nectar from the families Bombacaeae, Fabaceae, Convolvulaceae, Apocynaceae, Cactaceae and Rosaseae. We did not found evidence that species diets may be changing in relation to the presence of potential competitors. However, we found niche partitioning in daily activity patterns related to high density of *L. yerbabuenae*.

Key words: Competition, foraging behavior, nectarivory, *Leptonycteris yerbabuenae, Glossophaga soricina*

INTRODUCTION

Coexisting species with similar requirements may often be limited according to the degree of overlap in one or more dimensions of their niche. Therefore, animals have developed different strategies that reduce competition for resources (Briffa and Sneddon 2010; Griffin and Silliman 2011). Niche partitioning is one of the most important strategies that enable species coexistence (Schoener 1974) through the exploitation of resources in different ways (Griffin and Silliman 2011; Denzinger and Schnitzler 2013; Salinas-Ramos et al. 2015).

Niche segregation in bat species has been found to be driven by a combination of bat traits such as skull morphology, wing design, and body size (Bonaccorso and Gush 1987; Norberg and Rayner 1987; Fleming 1993a; Lou and Yurrita 2005; Mello 2009; Bloch et al. 2010; Denzinger and Schnitzler 2013). In addition to these specializations, physiological limitations, food properties, resource availability, and biotic interactions may also determine feeding behavior in bat species (Freeman 1995; Nicolson and Thornburg 2007; Ayala-Berdon et al. 2011; González-Terrazas et al. 2012). Nectarivorous bats are the highly specialized and dependent on food properties due to the elevated cost of flight (Winter and Helversen 1998; Hainsworth and Wolf 1972). Then diet may be considered the main constraint during competition, and species may need to develop strategies that enable coexistence.

Dimensions into which niche partitioning may usually occur are activity patterns (feeding time and feeding areas), niche flexibility, and migrations (Schoener 1974; Griffin and Silliman 2011). Niche segregation in time and diet are two of the main dimensions in which animals avoid competition for resources. In relation to diet, it has been observed that coexisting species present morphological and physiological adaptations that allow them not only to feed on different resources, but also to exploit them in different ways. For instance, body length and morphology of the oral apparatus may determine the nectar extraction efficiency in nectarivorous bats (González-Terrazas et al. 2012), therefore larger nectarivorous bats have been found preferring larger flowers when coexisting with smaller species (Fischer 1992), which suggests that size could be one of the factors regulating much of the axis into which niche partitions. Differences in feeding time are also common when species feed on similar resources (Griffin and Silliman 2011). Niche segregation in daily activity has been studied in several groups of mammals such as ungulates, felines and rodents (Basurto 2016, Bu et al. 2016), However for bats, little is known about the overlap between coexisting species (Ramírez-Pulido and Armella 1987).

The lesser long-nosed bat (*Leptonycteris yerbabuenae*) and the Pallas's long-tongued bat (*Glossophaga soricina*) are sympatric species in much of their distribution range. Some populations of *L. yerbabuenae* are migratory (Howell 1979; Cole and Wilson 2006), while *G. soricina* maintain resident populations throughout its distribution range (Gardner 1977; Álvarez et al. 1991; Herrera 1999). This causes a difference in temporal co-occurrence with *G.soricina* being present in the tropical dry forest of western México all year round while *L. yerbabuenae* can be found mainly from November to March (Sandoval-Soto 2013).

The arrival of a highly specialized nectarivorous, larger species may create temporal competition for resources between the migrant and the resident species. Creating the opportunity for alternative strategies in niche dimensions not seen during the months when migrant species is absent to originate. Niche partitioning between resident and migratory species has been investigated in birds, and have found that species may differ in their foraging behavior when coexisting (Salewski et al. 2003). However, it remains largely unknown to the best of our knowledge for bats whether the arrival of a migratory species leads to a change in resources exploitation to reduce competition. Investigating the occurrence of this partitioning would be important for specialized nectarivorous bats and especially for those in a habitat type with a high variation in food availability such as the tropical dry forest. We then hypothesized that the temporary arrival of a highly specialized migratory nectarivorous species could generate changes in the time patterns and use of food resources in a resident species such as *G. soricina*. Therefore, the aim of this study was to evaluate whether niche partitioning between *L. yerbabuenae* and *G. soricina* occurs in a Mexican tropical dry forest in these dimensions of the niche. During this period, we expected that the resident species would exhibit a change in both patterns of use of resources and daily activity as a possible strategy to avoid competition.

MATERIALS AND METHODS

-Study area

We conducted the study in the “La Bonetera” area in Lázaro Cárdenas, southern Michoacán, México (ca. 18°05'N, 102°25'W). The area has an extension of approximately 900 ha covered mainly by tropical deciduous forest and patches of semi-deciduous forest. It has a marked dry season from November through June, an average annual rainfall of 1276.8mm, and average annual temperature of 27 °C (Sandoval-Soto 2013).

-Study species

Leptonycteris yerbabuenae is distributed from southern Arizona and New México in the United States of North America to Honduras and El Salvador (Simmons 2005). Populations near 30° north latitude migrate southwards tracking flowering plants (Rojas-Martínez et al. 1999). *Leptonycteris yerbabuenae* is one of the largest nectarivorous, weighing in average 26 g (Cole and Wilson 2006). This species specializes in the consumption of nectar, although the consumption of fruits, pollen and insects, may also occur but considerably in less proportion (Howell 1979; Rojas-Martínez et al. 2012). *Leptonycteris yerbabuenae* can fly up to 100 km each night (Horner et al. 1998) and may form groups of up to 25 individuals as a way to maximize food time search (Howell 1979). Conversely, *Glossophaga soricina*, is a small bodied (9.6 g) (Álvarez et al. 1991) widely distributed bat, which ranges from northern México to northern Argentina (Álvarez et al. 1991). It has been observed that *G. soricina* maintains resident populations throughout its distribution range (Fleming et al. 1993 b), with a much more reduced mobility than other species, being able to fly up to three km per night searching for feeding areas (Aguiar et al. 2014). Although the large proportion of this species diet relies mostly on nectar, it can make use of fruits and insects to complement it (Gardner 1977; Herrera 1999).

-Bat sampling and pollen and feces collection

Bats were monthly sampled from April 2016 through March 2017, totalizing 60 net-nights. Sampling excluded June and October due to weather conditions. Six sampling sites were selected and sampled one night per month. The sampling scheme considered the inclusion of the two types of vegetation (tropical deciduous and semi-deciduous forest); full moon nights were avoided due to bats lunar phobia (Saldaña-Vázquez and Munguía-Rosas 2012). Eight mist-nets were set up at ground level at each sampling site. Nets were opened from 7:00 pm to 3:00am and checked every 30 minutes. These hours include the maximum activity peaks reported for most Glossophaginae (Horner et al. 1998). Pollen samples were collected from bats fur with fuchsine gelatin. For fecal samples, bats were temporally held in soft cotton bags until they defecated. Each fecal sample was preserved in 70% ethanol and placed in plastic vials for posterior analysis in lab (Riechers et al. 2003).

-Diet determination

Fecal samples were examined in the stereo microscope to determine the presence of pulps, fibers, seeds, insects and pollen. Each component was placed in separate vials. We only analyzed pollen grains because bats feed mainly on nectar and identification of diet items such as insects through insects' body parts and fruits through pulps and fibers are uncertain. We extracted pollen samples from feces and fur gelatin samples; samples were mounted as permanent pollen slides. Pollen was identified by using local reference collections and pollen keys (Roubik and Moreno 1991).

-Resource availability

To estimate floral resources available for bat species, we monthly counted chiropterophilic flowers on each sampling site. In addition, complementary surveys were carried out in a ratio of ~3 km outside the study area to search for potential resources for bats that were not recorded in the sampling sites. Pollen samples were collected from these plants to create a reference collection.

-Data analysis

The pattern of resource use was performed by calculating the percent area of each food item (PA) to know the main resources that are part of the diet of these bat species. This index is a modification of the volumetric method and is used when the size of the prey is very small (Hyslop 1980). In this method, stomach contents or feces are poured into a grid with a unit of known area and the space occupied by each resource in relation to the total consumed is counted.

We analyzed data of the consumption of each resource by bat species into two seasons: when both species coexist (November-February) and when they do not (March-October). This data was used to determine diet selectivity by Levin's index (Krebs 1998). This data was collected during the March-October period for *G. soricina*, while it was collected for both species during the co-occurrence period. Pianka´s index (Krebs 1999) was used to determine the two species diet overlap during the coexistence season. Numbers of pollen grains of each plant consumed were used as an indirect way of measure resource utilization for each bat species (Sánchez-Casas and Álvarez 2000; Krebs 2014).

Data of the capture hours (taken every 30 minutes) was used to generate the probability distributions that describe the activity patterns of the species with the package Overlap (Meredith and Ridout 2014) for R (R CoreTeam 2014). With this package, we also calculated the overlapping coefficient between species. This coefficient takes values from 0 to 1, where values closer to 0 represents no overlap and values closer to 1 represents identical activity patterns for the evaluated period (Meredith and Ridout 2016). We carry on this analysis in three stages. First we compared data from *G. soricina* between the July-August period and the November-December period, to assess the change in the activity patterns of this resident species. Then we split the co-occurrence into two periods. The first period included data of November and December for both species. These months correspond to those when *L. yerbabuenae* arrives to the area but in high density. The second period included data for both species for January and February, which corresponds to the months with less density of *L. yerbabuenae* individuals as this is the time when the spring migration to non-wintering grounds occurs. Because the number of observations of the minimum sample was less than 50, we used Δ1 as the coefficient of overlapping (Meredith and Ridout 2016).

RESULTS

-Bats abundance

We capture 112 *L. yerbabuenae* individuals. This species was present from November to March, with the largest number of individuals being captured in December (76%); and the lowest number of individuals captured was recorded at the end of February (0.05%). *Glossophaga soricina* was present throughout the year, with a total of 83 individuals captured.

-Diet

Fecal and pollen samples were collected from 106 *L. yerbabuenae* and 38 *G. soricina* individuals. Fecal samples were screened for food items, which were separated by type in pollen, pulp, fibers, seeds and insects. The percent area (PA) obtained for each type of resource indicated greater nectar consumption through pollen grains observed in fecal samples compared to the rest food items for both species (86% *L. yerbabuenae*, 46% *G. soricina*). This indicates that *L. yerbabuenae* almost doubles the consumption of nectar and pollen when compared to *G. soricina*. *Glossophaga soricina* also consumes a high percentage of both pulps (30%) and insects (16%) (Fig. 1).

Thirteen morphospecies of pollen were identified from six plant families in fecal and fur samples: Bombacaeae, Fabaceae, Convolvulaceae, Apocynaceae, Cactaceae and Rosaseae. Twelve plant species were identified in the diet of *G. soricina* throughout the year; however, only seven species appeared in its diet when both species co-occurred in the study site, and onto which competence could occur. The only plant species that *G. soricina* did not consume was *Ipomoea sp.2*. Conversely, *L. yerbabuenae* only used six of the 13 plant morphospecies, which belonged to three plant families: Bombaceae, Convolvulaceae and Fabaceae (Table 1).

Some plants were consumed exclusively by each bat species during co-ocurrence. On the one side, *G. soricina* also fed from *Opuntia sp*. and an unidentified plant, and on the other side, *L. yerbabuenae* used one extra species of *Ipomoea.*

-Niche breadth and niche overlap

Levin´s index indicated that during the time both species coexisted, the less specialized nectarivorous, *G. soricina*, had the highest niche breadth (Levin´s = 0.790, 95% confidence intervals = 0.561 - 1.020), and the more specialized nectarivorous species *L. yerbabuenae* had lower values (Levin´s = 0.479, 95% confidence intervals = 0.272 - 0.544). Analysis from *G. soricina* during the non- occurrence period (March-October) found similar values of Levin´s index to that observed when species co-occur (Levin´s = 0.750, 95% confidence intervals = 0.315 - 1.179). These results suggest not only that *G. soricina* is generalist and maintains this pattern regardless of the presence of the competing species, but also that *L. yerbabuenae* is selective in its diet when both species coexist. This is reflected in a low level of diet sharing as Pianka´s niche overlap index indicated that *L. yerbabuenae* and *G. soricina* shared only 31% of their diet when both species co-occur. This suggests low levels of diet competition between species as the generalist species adjust its diet to available resources.

-Resource availability

We found a highly fluctuation of available resources for bat species through the year, with 86% of the observed flowers occurred during the dry season. The availability of flowering resources reached the highest peak during January (40% of the total observed flowers), and the less availability of resources was observed from July to October (13% of total flowers), which corresponds to the rainy season (Fig. 2). The main species that presented flowers during the dry season were *Pseudobombax ellimpticum, Bahunia paulettia* and *B. ungulata*. On one hand, *P. ellipticum* contributed with 83% of the observed flowers, and was responsible for the flowering peak in January and February; on the other hand, *Bahuinia paulettia* and *B. ungulata* presented flowers from November to January, and contributed with 13% of flowers for the dry season. Other plant species that presented flowers in the study site during these months were *Ipomoea sp., Caliandra sp.* and *Opuntia sp*. For the rainy season we also found *Caliandra sp., Stemmadenia grandiflora* and some cacti species. Species such as *Ceiba pentandra* and *C. aesculifolia* were not found in the study site, but observed while performing flowering plants surveys in a radius of ~3km from the study site indicated these plant species could be present within the movement capabilities of the species.

-Activity patterns

First we analyzed data from *G. soricina* during July-August and November-December. Probability distribution results indicated that this species presented a change in their activity pattern between seasons. Activity patterns during July-August was 73% similar to that of November-December (confidence intervals = 50.5%, 91.6%). *Glossophaga soricina*´s period of activity was longer during July-August and presented one activity peak at 10:30 pm and another one at 3:00 am, these months correspond to those with the less density of nectarivorous bats in the area. During November-December, when *L. yerbabuenae* arrived to the study area, *G. soricina* reduced its activity, and maintained only one activity peak at 10:30 pm (Fig. 3a). It was observed that *L. yerbabuenae* and *G. soricina* share about 47% of their daily activity patterns (confidence intervals = 32.4%, 62.2% respectively) during November and December, when density of individuals was higher. However, the peaks of activity of these species were off one from each other. *Glossophaga soricina* recorded the highest activity peak at 10:30 pm. Meanwhile, activity peak of *L. yerbabuenae* occurred approximately at 2:00

am (Fig. 3b). Conversely, during the low *L. yerbabuenae* abundance period (January-February) both species shared 69% of their daily activity patterns (confidence intervals = 49.4%, 86.3% respectively). However, these species activity peaks were still off one from each other as *G. soricina* was more active at 11:00 pm and *L. yerbabuenae* had two peaks, one at 10:00 pm and a second one at 3:30 am (Fig. 3c). These data indicates that during periods of great density of individuals, activity time was highly divided between bat species; however, species extended their feeding time when there was a less density of nectarivorous bats in the area

DISCUSSION

-Bats abundance and resource availability

We found a greater number of nectarivorous bats from November to January. This data coincides with the greatest availability of flowering resources in the study area, and with the flowering pattern found in the tropical dry forest of México (Stoner et al. 2003). Flowering phenology has been proposed as an important factor inducing changes in nectarivorous bats population dynamics (Fleming 1982; Tschapka 2004). Our study builds up on the evidence supporting the idea that bats respond to changes in food availability. Higher bat abundance during seasons with greater food availability was also found by Stoner et al. (2003) in the tropical dry forest of western México during winter and spring, and by Cornejo et al. (2011) in the crasicaule shrub and the tropical dry forest of central, México during spring. Tropical dry forests provide the species with a large amount of floral resources that bats use in the winter. Migrating species such as *L. yerbabuenae*, take advantage of this areas to mate and forage during this season (Fleming et al. 2002).

At the end of February, *L. yerbabuenae* stop being captured in mistnets. This could indicate that the species has undertaken its migration to non-wintering grounds, to areas with more resource availability (Fleming et al. 1993 b; Medellín 2012). Possible explanations for the potential movements this species performs post-wintering staying is that individuals who migrated from the northern México, return to the north to give birth and form maternity colonies during the spring (Cockrum 1991).Other individuals who give birth during the winter could move to central México which is characterized with lots of columnar cacti blooming during the spring (Cornejo et al. 2011), according to Fleming et al. (2002) this populations could mate in this areas in May and June. Other studies have demonstrated that populations below 21° latitude do not migrate (Rojas-Martínez et al. 1999); therefore, an alternative explanation is that some individuals do not migrate latitudinally, but performed altitudinal and local movements instead. This is supported by the fact that two individuals of *L. yerbabuenae* were captured in mistnets during August (2016 and 2017 respectively) approximately 24 kilometers from our study site (Bucio-Jiménez and Chávez-Estrada, unpublished data). However, these are only observations of a few individuals, and more information is needed to determine actual residency trends of this population

-Niche partitioning

During the time both species coexisted, *G. soricina*, had higher values of niche breadth than *L. yerbabuenae*. Niche analysis suggests low levels of interspecific competition between bat species as *G. soricina*´s pattern of niche breath was similar between seasons regardless of the presence of *L. yerbabuenae*. This idea is supported by the fact that although bat species shared five of the eight resources that were used during coexistence, the proportion of use of each resource was different for each bat species. This scenario caused low levels of diet overlap between bats. *G. soricina* has previously been reported to be more plastic than *L. yerbabuenae* in what they eat (Sánchez-Casas and Álvarez 2000; Sandoval-Soto 2013) and then the former bat species could be more likely to be the one shifting to available resources (Gardner 1977; Herrera 1999).

Some studies have suggested that coexistence between sympatric species is probably enabled by differences in their abundance and in their temporal feeding strategies, such is the case of *Glossophaga commissarisi* and *Hylonycteris underwoodi* in the rainforest of Costa Rica (Tschapka 2004), and of some nectarivorous species in the tropical dry forest and columnar cacti areas Southward of the study area along the pacific coast of México (Ibarra-López 2012).

In the tropical dry forest of Michoacán, we observed that *Leptonycteris yerbabuenae* and *G. soricina* showed differences in patterns of resource use. Percent area for each food item showed that *L. yerbabuenae* feeds mainly on floral resources in comparison with *G. soricina*. These observations coincide with the feeding habits reported for these bat species (Gardner 1977; Herrera 1999; Ibarra-López 2012).

-Activity patterns

Probability distribution results indicated that *G. soricina* presented a change in their activity pattern between seasons. During July-August, the activity pattern probability distribution for *G. soricina* expanded for a longer period of time, being active until 3:30 am. One plausive explanation for this is that in these months there was less abundance of other nectarivorous bats, and *G. soricina* should not compete for nectar with these species despite the fact that there is a low availability of floral resources. Beside, during these months *G. soricina* also modify its feeding habits to a more omnivorous diet, and it has been observed that activity pattern may be sometimes influence by prey activity (Anthony et al. 1981, Salvarina et al. 2018).

After the arrival of *L. yerbabuenae*, the activity patterns of G. soricina changed and reduce its activity. We found that activity time was highly divided between bat species during the months with higher density of bats; however, species extended their feeding time when there was a less density of nectarivorous bats in the area. The increase in density of bats during November-December is consistent with the northern migration of *L. yerbabuenae* in the winter (Wilkinson and Fleming 1996), then relating the shift in activity patterns with the migrating behavior in bats. This association has not been stablished in bats, and could indicate a seasonal flexibility in behavioral strategies to cope with a larger and potentially more competitive migrating species. When considering diet data along with the activity pattern in concert, we could argue that interspecific differences in foraging time and the great availability of floral resources in the tropical dry forest may reduce interspecific competition even when bats feed on similar resources. Similar results have been observed in frugivorous medium size mammals, whom feed on the same fruits at different time of the day to avoid competition (Basurto 2016), and some other studies have observed that carnivore mammal's species with higher activity overlap, had more differences in diet, also as a strategy to reduce competition (Bu et al. 2016).

Should these activity peaks be related to feeding activity (Horner et al. 1998), they would indicate that each species segregates in time in order to avoid interspecific competition. Evaluations of activity patterns in *L. yerbabuenae* report the species leaves roosting sites shortly after sunset and returns by 3:30 am. Evaluations of the availability of food resources indicate nectar production occurs between 12 pm to 2 am (Horner et al. 1998). Then, the activity pattern in our study could potentially indicate the time when bats went out to their feeding areas and while returning to their roost, but not in the exact moment they feed. Recent research by Rodríguez-Ramírez (2017) evaluated the floral visits of bats to *Bahuinia sp*. at our study site, and observed that *L. yerbabuenae* and *G. soricina* forage at different time of the night, and that species take turns to visit the flowers when they feed on the same tree. Foraging activity peaks may be related to high production of nectar during the night, and bats can spent the rest of the time carrying other activities, such as searching for new foraging areas, reproduction or rest (Horner et al. 1998). This suggests that the differences in activity time could still be related to interspecific foraging differences.

After analyzed the diet and activity patterns in these two bat species, we did not find evidence that species diet may be changing in relation to the presence of potential competitors. However, we found niche partitioning in daily activity patterns related to high density of *L. yerbabuenae*. Both species extended foraging hours when there was less density of individuals; during this same period, the bigger species presented two foraging peaks. This result may suggest that the nectarivorous bat species modify their behavior in presence of one another, in order to avoid competition.

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Ethical statement

All applicable national guidelines for the care and use of animals were followed.

Conflict of interest:

The authors have no conflict of interest.

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Table 1. Percentage of individuals of each species that consume each floral resource. Consumption was determined by pollen samples of *L. yerbabuenae* (n=106) and *G. soricina* (n=38) in the tropical dry forest of Lázaro, Cárdenas, Michoacán. *G. soricina** column indicates the resources that are used by this species at the no coexistence period; the other *G. soricina* column indicates the resources that are use at the time of coexistence. Because each individual can consume several resources, the sum of the percentages is above 100.

Family	Species	*G. soricina**	*G. soricina*	*L. yerbabuenae*
Bombacaceae	*Ceiba pentandra*	**2.6**	**21.05**	**34.0**
	Ceiba aesculifolia	**2.6**	0.0	0.0
	Pseudobombax ellipticum	**7.9**	**13.2**	**15.1**
Fabaceae	*Bahuinia ungulata*	**0.0**	**34.2**	**81.1**
	Bahuinia pauletia	**2.6**	**28.9**	**12.3**
	Inga vera	**10.5**	0.0	0.0
	Calliandra sp.	**2.6**	0.0	0.0
Convolvulaceae	*Ipomoea sp. 1*	**10.5**	**13.2**	**11.3**
	Ipomoea sp. 2	0.0	0.0	**4.1**
Apocynaceae	*Stemadenia grandiflora*	**5.3**	0.00	0.0
Cactaceae	*Opuntia sp.*	**7.9**	**5.3**	0.0
	Morphospeceis 1	**2.6**	0.0	0.0
Rosaceae	Morphospecies 2	**7.9**	**26.3**	0.0

Figure legends

Fig. 1. Resource use of *L. yerbabuenae* and *G. soricina*, determined by the percent area of the different food items obtained in fecal samples of each species. April 2016 to March 2017 in "La Bonetera", Michoacán, México. Standard errors are display in lines above the bars.

Fig. 2. Standardized proportional change of flower availability of plants consumed by nectarivorous bats in "La Bonetera", Michoacán, México. Data refers to the number of chiropterophilic flowers observed bimonthly related to the total of chiropterophilic flowers during April 2016 – March 2017.

Fig. 3. Daily activity patterns of *L. yerbabuenae* and *G. soricina*. Lines indicate Kernel density for each species. Δ_1: corresponds to the coefficient of overlapping. a) Indicate overlap between *G. soricina* individuals, dotted line correspond to data from November- December, while continuous line corresponds to July-August. b) Overlap between species during the high *L. yerbabuenae* abundance period of November and December. c) Overlap between species during the low *L. yerbabuenae* abundance period of January and February. In fig. 3b and 3c dotted line indicate *G. soricina*, and continuous line indicate *L. yerbabuenae*.

Figures

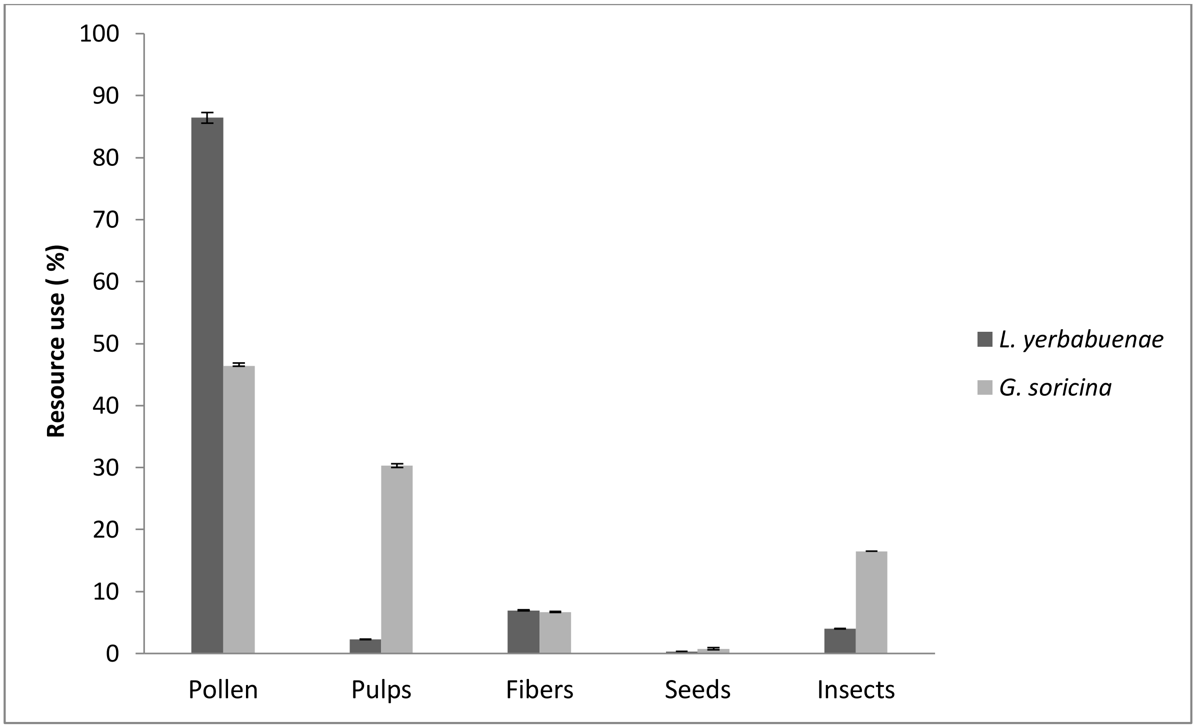

Fig. 1.

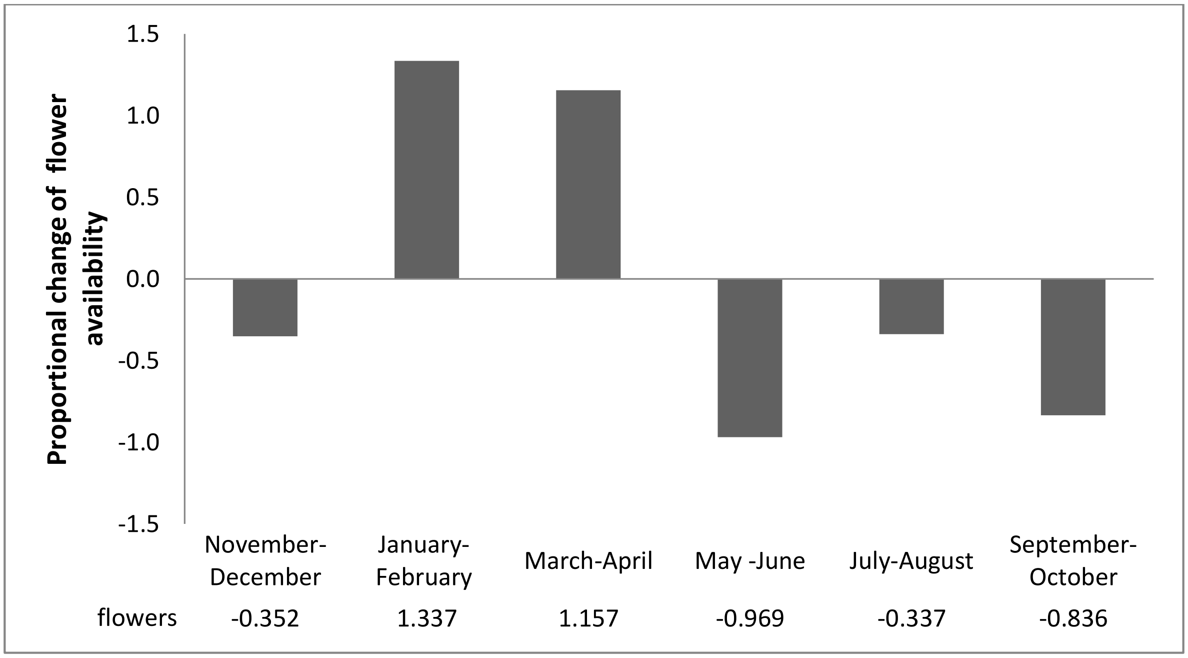
Proportional change of flower availability
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
November-December
January-February
March-April
May -June
July-August
September-October
flowers
-0.352
1.337
1.157
-0.969
-0.337
-0.836

Fig. 2.

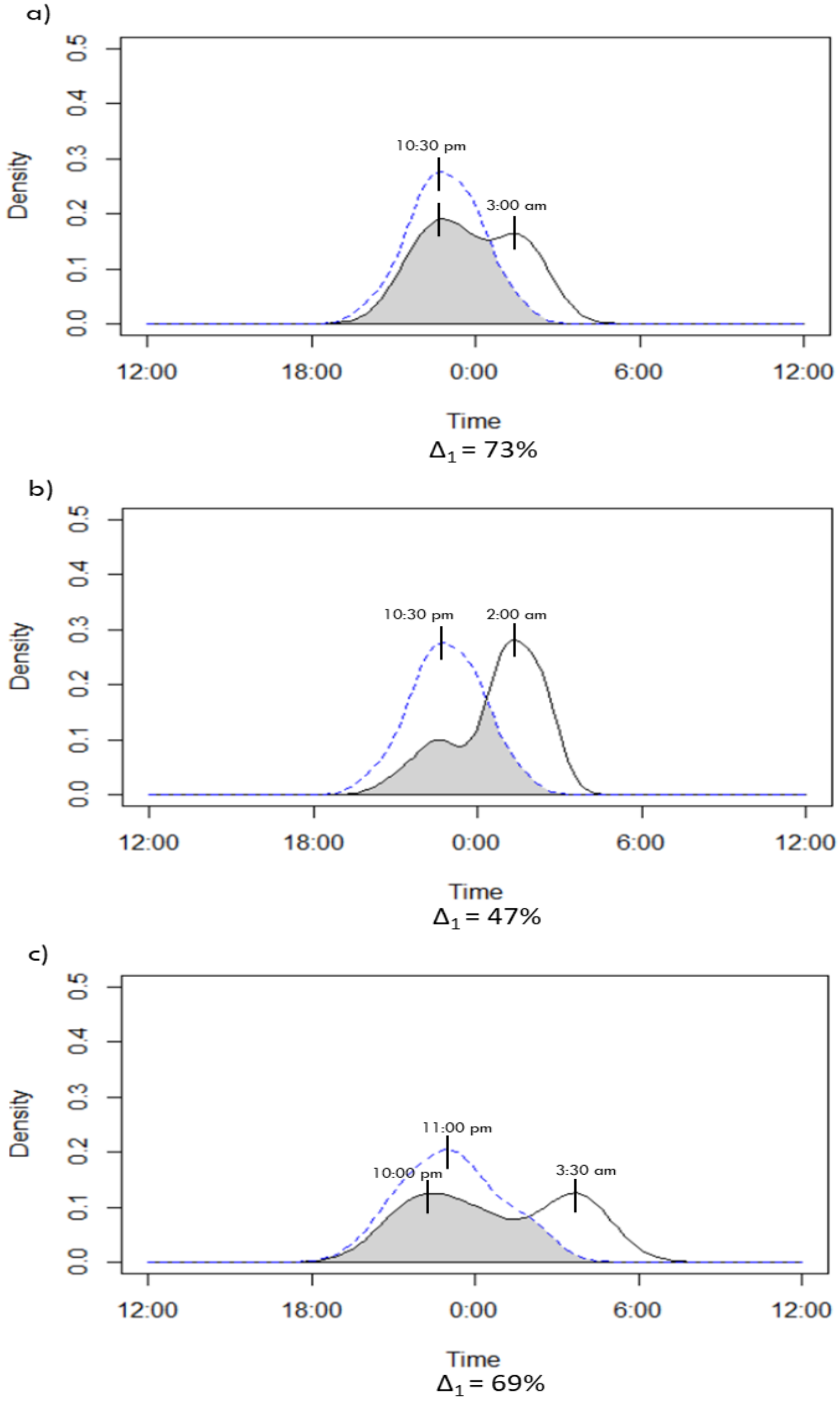
a)
Density
0.0
0.1
0.2
0.3
0.4
0.5
10:30 pm
3:00 am
12:00
18:00
0:00
6:00
12:00
Time
$\Delta_1 = 73\%$
b)
Density
0.0
0.1
0.2
0.3
0.4
0.5
10:30 pm
2:00 am
12:00
18:00
0:00
6:00
12:00
Time
$\Delta_1 = 47\%$
c)
Density
0.0
0.1
0.2
0.3
0.4
0.5
11:00 pm
10:00 pm
3:30 am
12:00
18:00
0:00
6:00
12:00
Time
$\Delta_1 = 69\%$

Fig. 3.

CAPÍTULO 2

Food selection and feeding patterns in nectarivorous bats: *Leptonycteris yerbabuenae* and *Glossophaga soricina*

FORMATO DE LA REVISTA: OECOLOGIA

Food selection and feeding patterns in nectarivorous bats: *Leptonycteris yerbabuenae* and *Glossophaga soricina*

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[1] Declaration of authorship

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[1]Author Contributions: ASM and YHD performed the experimental design and improved the manuscript; ACE performed the experimental design, experiments, analyzed the data and wrote the manuscript.

ABSTRACT

Sympatric species reduce competition for resources due to differences in one or more dimensions of their niche. Biotic interactions between pollinators, as well as variations in the availability and quality of resources, are important factors that determine food selection in bats. Nectarivorous species *Leptonycteris yerbabuenae* and *Glossophaga soricina* coexist temporarily in much of their distribution. These species have similar requirements, but differ in the way of obtaining the food. Previous field studies have not observed competition for resources when evaluated the diet of these species, however, it is not clear how competition is actually involved or if this segregation is based on resources characteristics. Therefore, we analyzed nectar selection and feeding patterns in these bat species under captive conditions. We conduct experiments in which we control for resource type and availability by offering the bats different artificial nectar solutions while we further removed interspecific interactions. Solutions differed in concentration and type of sugar, and some of these were similar to chiropterophilic plant species. Bat species presented differences in food selection, *G. soricina* feeds mainly on those resources similar to *Ipomoea* and sugar sucrose. Conversely, *L. yerbabuenae* preferred those similar to cacti. In addition, the feeding time of each solution was also different. These results may suggest low levels of competition between species under conditions of abundance of resources and low density of individuals, however these conditions are not always found in nature, and patterns may change under conditions of food scarcity, and high density of competitors.

Key words: Foraging, food preference, nectarivory.

INTRODUCTION

The coexistence between sympatric species is favored when species use resources in different ways, commonly call niche partitioning (Schoener 1974; Griffin and Silliman 2011; Denzinger and Schnitzler 2013; Salinas-Ramos et al. 2015). Two of the main dimensions into which niche partitioning may usually occur are activity patterns in feeding time and niche flexibility in diet (Schoener 1974; Griffin and Silliman 2011). The elevated cost of flight of nectarivorous species such as birds and bats, causes these species to be highly dependent on nectar properties such as energy content, sugar type, and viscosity among others (Winter and Helversen 1998; Hainsworth and Wolf 1972). Then this high energetic dependence may result in strategies to avoid competition among sympatric species (Tschapka 2004).

Plants that are pollinated by bats produce nectar as the main reward offer to pollinators, and their properties can vary with environmental conditions, species characteristics and biotic interactions. Nectar is composed mainly of sugar and water, although it can also contain proteins, amino acids, lipids, organic acids, and antioxidants (Baker et al. 1998). Plant species can produce from 100 µl to 20 ml of nectar in one night (Tschapka and Dressler 2002; Nicolson and Thornburg 2007). This may contain glucose, fructose and sucrose as principal sugar types, and sugar concentration can vary from 3% to 40% (Baker et al. 1998, Rodríguez-Peña et al. 2007, De Santiago 2013), being common to find diluted nectars between 18 and 21% (Von Helversen and Reyer 1984; Baker et al. 1998; Rodríguez-Peña et al. 2016). Despite variations in the properties of nectar, experimental studies have not observed differences in bats preference for sugar types, but for the concentration and energy content (Winter and Stich 2005; Rodríguez-Peña et al. 2007; De Santiago 2013).

Feeding behavior in bat species seems to be influenced by several factors, such as bat morphological specializations, physiological limitations, food properties and resource availability. All these elements may determine what a species is able to eat (Freeman 1995; Nicolson and Thornburg 2007; Ayala-Berdon et al. 2011; González-Terrazas et al. 2012). Then these characteristics may foster the segregation of bat species based on traits, and then species with similar traits may increase the likelihood of competition.

Species such as, *Leptonycteris yerbabuenae* and *Glossophaga soricina* coexist temporarily in much of their distribution range. These species differ in morphological characteristics associated with the foraging mode; on the one side, *L. yerbabuenae* is considered highly specialized in the consumption of nectar (Howell 1979; Cole and Wilson 2006), while *G. soricina* is generalist (Gardner 1977; Álvarez et al. 1991; Herrera 1999).

These two species normally do no coexist during most of the year, and *L. yerbabuenae* co-occurs with *G. soricina* during the winter in western México when they may compete for resources given their similar requirements. Despite this, in previous studies we did not find evidence that the species´ diets change in relation to the presence of potential competitors under natural conditions (Chávez-Estrada, in prep); however, it is not clear how competition is actually involved or if this segregation is based on resources characteristics. We hypothesize that if competition is not involved in species segregation, the pattern observed in the field will be maintained once species are released from potential competition. Then floral resources characteristics such as nectar quality and amount could be driving the feeding pattern. Previous studies also indicate that each species has different activity peaks during the night, and the duration of these peaks becomes narrower when both species coexist (Chávez-Estrada, in prep), then the duration of these peaks may increase when compared to those found in the filed once competition is released. Therefore, we analyzed nectar selection and activity patterns in captivity and under not competitive scenarios.

MATERIALS AND METHODS

-Study species

Leptonycteris yerbabuenae is one of the largest nectarivorous bats in America (Cole and Wilson 2006), due to its bigger size, this species can fly up to 100 km each night to reach feeding areas (Horner et al. 1998), and northern populations performs migrations during the winter, tracking flowering plants (Rojas-Martínez et al. 1999). This species is also one of the most specialists on the consumption of nectar, although the consumption of insects and fruits may also occur (Howell 1979; Rojas-Martínez et al. 2012). Conversely, *G. soricina* is a smaller nectarivorous bat (Álvarez et al. 1991), and has a much more reduce mobility than other species, being able to fly up to three km per night searching for feeding areas (Aguiar et al. 2014). The presence of resident *G. soricina* populations throughout its distribution range occurs, probably as the result of its low mobility (Fleming et al. 1993). The diet is based mostly on nectar; however, the consumption of fruits and insects is not uncommon (Gardner 1977; Herrera 1999).

-Study site and bat sampling

Bats were collected in the “La Bonetera” area in Lázaro Cárdenas, southern Michoacán, México (ca. 18°05'N, 102°25'W). The area is covered mainly by tropical deciduous forest and patches of semi-deciduous forest. It has a marked dry season from November through June, and average annual temperature of 27 °C (Sandoval-Soto 2013). Six species of nectarivorous bats have been reported in the area, being *L. yerbabuenae* and *G. soricina* the most abundant species (Sandoval-Soto 2013; obs. pers.). We used mist nets at ground level to capture 6 non-reproductive adult males of *L. yerbabuenae* and 6 non-reproductive adult males of *G. soricina* (SEMARNAT; permit number SGPA / DGVS / 03702/17).

-Care and housing of bats

All bats were transferred to the experimental laboratory in Morelia, México. Bats were marked with plastic collars and health status was constantly monitored. We kept bats inside cages covered with shade cloth (0.75 x 0.75 x 0.75 m) in groups of three individuals. The laboratory remained in darkness at night and little illumination during the day; temperature was about 26-27 °C and relative humidity about 50% similar to other studies (Rodríguez-Peña et al. 2013). These conditions were similar to those in the captured area. Bats were fed daily at 8:00pm with a maintenance diet; composed by milk powder, cereals, sugar and fruit (mango or banana), complemented with vitamins and minerals (multivitamin tonic, "Cariño", México) (Mirón et al. 2006).

- Experimental design

We prepared artificial nectar solutions (Table 1) to evaluate the preference for sugar type and sugar concentration. Some of these solutions were similar to chiropterophilic plants that are commonly consumed by bats: *Ipomoea ampullaceae, Ceiba aesculifolia* and *Acanthocereus occidentalis* (Rodríguez-Peña et al. 2016). In addition, we also prepared solutions of single sugars at a concentration of 20% (w/w): the hexoses glucose and fructose, and the disaccharide sucrose. Pure water was also place as a control.

To evaluate food selection, a total of 12 trials were made with six individuals per species. Every night we placed one individual in the experimental area. This area consisted in a larger cage (3.6 x 1.6 x 2.6 m) with two resource patches, placed at a high of 1m at opposite sides of the cage. Each patch had seven feeders filled with 15 ml of solution (two for each type of solution) and placed randomly inside the patch. In addition, to account for changes in volume or concentration, we measure evaporation using control feeders for each solution, these feeders were covered with mesh to prevented bats from feeding on them.

Bats behavior was recorded during the night using two night vision cameras, focusing the food patches. Videos started at 20:00 hrs and finished by 7:00 am. For analysis, we discarded the first recording hour because bats took about an hour to start feeding after the solutions had been placed. Videos were review in slow motion using the software VLC-media-player 2.2.6. To evaluate foraging and activity patterns, we registered each time the bats approached to a feeder and drink from it. We also registered the feeder they visited and the time they fed on.

-Data analysis

To analyze if there were significant differences between treatment preferences, a GENMOD procedure was performed using software SAS 2003 version 9.3. We use frequency of visits to each solution per hour as the dependent variable, using a Poisson distribution and a log link function. We establish activity patterns per hour during the night by using data of the time at which each event occurred.

RESULTS

A total of 132 video hours were recorded for each bat species. In the experiments, *G. soricina* individuals performed a higher number of feeding events during the night, with an average of 102 visits per night (confidence intervals= 41.57, 162.77, n=6). Conversely, *L. yerbabuenae* individuals recorded a lower number of feeding events, with an average of 65 visits each night (confidence intervals = 27.25, 103. 74, n=6).

Significant differences were found between frequencies of visits to each type of solution by bat species. *Leptonycteris yerbabuenae* visited more often those feeders with nectar similar to cacti (*A. occidentalis*) (χ^2= 129.32, df= 6, p<0.0001), while *G. soricina* had a higher number of visits to feeders with solution similar to *Ipomoea ampullaceae* (χ^2= 223.03, df= 6, p<0.0001); we also observed that each bat species recorded a low number of visits to the preferred solution by the other species (Fig. 1). For the rest of the solutions, sucrose solution was visited mainly by *G. soricina*, while fructose and glucose solutions were recorded with similar use by both bat species. Conversely, water and *Ceiba aesculifolia* solution registered the lowest number of visits for the two bat species. Bat species not only fed from different solutions but also at different time. On the one hand *L. yerbabuenae* presents a feeding peak at 3:00 am (χ^2= 55.28, df=11, p<0.0001), and on the other hand, *G. soricina* had the highest number of feeding events around midnight (χ^2= 119.08, df=11, p<0.0001). The frequency of visits increases during the first hours until reaching its maximum peak and then decreases for both species (Fig. 2).

Frequency of visits to each treatment varied throughout the night. Apparently, bats made some recognition visits to the feeders and then choose the resources they used the rest of the night (Fig. 3). In the case of *L. yerbabuenae*, the consumption of water is restricted only to the first hours of feeding, later it is not consumed during the rest of the night. Conversely, *G. soricina* maintained water consumption throughout the night, although the frequency of visits was low. Both species alternated nectar consumption between different solutions. However, it can be observed that from 11:00 pm on, *L. yerbabuenae* fed mainly on nectar similar to cacti. This pattern was maintained until 6 am, when it changed for sucrose and *Ipomoea* solutions (Fig. 3). *G. soricina* also alternated the consumption among the different solutions before midnight, but after that time it mainly fed on *Ipomoea* and sucrose (Fig 3).

DISCUSSION

Our results agree with what we initially hypothesize. We found differences in resource use between bat species in time axis as well as in diet selection. *G. soricina* were more generalist than *L. yerbabuenae*, while *L. yerbabuenae* was selective and chose the most energetic resources. Then one possible explanation is that resource characteristics such as nectar quality could be driving the feeding pattern. In relation to the activity patterns, we observed that once species were released from competition, species showed differences in their activity peaks. These peaks of activity were similar to those found previously in the field (Chávez-Estrada, in prep). Our results also indicate that the duration of the feeding time by species increase when compared to that found previously during high density of bats (Chávez-Estrada, in prep). Then these results indicate that the presence of potential competitors may be influence feeding activity in bat species.

-Patterns of resource utilization

Our experiments show differences in number of feeding events, feeding preferences and feeding time by bat species and by treatments. Some authors have suggested that feeding behavior in bats species seems to be influenced by several factors, such as bat morphological specializations, physiological constraints, nectar properties and resource availability (Freeman 1995; Nicolson and Thornburg 2007; Ayala-Berdon et al. 2011; González-Terrazas et al. 2012), therefore, our results can be explained by a combination of factors.

In relation to the number of feeding events, *G. soricina* was the species that performed a large number of visits to all treatments. Several explanations that include both bat species and resource characteristics could account for this pattern. These results may be related to morphological characteristics that enable nectar feeding habits in bats (Freeman 1995). Some studies have demonstrated that morphological specialization such as the length of the oral apparatus and the tongue, are positively related with nectar extraction efficiency (González-Terrazas et al. 2012). The specialized species of *L. yerbabuenae* is more efficient when extracts nectar than the less specialized nectarivorous *G. soricina* (González-Terrazas et al. 2012), therefore, *G. soricina* needs to perform a higher number of floral visits than *L. yerbabuenae* to extract the same volume of nectar.

Floral visits may also depend on nectar concentration and nectar properties. Some studies have shown that nectar properties, especially viscosity, can increase with nectar concentration, making it harder to consume (Baker 1975; Kingsolver and Daniel1983). This makes this resource more difficult to exploit despite its benefits to those less efficient species. Therefore, it may be more efficient feeding on intermediate concentrations to a less specialized species than feeding on more diluted or concentrated nectars (Baker 1975; Kingsolver and Daniel1983). These agree with our experiments when we observed the less efficient *G. soricina* preferred less concentrated and energetic nectars similar to Ipomoeas. Apparently bats can compensate low energy intake by increasing feeding time and feeding events (Ayala-Berdon et al. 2011). Conversely, *L. yerbabuenae* fed mainly on cacti solutions, which were also the most concentrated and energetic resources offered in our experiments. *L. yerbabuenae* is one of the largest nectarivorous bat species, and feeding on the most concentrated solutions enable bats to enhance daily energy budget with less feeding events (Helversen and Reyer 1984; González-Terrazas et al. 2012).

Other explanations to the pattern of visit may be related to physiology. Since nectar is composed mainly on sugar and water (Baker et al. 1998), feeding behavior is also determined by physiological bat capacities to digest sugars and to eliminate water excess (Ayala-Berdon et al. 2011). Consumption of pure water is not expected to occur in nectarivorous bats as it may be obtained from nectar; however, some studies have shown that nectarivorous species do not drink extra water unless nectar is up to 50% of concentration (Helversen and Reyer 1984). These results contrast to our experiments, in which we observed that *G. soricina* maintenance little water ingestion during all night even with a low concentration. Water consumption in nectarivorous species remains largely unknown, and further research is needed.

Resource availability is another factor that has been related to food selection in bats (Ayala-Berdon et al. 2009; Laurindo 2017). Previous studies in tropical dry forests have found that Bombacaceous plant species are one of the most important resources for nectarivorous bats (Stoner et al. 2003; Quesada et al. 2003). Since bats were collected in a tropical dry forest, we expected that bats would feed mainly on these solutions types. However, nectar similar to *C. aesculifolia* was one of the less visited resources in our experiments. On plausive explanation is that nectar quality and availability of resources could be acting in concert in the selection of food resources. One previous study in the same study area found that there is a plant species turnover, with *Pseudobombax ellipticum* being the most common species in the diet during its massive flowering (Chávez-Estrada, in prep). Despite this, when both species were released from competition and were allowed to consume on any resource the Bombacaceous nectar was not preferred. These points to the possibility that the consumption of this nectar is more due to the large availability of flowering plants rather than to its quality.

-Patterns in feeding time

Feeding activity patterns were also different between species. Peaks of maximum feeding observed in our experiments agree with the results previously found in the field, but the duration of the feeding time increase when compared to those found during high density of bats (Chávez-Estrada, in prep); *G. soricina* performs a higher number of feeding events around midnight which is earlier than the maximum feeding hour of *L. yerbabuenae*. Field studies have suggested that foraging activity peaks may be related to a higher production of nectar during the night (Horner et al. 1998), and differences in feeding patterns may reduce competition for resources; however, in our experiments nectar was available for bats throughout all night; one possible explanation is that activity and feeding patterns are not only related to food characteristics but also to the species intrinsic characteristics (Fragaszy et al. 2004)

In conclusion, our data on food selection and feeding patterns in this two bat species in captivity suggests differences in resource use between these two bat species in time axis as well as in diet selection. Therefore, these agree with our initial statement, and we think that species should not compete when coexisting. However, in natural conditions there are many factors that can influence foraging behavior, such as biotic interactions, food quality and quantity, physiological demands and limitations, among others (Ayala-Berdon et al. 2009; Laurindo 2017). Since our experiments were carried out under high resource abundance and low density of individuals, we suggest similar future experiments in which interactions are taking into account.

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Ethical statement

All applicable national guidelines for the care and use of animals were followed.

Conflict of interest:

The authors have no conflict of interest.

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Table 1. Composition of artificial nectar solutions given to bats on each trial. Plant properties are based on Rodríguez-Peña et al. (2016).

Solution	Nectar concentration (°Brix)	% Glucose	% Fructose	% Sucrose	Energy content in 100gr of solution (kcal)
Ipomoea ampullaceae	24.42	40.93	46.58	14.49	95.18
Ceiba aesculifolia	16.85	47.18	49.82	2.99	65.33
Acanthocereus occidentalis	27.13	17.06	28.97	53.98	105.39
Glucose	20	100	-	-	75.00
Fructose	20	-	100	-	80.00
Sucrose	20	-	-	100	77.4
Water	-	-	-	-	0.00

Figure legends

Fig. 1. Average frequency of visits per treatment. Significant differences were found for *Leptonycteris yerbabuenae* ($_{\chi}{}^{2}$= 129.32, df= 6, $p<0.0001$) and *G. soricina* ($_{\chi}{}^{2}$= 223.03, df= 6, $p<0.0001$);

Fig. 2. Average frequency of visits per hour. Bat species fed from different solutions at different time. *L. yerbabuenae* ($_{\chi}{}^{2}$= 55.28, df= 11, $p<0.0001$), *G. soricina* ($_{\chi}{}^{2}$= 119.08, df= 11, $p<0.0001$).

Fig. 3. Alluvial plot showing frequency of visits to each solution during different hours for *G. soricina* and *L. yerbabuenae*.

Fig. 4. Percentage of visits to each solution during different hours. a) Data of *L. yerbabuenae,* b) Data of *G. soricina.*

Figures

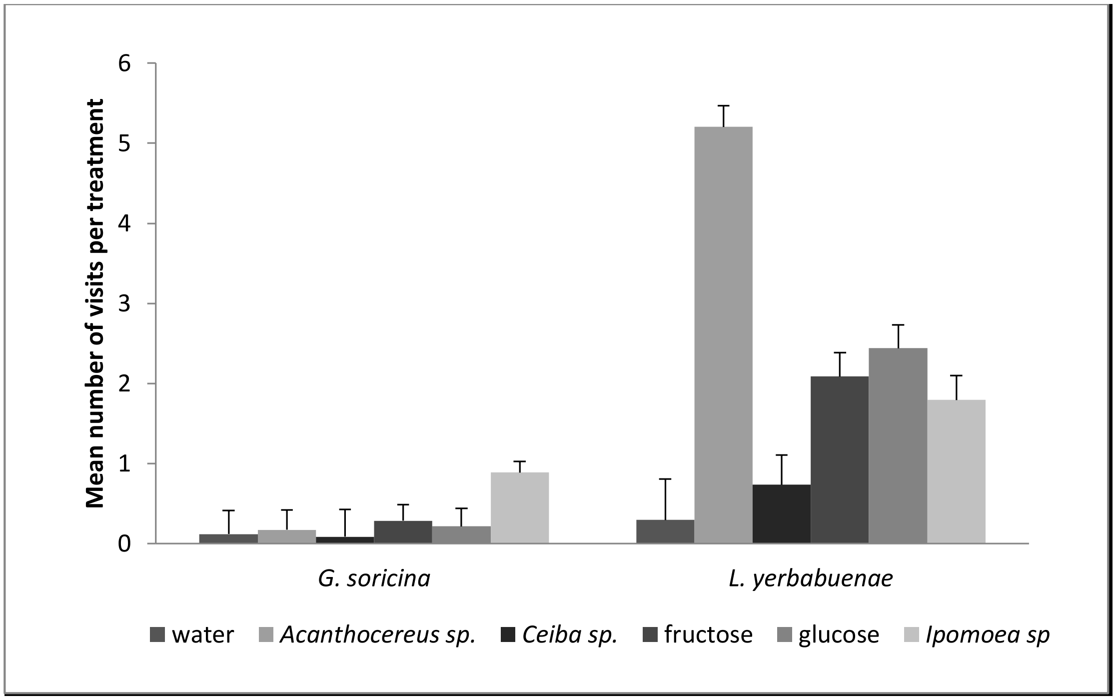

Fig. 1.

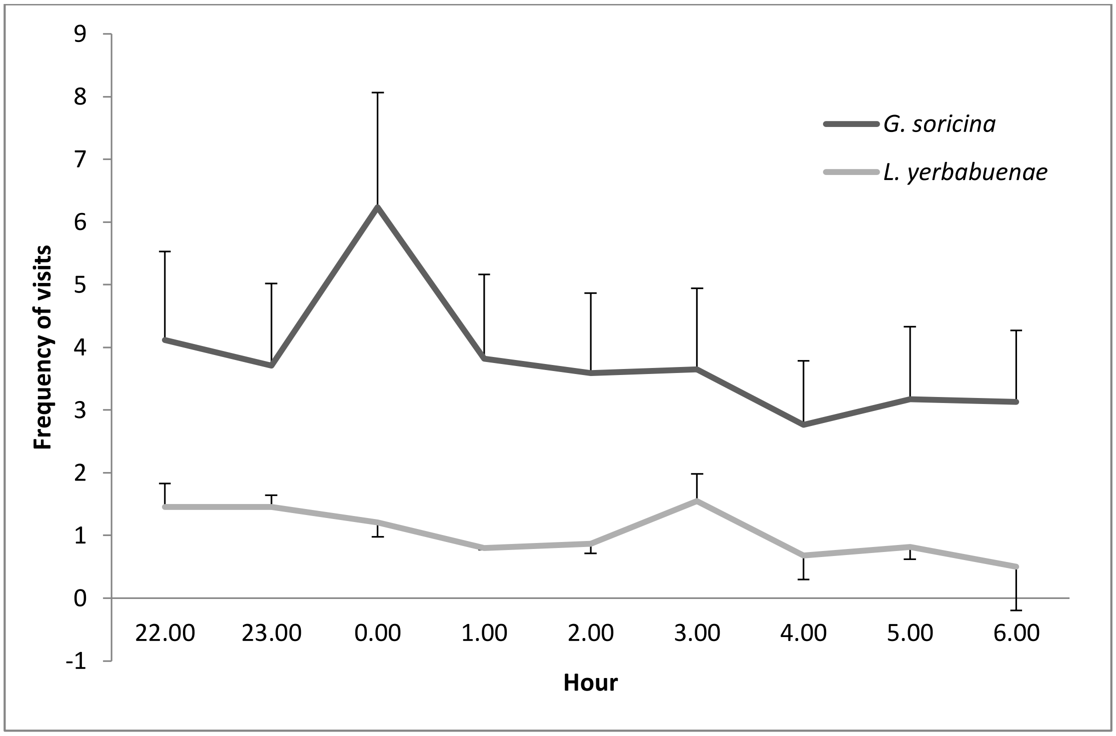
9
8
7
6
5
4
3
2
1
0
-1
Frequency of visits
G. soricina
L. yerbabuenae
22.00
23.00
0.00
1.00
2.00
3.00
4.00
5.00
6.00
Hour

Fig. 2.

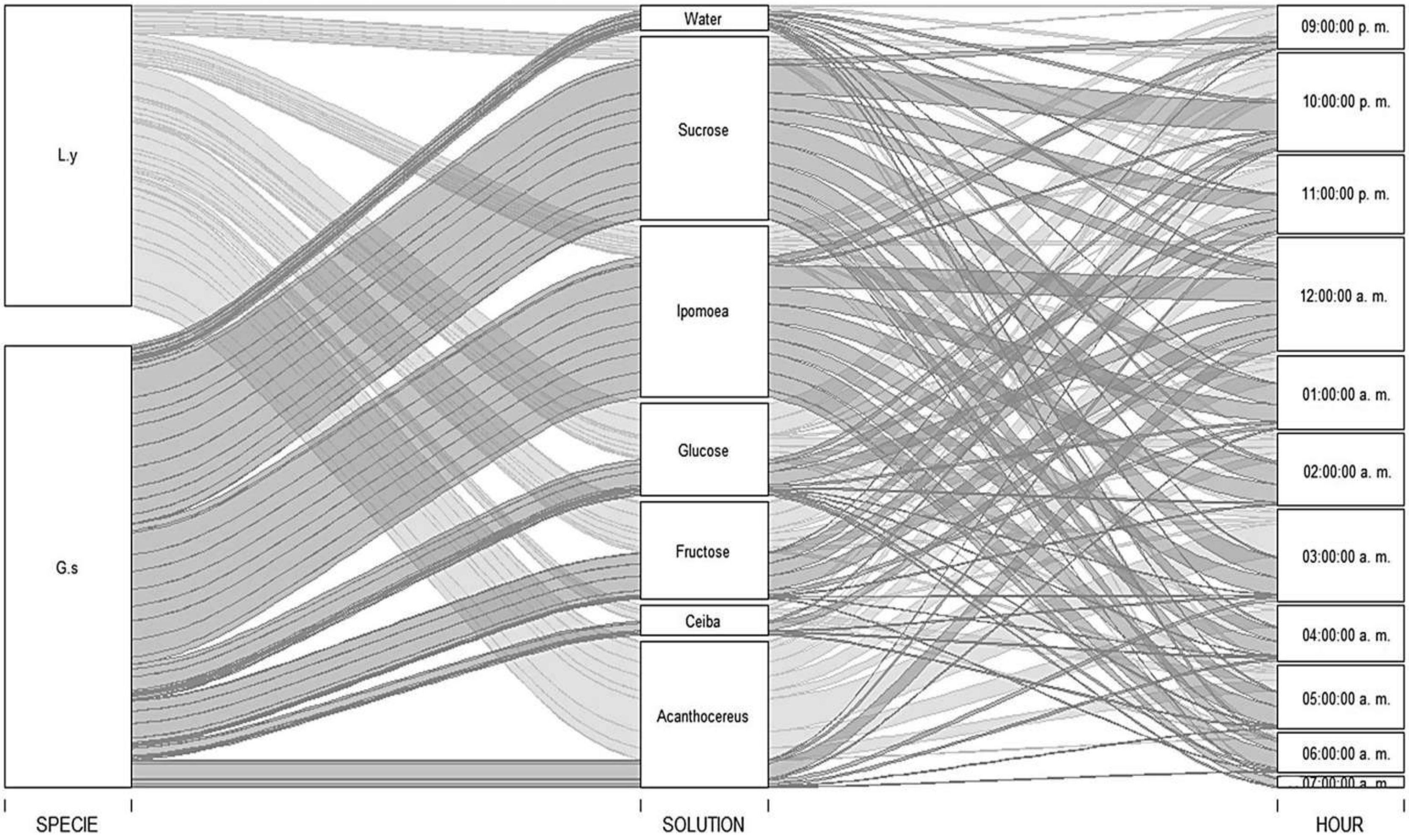
L.y
G.s
Water
Sucrose
Ipomoea
Glucose
Fructose
Ceiba
Acanthocereus
09:00:00 p. m.
10:00:00 p. m.
11:00:00 p. m.
12:00:00 a. m.
01:00:00 a. m.
02:00:00 a. m.
03:00:00 a. m.
04:00:00 a. m.
05:00:00 a. m.
06:00:00 a. m.
07:00:00 a. m.
SPECIE
SOLUTION
HOUR

Fig. 3

DISCUSIÓN GENERAL

Nuestros resultados sugieren diferencias en la dieta y en los patrones de actividad diaria de las especies de murciélagos. Observamos que la selección del alimento y la amplitud del nicho de las especies no están relacionadas con la presencia de competidores potenciales; lo anterior debido a que *G. soricina* se comportó como un depredador generalista y mantuvo su patrón de amplitud de nicho a pesar de la presencia de *L. yerbabuenae*, además en los experimentos de cautiverio prefirió recursos con contenido energético intermedio; mientras que *L. yerbabuenae* fue especialista en el consumo de néctar y en los experimentos de cautiverio prefirió aquellos recursos con mayor aporte energético. Una posible explicación es que la disponibilidad y aporte energético de los recursos podrían estar influenciando el patrón de alimentación observado. En relación a los patrones de actividad diaria, las especies presentaron diferencias en los picos de actividad, esto parece estar influenciado por la presencia de otros individuos; ya que el tiempo que cada especie invierte en alimentarse aumenta cuando existe baja densidad de individuos, posiblemente como una estrategia para reducir la competencia por los recursos en condiciones naturales.

-Abundancia de murciélagos y disponibilidad de recursos

La mayor cantidad de murciélagos nectarívoros fue capturada durante la temporada seca, lo cual coincidió con la mayor abundancia de flores en el área de estudio. Este mismo patrón ha sido observado por otros autores en el bosque seco y el matorral crasicaule de México (Stoner et al. 2003; Cornejo et al. 2011), lo cual sugiere que la fenología de floración de las especies quiropterofílicas es un factor importante en la dinámica de las poblaciones de murciélagos nectarívoros (Fleming 1982; Tschapka 2004).

-Dieta y análisis de nicho

La dieta de los murciélagos estuvo compuesta por ocho especies de plantas diferentes durante el tiempo en el que coexisten. *G. soricina* presentó mayor amplitud de nicho, lo que significa que es una especie memos especialista en comparación con *L. yerbabuenae*. Lo anterior coincide con los hábitos alimenticios reportados para estas especies (Gardner 1977; Howell 1979; Herrera 1999; Ibarra-López 2012; Rojas-Martínez et al. 2012). Además, observamos que el patrón de amplitud de nicho de *G. soricina* no fue modificado por la presencia de *L.*

yerbabuenae. Aunque las especies compartieron cinco de los ocho recursos utilizados durante la coexistencia, la proporción de uso de cada recurso fue diferente para cada especie de murciélago, lo que ocasionó bajos niveles de traslape en dieta de estas especies.

En los experimentos en cautiverio, *G. soricina* mantuvo el patrón observado en campo y fue más generalista que *L. yerbabuenae.* Además, observamos diferencias en la preferencia del recurso. Por un lado, *L. yerbabuenae* realizó un menor número de eventos de alimentación y prefirió aquellos recursos que presentaron mayor contenido energético; por otro lado, *G. soricina* realizó un mayor número de visitas a recursos con menor aporte calórico. Por lo tanto, es posible que las propiedades del néctar influyan en la selección de los recursos. Además de las características y disponibilidad del alimento, otros autores también han sugerido que el comportamiento alimentario en las especies de murciélagos está influenciado por las especializaciones morfológicas y las limitaciones fisiológicas de las especies (Freeman 1995; Nicolson y Thornburg 2007; Ayala-Berdon et al. 2009; González-Terrazas et al. 2012).

-Patrones de actividad

Se observaron diferencias entre los picos de alimentación de las especies de murciélagos. Algunos estudios han sugerido que los picos de alimentación pueden estar asociados a la mayor producción de néctar de las especies quiropterofílicas (Horner et al. 1998). Sin embargo, en nuestros experimentos el néctar estuvo disponible durante toda la noche; por lo que es posible que los patrones de alimentación no solo estén relacionados con las características del alimento sino también con las características intrínsecas de las especies (Fragaszy et al. 2004). Por otro lado, también observamos que el tiempo invertido en la alimentación parece estar relacionado con la densidad de individuos. Lo anterior debido a que el tiempo de actividad estuvo altamente dividido entre las especies de murciélagos durante los meses con mayor número de individuos, sin embargo, estas especies extendieron su tiempo de alimentación cuando había una menor densidad de murciélagos nectarívoros en el área. Este mismo patrón fue observado durante el trabajo de laboratorio. Lo anterior, podría indicar una flexibilidad estacional en las estrategias de comportamiento de los murciélagos para hacer frente a los cambios en la dinámica de las poblaciones y a la llegada de especies migratorias potencialmente más competitivas. Es posible que las diferencias interespecíficas en el tiempo de búsqueda de alimento y la gran disponibilidad de flores en el bosque tropical seco puedan reducir la competencia interespecífica incluso cuando los murciélagos se alimentan de recursos similares. Otros estudios en mamíferos medianos han también han observado diferencias en los horarios de alimentación de especies con dietas similares (Basurto 2016; Bu et al. 2016).

En conclusión, después de analizar la dieta y los patrones de actividad en estas dos especies de murciélagos, no encontramos evidencia de que la dieta de las especies pueda estar cambiando en relación con la presencia de competidores potenciales, pero sí encontramos segregación de nicho en los patrones de actividad diaria relacionados con la alta densidad de *L. yerbabuenae*. Por lo tanto, creemos que las especies no deberían competir cuando coexisten. Sin embargo, en condiciones naturales hay muchos factores que pueden influir en el comportamiento de alimentación, como las interacciones bióticas, la cantidad y calidad de los alimentos, las demandas y limitaciones fisiológicas, entre otros (Ayala-Berdon et al. 2009; Laurindo 2017). Dado que nuestros experimentos se llevaron a cabo con una gran abundancia de recursos y baja densidad de individuos, sugerimos experimentos similares en los que las interacciones sean tomadas en cuenta.

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