



DIETARY VARIATION AND REPRODUCTIVE STATUS OF *Mormoops megalophylla* (CHIROPTERA: MORMOOPIDAE) IN A CAVE OF NORTHEASTERN ANDES FROM COLOMBIA

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ABSTRACT. Dietary studies of insectivorous bats are critical for a comprehensive analysis of their ecological role in pest control. Several factors including seasonality, reproductive status and sex may influence dietary specialization. However, data on insectivorous bat diet are scarce, especially in Mormoopidae family. Here, we analyzed the dietary variation of *Mormoops megalophylla* (Peters, 1864) between sexes, reproductive states and climatic seasons in Macaregua cave, located in Northeastern Andes of Colombia. We collected fecal samples and vaginal smears from 377 individuals. We assess differences between sexes in the frequency of insect consumption and we estimate dietary breadth in reproductive and non-reproductive bats. *Mormoops megalophylla* has a highly specialized diet, selecting primarily for Lepidoptera insects. There were no differences between sexes, but wider dietary breadth was found in reproductive bats in comparison to non-reproductive bats. Probably, the specialization on Lepidoptera insects is explained by the high amounts of caloric energy that these insects can offer. It was remarkable the upward trend in Lepidoptera consumption from reproductive bats during the wet season, when moths are available. By contrast, non-reproductive bats increased Lepidoptera consumption in the dry season, possibly to prepare for the next reproductive events. The analysis of diet over time suggests variations between climatic seasons and reproductive states; that is, when bats are reproductively active, they increase the amount of Lepidoptera consumption in the wet season to supply their energy requirements during reproduction. These results provide key information about the ecology of *M. megalophylla* in the northern part of its South American distribution.

RESUMEN. Variación en la dieta y estado reproductivo de *Mormoops megalophylla* (Chiroptera: Mormoopidae) en una cueva del noreste de los Andes de Colombia. Los estudios de dieta en murciélagos insectívoros son fundamentales para un análisis exhaustivo de su papel en el control de plagas. Varios factores como la estacionalidad, el estado reproductivo y el sexo, pueden incidir en la especialización de la dieta. Sin embargo, información sobre la dieta en murciélagos insectívoros es escasa, especialmente en la familia Mormoopidae. Analizamos la variación en la dieta de *Mormoops megalophylla* (Peters, 1864) entre sexos, estados reproductivos y estaciones climáticas en la cueva Macaregua, en los Andes nororientales colombianos. Recolectamos muestras fecales y citologías vaginales de 377 individuos. Evaluamos las diferencias entre sexos en la frecuencia del consumo de insectos y estimamos la amplitud de dieta en murciélagos reproductivos y no reproductivos. *Mormoops megalophylla* presenta una dieta especializada en lepidópteros. No hubo diferencias entre sexos, pero hubo mayor amplitud de dieta en murciélagos reproductivos en comparación con los no reproductivos. La especialización en lepidópteros se puede explicar por las altas cantidades de energía que proveen estos insectos. Fue notable el incremento en el consumo de lepidópteros en murciélagos reproductivos durante la estación húmeda, que es cuando hay más polillas. Contrariamente, murciélagos no

reproductivos aumentaron el consumo de lepidópteros en la estación seca, como preparación para futuros eventos reproductivos. El análisis de la dieta en el tiempo sugiere variaciones entre estaciones climáticas y estados reproductivos; individuos reproductivos consumen más lepidópteros en época húmeda supliendo sus requerimientos energéticos durante la reproducción. Estos resultados proporcionan información clave de la ecología de *M. megalophylla* en el norte de su distribución sudamericana.

Key words: feeding habits, insectivorous bats, Macaregua Cave, reproduction, vaginal smears.

Palabras clave: citologías vaginales, cueva Macaregua, hábitos alimentarios, murciélagos insectívoros, reproducción.

INTRODUCTION

Approximately three-quarters of bat species are insectivores (Hutson et al. 2001; Aguirre 2007). The Neotropical region harbors more than the half of the species of insectivorous bats (Maas et al. 2016), however, the knowledge of natural history traits such as dietary composition is scarce (Fabián et al. 1990; Willig et al. 1993). Dietary studies of insectivorous bats are imperative for a comprehensive analysis of their ecological role as regulators of insect populations (Debelica et al. 2006; Maas et al. 2016; Kemp et al. 2019; Castillo-Figueroa 2020a). Several factors influence dietary specialization; for instance, intrinsic factors related with body size, developmental or reproductive status and sex, as well as extrinsic factors associated to seasonality, spatial distribution and nutritional value of food items may affect feeding behavior of bats (Bohlender et al. 2018).

The insectivorous bat family Mormoopidae contains genera *Pteronotus* and *Mormoops*. In Colombia, *Mormoops* is represented by a single species: *Mormoops megalophylla* (Peters, 1864). This species is distributed from southern USA (Arizona and Texas) to northern Peru in South America (Dávalos et al. 2008) and is found in a variety of habitats which comprises tropical forests, savannas, and desert environments, among other ecosystems (Nowak 1991). In Colombia the species has been reported in the Caribbean and Andean regions, in Antioquia, Santander, Tolima, Bolivar, Cesar, Córdoba, La Guajira and Sucre departments (Solari et al. 2013). However, little is known about the ecology of *M. megalophylla*. For example, there are only two dietary studies (Easterla & Whitaker 1972; Boada et al. 2003) but none of them studied dietary variation between sexes, reproductive status, and climatic season.

In Colombia, dietary studies have been conducted mainly on frugivorous bat species (Estrada-Villegas et al. 2007, 2010a; Ríos-Blanco & Pérez-Torres 2015; Suárez-Castro & Montenegro 2015; Aroca et al. 2016;

Montoya-Bustamante et al. 2016; Bohlender et al. 2018; Cely-Gómez & Castillo-Figueroa 2019). The few contributions focused on insectivorous bats' diet have studied species from families Molossidae and Emballonuridae (Arata et al. 1967; Ramírez-Chaves et al. 2008; Cruz-Parrado et al. 2018), but none has investigated the feeding habits of Mormoopidae species. The presence of large colonies of *M. megalophylla* in caves of Santander department has been recorded (Muñoz-Saba et al. 2013; Pérez-Torres et al. 2015). Caves are ideal sites for dietary and reproductive investigations because of the high number of individuals that can be captured, which becomes critical in ecological studies given the difficulty of insectivorous bat sampling in other habitats such as forests (Sosa et al. 1996; Estrada-Villegas et al. 2010b).

We explored dietary attributes of a population of *M. megalophylla* in a cave of Northeastern Andes of Colombia (Macaregua cave). Our objectives were: 1) describe its diet composition, 2) evaluate the existence of dietary differences among sexes and parse out dietary breadth between reproductive states of individuals, and 3) analyze dietary variation along the two annual climatic seasons (dry and rainy season). Because some studies have shown no significant differences in feeding habits between males and females of insectivorous bats (Gamboa & Díaz 2018), but also have shown the increase of insect consumption during reproductive season (Sosa et al. 1996), we expect to observe no differences between sexes and higher dietary breadth in reproductive bats than non-reproductive bats. As food availability is not uniform during all the year, we expect to record variations in the proportion of insect consumption in the two climatic seasons.

MATERIALS AND METHODS

Study site

Macaregua cave is located in Santander department, municipality of Curití (centroid of the study area: 6°39'36.2" N 73°06'32.3" W; Fig. 1), in an elevation of 1 566 meters (Pérez-

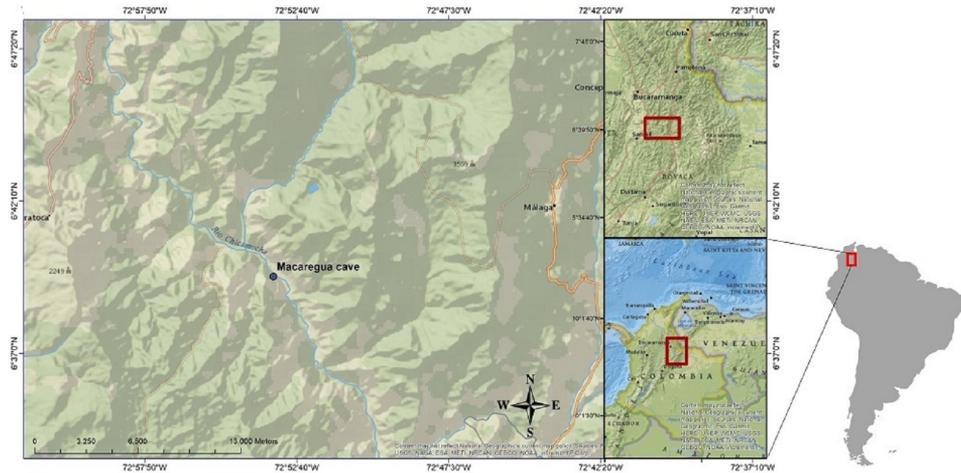


Fig. 1. Location of Macaregua cave (Santander, Colombia).

Torres et al. 2015). The cave is immersed in a remnant of tropical dry forest and agricultural fields of tobacco, maize, beans and coffee. Three insectivorous species inhabit this cave, of which *Mormoops megalophylla* is the most abundant (Pérez-Torres et al. 2015).

Bat sampling

Five field trips were conducted from April 2013 to January 2014, covering both dry season (December, January) and wet season (April, August, September). In each of the field trips, and with the intention of capturing the bats with their full stomachs after feeding, we positioned a mist net (2x6 m) at the entrance of the cave from 2:00 to 7:00 hours (Fig. 2). Each bat captured was placed in a cloth bag for maximum 30 minutes to collect its fecal samples. Standard external body measurements, sex, age category, and reproductive status were recorded for each individual (Kunz & Parsons 1988). Before liberation, we marked each bat's forearm with a numbered aluminum-ring. To avoid repeat fecal samples from individuals, we individually marked each bat punch-marking numbers into their wing membranes with tattoo pliers for small domestic animals according to Bonaccorso & Smythe (1972). Voucher specimens (MUJ 1724-MUJ 1725) were deposited in Mammalian Collection at the Museo Javeriano de Historia Natural of Pontificia Universidad Javeriana (MPUJ-MAMM) in Bogotá, Colombia.

Fecal samples and vaginal smears

The samples were examined following the methodology described by Whitaker et al. (2009). All insect parts (e.g., legs, antennae, proboscis, head, tarsal, and tarsal claws) were separated and identified to order category using taxonomic keys of Kristensen (1999) and Borror & White (1970). Samples were also analyzed by professional entomologists from Pontificia Universidad Javeriana (Dimitri Forero) and CORPOICA institution (Edgar Palacio) to confirm identification. The reproductive status of male bats was determined by examining testes (scroted or not). The reproductive status of female bats was determined based on

vaginal smears according to Vela-Vargas et al. (2016). These were analyzed using a microscope (Nikon Eclipse E400), in which the percentage of cells in the different estrous cycle's stages were established. Females were reproductive when they presented a dominance of nucleated superficial cells (proestrus), enucleated superficial cells (estrus), and intermediate cells (metestrus), and were considered as non-reproductive when presented parabasal cells (anestrus) (Vela-Vargas et al. 2016; Stukenholtz et al. 2018).

Data analysis

We determined the percentage of reproductive and non-reproductive females and males. We applied the Levins index ($B=1/\sum pi^2$) to determine dietary breadth (Levins 1968), and we also used the Hulbert correction ($Ba=B-1/B-n$) in order to scale diet breadth from 0 to 1 (Hulbert 1978), where pi is the proportion of individuals consuming a particular prey item i and n is the number of possible resource states (Gamboa & Díaz 2018). In Hulbert correction, a value of 0 represents that all individuals consume a single food item (more specialist), and 1 when all individuals consume the totality of food items that are available (more generalist) (Hulbert 1978). We analyzed the frequencies of consumption of members of the different insect orders found in the fecal samples. To determine whether the observed frequency of food items consumed were different between the sexes, we applied Chi-square tests (χ^2), using a level of significance of 0.05. We also analyzed whether insect consumption of reproductive and non-reproductive males and females were associated to seasonal variation. By doing so, we assessed consumption frequencies of each of these reproductive categories in each month through χ^2 test.

RESULTS

Bat population and food items consumed

We captured 377 individuals during the five field trips. From these, 164 were females (40.66% re-

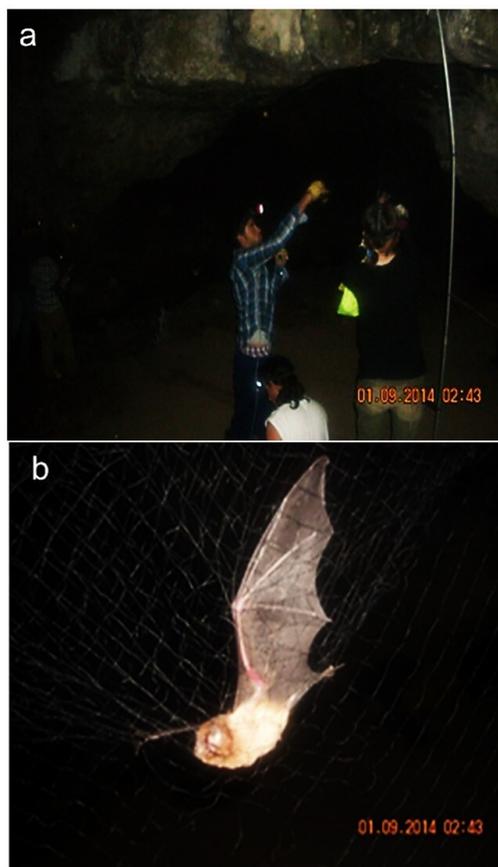


Fig. 2. Bat sampling at Macaregua cave (Santander, Colombia). a) Mist net at the entrance of the cave; b) individual of *Mormoops megalophylla* captured.

productive and 59.34% non-reproductive) and 213 were males (18.71% reproductive and 81.29% non-reproductive). Regarding females, 92.7% were adults and 7.3% subadults. For males 94% were adults, 5.6% were subadults and 0.4% were juveniles. Overall, 85 fecal samples were obtained. Fragments of tibiotarso and tarsal claws of Lepidoptera were the commonest remains in the feces (**Fig. 3; Table 1**). Due to the large number of fragmentary structures found in fecal samples, it was not possible to differentiate among morphospecies. However, a higher frequency of fragments belong to Lepidoptera order was found, followed by Hemiptera and Hymenoptera orders, respectively (**Table 1**). Therefore, the diet of the population of *M. megalophylla* from Macaregua cave is based mainly on Lepidoptera insects.

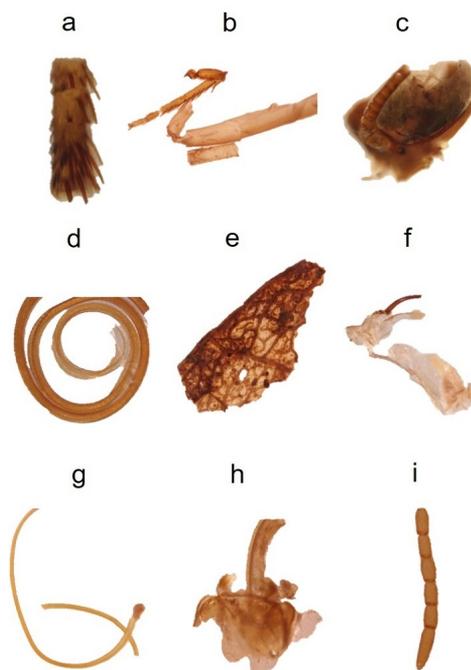


Fig. 3. Insect fragments found in the diet of *Mormoops megalophylla* at Macaregua cave (Santander, Colombia). a) Tarsus from a Lepidoptera; b) tarsus and tarsal claws from a Lepidoptera; c) eye and antenna from a Lepidoptera; d) proboscis from a Lepidoptera; e) wing from a Hemiptera; f) frenulum from a Lepidoptera; g) frenulum and proboscis from a Lepidoptera; h) head from a Lepidoptera; and i) antenna from a Hymenoptera.

Dietary variation between sexes and reproductive status

There were no significant differences in diet composition between males and females ($\chi^2=4.01$; $n=85$; $df=1$; $p=0.406$), but according to Levin index we found a higher dietary breadth in females ($B=1.05$; $B_a=0.05$) than males ($B=1.02$; $B_a=0.02$). Similarly, reproductive males ($B=1.21$; $B_a=0.28$) and reproductive females ($B=1.13$; $B_a=0.15$) showed a higher dietary breadth in comparison to non-reproductive males ($B=1$; $B_a=0.01$) and non-reproductive females ($B=1$; $B_a=0.01$).

Dietary variation along annual seasons

We found an association between reproductive status of bats and insect consumption in each month ($\chi^2=180.58$; $n=85$; $df=12$; $p<0.0001$). When comparing the consumption of Lepidoptera insects between reproductive and non-reproductive males, there is an increasing tendency in reproductive males dur-

Table 1

Food items found in the diet of *Mormoops megalophylla* at Macaregua cave (Santander, Colombia).

Insect order	Insect part	Percentage of fragments (%)
Lepidoptera (98.2%)	Tibia and tarsus	37.2
	Proboscis	10.6
	Antennas	19.4
	Head	4.3
	Frenulum	9.4
	Tarsus and claws	13.9
	Femur, warm and tarsal	3.4
Hemiptera (1.2 %)	Tarsus and claws	0.6
	Wings	0.6
Hymenoptera (0.6%)	Antennas	0.6

ing the wet season. Conversely, in the dry season, the trends are reversed, as reproductive males consumed less Lepidoptera, while non-reproductive males increase their consumption of insects of this Order (Fig. 4a). In the case of females, the reproductively active individuals showed one peak of increase of Lepidoptera consumption in the wet season (August), and one in the dry season (December), with a decrease in January. The non-breeding females showed one peak of consumption in the wet season (September), and an increase in the dry season (January) (Fig. 4b).

When comparing reproductive males and females, a similar pattern is presented: the maximum peak is at the beginning of dry season and the minimum peak is at the beginning of the wet season, with an increasing tendency during this climatic season (Fig. 4c). Finally, when comparing the proportion of lepidopteran consumption between non-reproductive males and females, we observed a similar pattern from the end of the wet season (September), with a peak of Lepidopteran consumption in January, on the dry season (Fig. 4d).

DISCUSSION

Our study showed a high dietary specialization of *M. megalophylla* towards the consumption of Lepidoptera insects (Table 1). Stomach collections from individuals of *M. megalophylla* suggest this bat feeds mainly on large-bodied moths. This result is consistent with the report of Easterla & Whitaker (1972), who found a 100% frequency of consumption of Lepidopteran moths based on the examination of

stomach content of two individuals. Based on this, *M. megalophylla* can be considered as a rare species due to its specialization in the use of trophic resources (Yu & Dobson 2000). We also found fragments of Hemiptera (Fig. 3e) and Hymenoptera (Fig. 3i) insects but in less proportion. Additionally, other studies have reported consumption of Dermaptera and Coleoptera (Boada et al. 2003).

As *M. megalophylla* has a large size when compared to other insectivores (Forearm length mean: 54.5 mm) (Rezutek & Cameron 1993; Castillo-Figueroa 2020b), this species needs the consumption of high-energy resources such as Lepidoptera. For example, moths of the Saturniidae family can have between 52% to 80% of the protein in dry matter (Bukkens 2005), being thus a suitable food item to satisfy the daily energy demand of these large insectivores. Moreover, soft-bodied insects may be common in the diet of this species due to its cranio-dental morphology characterized by smaller dilambodont teeth, thinner jaws and gracile skull (Freeman 1981, 1998; Rezutek & Cameron 1993). This is also the case of vespertilionids that are moth specialists such as *Euderma maculatum* and species of *Plecotus*, in which typical cranio-dental traits include numerous but smaller teeth, smaller canines, gracile skulls, long thin jaws, and little or no cranial crest development (?).

Based on Wilson (1973), reproductive cycles of insectivorous bats depend on the insect abundance according to the seasonal fluctuations. In this sense, it was remarkable the upward trend in Lepidoptera consumption from reproductive bats during the wet season, when moths are available (Torres-Flores 2013). Strict insectivores tend to eat larger and softer-bodied preys including chewing herbivores such as Lepidoptera larvae during the breeding season (Maas et al. 2016). This agrees with results of Gamboa & Díaz (2018) in Argentina, where many species of Lepidoptera are abundant on wet season because of higher abundance of food resources.

Reproductive males and females must consume enough resources to be reproductively active; for instance, females might have a greater consumption of resources in active periods since it requires the intake of a large amount of nutrients for the processes of gestation, lactation, and rearing of their offspring (Racey 1982; Kunz et al. 1995; Lee & McCracken 2002; Voigt 2003). Lactation is, undoubtedly, the most energetically costly period (Speakman 2008) in which bats increase the consumption of insects during the early weeks of lactation to milk production and export (Kunz et al. 1995). By contrast, non-reproductive

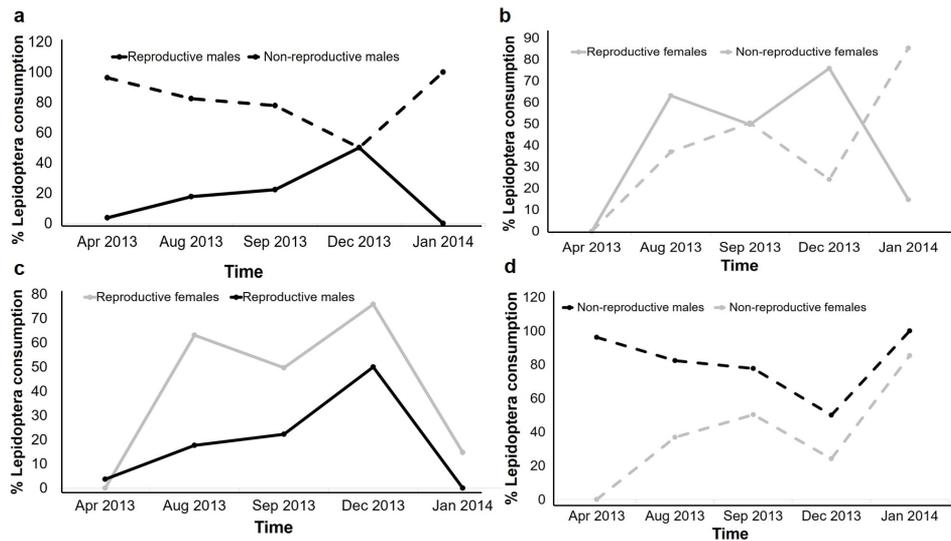


Fig. 4. Dietary variation over time comparing: a) reproductive males vs non-reproductive males; b) reproductive females vs non-reproductive females; c) reproductive males vs reproductive females; and d) non-reproductive males vs non-reproductive females of *Mormoops megalophylla* at Macaregua cave (Santander, Colombia).

bats increased Lepidoptera consumption in the dry season, perhaps to prepare for next reproductive events, and particularly males, decreased their consumption in the wet season (Fig. 4a). According to MacArthur & Pianka (1966), an optimal forager adjusts the time in each strategy to maximize its net energy reserve, which can occur with the non-reproductive males, where they can present a period of high proportion of consumption (dry season) and another of low consumption (wet season).

Even though the main objective of our study was to analyze the dietary variation of *M. megalophylla* between sexes and reproductive states in five months of the year including both the dry and the rainy seasons, it was not possible to infer the reproductive pattern of the species. To do so, a continuous monitoring (monthly) of the reproductive status of females and males is necessary to define the reproductive cycle. Additionally, according to preliminary observations performed in Macaregua cave, males spend most of the time during the year in this site while females arrive in particular times (mainly for their reproduction), leaving then the cave. Due to this, there are no females all the time in the cave and the fate of them when they leave the cave is unknown. It is critical, therefore, to study the reproductive cycle of this species to better relate the reproductive patterns to the diet as has been conducted in other species

such as *Carollia perspicillata* (Alviz & Pérez-Torres 2020).

Further studies should have a better taxonomic resolution of insects in dietary analysis. In our study, we confirm the specialization in Lepidoptera insects as Easterla & Whitaker (1972) have pointed out, but it might be that at the family or genus level *M. megalophylla* consumes different items and its diet is broader by the analysis scale. We recommend determining more accurately the morphospecies of Lepidoptera insects that belong to *M. megalophylla* diet using other techniques such as DNA metabarcoding of fecal samples, which can offer valuable insights into the dietary preferences of bats and their potential role as pest suppressors (Kemp et al. 2019). The application of DNA metabarcoding along with sequence-based assays of prey remain in feces have confirmed the diversified diets of several species of insectivorous bats (McCracken et al. 2012). In particular, the taxonomic identification of preys to the species level is more complicated in soft-bodied insects such as moths, many of which are agricultural pests that trigger highly destructive irruptions to crops of economic importance (McCracken et al. 2012). In this way, the consumption of potential pest insects can be associated with future studies that address the use of bats as possible biological controllers. Also, to have a more accurate idea of the insect composition in the study site, we recom-

mend either to search for a reference collection of insects (focused on location or similar ecosystem) or to include (parallel) insect sampling techniques in order to know more about available resources for insectivorous bats.

In sum, *M. megalophylla* is specialized in the consumption of Lepidoptera insects, probably because of the high amounts of caloric energy that moths can offer to them. We found no differences in insect consumption between males and females, but reproductive males and reproductive females have greater dietary breadth, perhaps as a result of the higher energy demand associated to reproductive events. Finally, lepidopteran consumption varies seasonally and according to sexual activity.

ACKNOWLEDGMENTS

To Elías Gómez and Flor Daza, owners of the property where Macaregua Cave is located, for allowing access to the cave and lodging in their premises. To the Laboratorio de Ecología Funcional (LEF), at Pontificia Universidad Javeriana (Bogotá, Colombia), especially to Estefanía Delgado for her assistance in the capturing of bats. To Dimitri Forero and Edgar Palacio for their help in the taxonomic identification of the structure fragments of insects. To Laura L. Garzón-Salamanca for her help in the preparation of the map in Fig. 1 and the graphs in Fig. 4. Finally, we are very grateful to Erin Stukenholtz for insightful comments on the manuscript and the revision of the English style. The collecting license was transacted through the project “Ecology of bats in cave systems in the department of Santander” supported by the Pontificia Universidad Javeriana (ID 5696). Finally, to the editor and the two anonymous reviewers for important comments and suggestions that substantially improved this paper.

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