

A difference between sexes: temporal variation in the diet of *Carollia perspicillata* (Chiroptera, Phyllostomidae) at the Macaregua cave, Santander (Colombia)

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Abstract

A difference between sexes: temporal variation in the diet of Carollia perspicillata (Chiroptera, Phyllostomidae) at the Macaregua cave, Santander (Colombia). Organisms adjust their foraging strategies to optimize the energetic costs during foraging with respect to benefits gained. These strategies are usually different in males and females due to their specific requirements during reproduction. Knowing the temporal dietary composition and variation may help us understand how intrinsic factors can influence diet during the breeding season. Seba's short-tailed fruit bat (*Carollia perspicillata*) plays an important role in seed dispersal throughout the Neotropics. Seasonal dietary changes related to resource availability have been documented but dietary differences between males and females have not been analyzed. We tested the hypothesis that dietary breadth increases and varies between males and females of *Carollia perspicillata* during the breeding season. We collected 295 fecal samples (from 236 males and 182 females) between June 2012 and April 2013 at the Macaregua cave (Santander, Colombia). Sex, diet and overlap were recorded. Time series analysis of dietary variation were estimated and related to food (fruits and flowers) availability. Males were found to include 18 seed morphospecies within their diet, while females included 16 seed morphospecies. *Ficus*, *Vismia* and *Acacia* were the most commonly consumed plant genera within the diet of both males and females. The time series analysis throughout the year indicated that males had greater dietary diversity than females. Dietary richness for males peaked multiple times, while dietary richness for females peaked only once during the transition period between pregnancy and lactation. We recorded significant sex differences in the value of importance of plants in the diet, evenness, and dominance of plant species consumed, as well as differential consumption over the seasons. Knowing the variations in the diet allows us to address the differences between the foraging strategies that females and males use in response to energy demands, movement patterns and habitat use. This is essential to understand all those processes that organisms must carry out for their survival and maintenance.

Key words: Bats, Conservation, Feeding ecology, Foraging, Nutrition

Resumen

Una diferencia entre sexos: variación temporal en la dieta de Carollia perspicillata (Chiroptera, Phyllostomidae) en la cueva de Macaregua, en Santander (Colombia). Los organismos ajustan sus estrategias de alimentación para optimizar la energía invertida en la búsqueda de alimento respecto a la energía obtenida. Estas estrategias suelen ser distintas entre machos y hembras debido a los requerimientos específicos durante la reproducción. Conocer la composición de la dieta y su variación en el tiempo puede ayudarnos a entender la forma en que los factores intrínsecos pueden influir en la dieta durante la época reproductiva. *Carollia perspicillata* es una de las especies más importantes en el proceso de dispersión de semillas del Neotrópico. Se han documentado cambios estacionales en la dieta relacionados con disponibilidad de recursos, pero no se han descrito las diferencias en la alimentación entre ambos sexos. Evaluamos la hipótesis que en la época reproductiva, la dieta se vuelve más variada y se diferencia entre machos y hembras de *Carollia perspicillata*. Entre junio de 2012 y abril de 2013 se obtuvieron recolectaron 295 muestras de materia fecal (de 236 machos y 182 hembras) en la cueva de Macaregua, en Santander (Colombia). Se registraron el sexo, la dieta y el solapamiento. Se realizaron análisis de series cronológicas de la variación de la dieta y se relacionaron con la disponibilidad de alimento (frutos y flores) a lo largo del tiempo.

En su dieta se identificaron 18 morfoespecies de semillas para machos y 16 para hembras. Las especies más consumidas fueron de los géneros *Ficus*, *Vismia* y *Acacia*, tanto en machos como en hembras. El análisis de series cronológicas realizadas durante el año mostró que la diversidad de la dieta de los machos fue mayor que la de las hembras. Mientras que los machos presentaron más de un pico de riqueza de la dieta, las hembras mostraron solo uno que coincidió con el período de transición entre el embarazo y la lactancia. Se observaron diferencias significativas entre sexos en cuanto al valor de la importancia de las plantas en la dieta, a la riqueza y dominancia de las especies vegetales consumidas, además de un consumo diferenciado según la época del año. Conocer las variaciones que ocurren en la dieta nos permite abordar las diferencias entre las estrategias de alimentación que las hembras y los machos utilizan en respuesta a las demandas de energía, los patrones de movimiento y el uso del hábitat. Esto es esencial para comprender todos los procesos que los organismos deben llevar a cabo para su supervivencia y mantenimiento.

Palabras claves: Murciélagos, Conservación, Ecología de la alimentación, Alimentación, Nutrición

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Introduction

Carollia perspicillata is the most abundant and widely distributed member of the genus *Carollia* (Fleming, 1988) and it is found in most evergreen forests in the neotropics (Cloutier and Thomas, 1992). Its diet is composed of a variety of fruits, flowers and insects. It is one of the main seed dispersers, helping to maintain plant heterogeneity, principally through the dispersion of pioneer plant species such as *Piper* and *Cecropia* (Barboza–Márquez and Aguirre, 2010; Kunz et al., 2011). Species of the genera *Piper* and *Solanum* comprise most of its diet, followed by a large variety of secondary plant species of the genera *Cecropia* and *Vismia* (Barboza–Marquez and Aguirre, 2010; Sánchez et al., 2012). During the dry season, when fruit production is low, its diet is mainly composed of nectar and pollen (Charles–Dominique, 1991; Cloutier and Thomas, 1992). Diet analyses have shown that *C. perspicillata* also consumes insects, possibly as a dietary supplement due to the low protein content of fruits (Mello et al., 2004a).

The dietary variation of *C. perspicillata* has been described in Costa Rica (Fleming and Heithaus, 1986), Rio de Janeiro and southeastern Brazil (Marinho–Filho, 1991; Mello et al., 2004a), but diet variation between males and females has not been reported. Dietary differences between males and females could be the result of seasonal changes of resources or energetic demands during different reproductive stages. According to reports, females' energetic demands increase continuously from fertilization to time of weaning (Sánchez et al., 2012). This is reflected in a 45 % increase in food consumption from pregnancy to lactation (Dietz and Kalko, 2006). Males only increase their energetic demands during gonad development and spermatogenesis (Cryan and Wolf, 2003; Pfeiffer and Mayer, 2013). Therefore, there likely exists a difference between male and female dietary items as sexes exhibit different energetic demands during their reproductive seasons. Understanding temporal dietary variation of this species might therefore allow us to explain behavioral traits, the relationship with the plants they feed on, their foraging patterns, and variations between males and females.

We analyzed the temporal variations of dietary preferences for male and female *C. perspicillata* in a cave in eastern Colombia, and evaluated the relationship of these changes with reproductive stages and resource availability. We evaluated whether the richness of the diet was greater during the breeding season, both for females (pregnant or lactating) and for males (scrotal testes), and also whether the amplitude of the diet of females was greater than that of the males, regardless of the season. We hypothesized that, due to the differences in energetic demands between males and females in relation to their reproductive seasons and foraging activities, a temporal variation in the components of the diet between sexes would be evident. Since the females present an increase in nutritional requirements during pregnancy and lactation, there would

be marked variations throughout the year due to the increase in the consumption of food items during these reproductive seasons.

Material and methods

Macaregua cave (6° 39' 36.2" N; 73° 6' 32.3" W) is located in Las Vueltas, Municipality of Curití, Santander, Colombia at an elevation of 1.566 m, embedded in a remnant of tropical dry forest (fig. 1). The average annual precipitation is 1.499 mm, with the highest peak of rainfall (285 mm) occurring in April– May and a second lower peak in September– October (GELT, 2013). The entrance to the cave is surrounded by tropical dry forest vegetation. Inside the cave there is a dry room of about 80 m long, and a moist room of about 610 m long with a running stream (Perez–Torres et al., 2015).

Sampling was conducted every two months between June 2012 and June 2013 to include both the dry and wet seasons. Bats were captured using cone traps and a mist net (6 x 3 m) located at the entrance to the cave, at between 02:00 and 05:00 h for four days each sampling month. The bats were mainly trapped when returning to the cave after foraging (Fleming and Heithaus, 1986; Charles–Dominique, 1991). Each individual was marked with forearm bands. Bats captured with traps were placed in individual cloth bags for 30' to 1 hour (Galindo–González, 1998; Heer et al., 2010; Mello et al., 2004b) to obtain fecal samples. Data collected for each individual were sex (male, female), reproductive status (males: testicles impalpable, inguinal or scrotal; females: active, inactive, pregnant, lactating) (Burnett and Kunz, 1982; Kunz and Anthony, 1982; Anthony, 1996), weight, and morphological measurements (Schmieder et al., 2015). Fecal samples were stored individually in microcentrifuge tubes with 70 % ethanol. The seeds found in the samples were separated according to morphology (size, color and shape) and initially classified by morphotype. Seeds were identified with the help of specialists, by comparing the morphotypes with reference collections at the Museum and Herbarium of Pontificia Universidad Javeriana and with specialized literature (Lobova et al., 2009).

To characterize the resource availability, vegetation sampling was conducted using five 50 m x 2 m transects (Dinerstein, 1986) located in the vicinity of the cave. The farthest transect was located at 4 km away from the cave and the closest was at 500 m. In addition, once the seeds retrieved from fecal samples were identified, phenological observations were made during each field trip in all established transects. Every day during the field trips the identified species of plants were examined in order to estimate the relative proportion of flowers and fruits during each sampling month. To check the reproductive status, the species of plants were characterized into four categories: 1) inactive (no flowers or fruits), 2) flowering (more flowers than fruits), 3) intermediate (same amount of flowers and fruits), and 4) fructification (more fruits than flowers) (Mello et al., 2004a, 2004b).

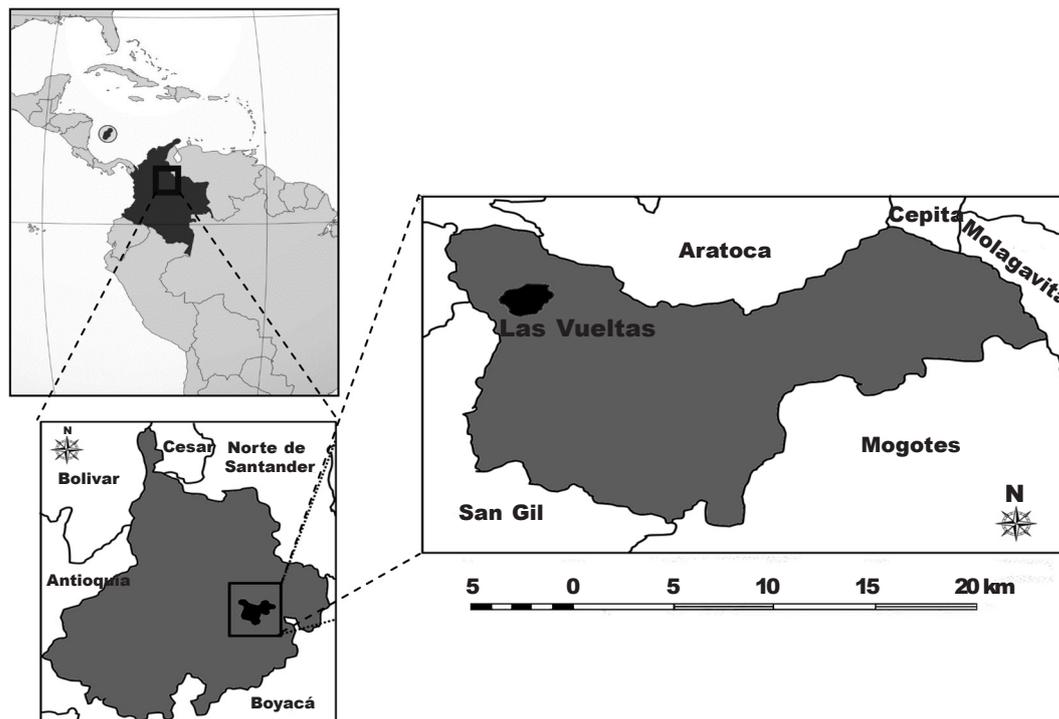


Fig. 1. Study area location in Vereda Las Vueltas, Municipality of Curití, Santander (Colombia). General information on the location of the country, the department and the village where the sampling was carried out is included.

Fig. 1. Ubicación de la zona de estudio en Vereda Las Vueltas, en el municipio de Curití, Santander (Colombia). Información general sobre la ubicación del país, el departamento y la aldea en los que se llevó a cabo el muestreo.

We analyzed the species composition and abundance of each dietary item consumed by both females and males. The number of samples in which a food item was found was taken into account in relation to the total number of samples analyzed. Diet breadth was evaluated using Levin's standardized index (B) following the assumptions proposed by Krebs (1998), where $B = Y^2 / (\text{total number of sampled individuals})$, R represents the total resources; s , total species; and N_j , number of individuals found using the j resource. Diet overlap was estimated using a simplified Morisita index (C_{Hj}) (Krebs, 1998), where $CH = \sum_{i=1}^n p_i^2$, p_i represents the proportion of the resource i from the total resources used by males and females, j y k ($i = 1, 2, 3, \dots, n$). A confidence level of 95% was taken into account in all analyses. Temporal dietary behavior was analyzed using a time series analysis (Box et al., 1994; Ziebarth et al., 2010), defined as a succession of observations of a variable taken in several instants of time. This test was used to model the mechanism that gives rise to the series observed through time. To run the test, we took time (independent) versus items consumed by males and females (dependent), and several variables of the time series analysis such as

the media, medium, trend, coefficients of symmetry and kurtosis. The normality of the test was analyzed using the Jarque–Bera estimate. Finally, consumption ratios between males and females were compared with an odds ratio test and we assessed temporal covariation between sexes using a Spearman's rank correlation test (Zar, 2010).

Results and discussion

During the sampling period, 236 males (56.46%) and 182 females (43.54%) were captured. In total, 160 fecal samples were collected from males and 135 from females. From these samples, 18 seed morphospecies were found in the fecal samples of males, and 16 seed morphospecies were found in fecal samples of females (table 1). *Ficus*, *Vismia* and *Acacia* were the most common plant genera, including more than 50% of the diet for both sexes. Males most frequently consumed *Ficus gigantocyce* (29.82%), followed by *Vismia glaziovii* (16.67%) and *Acacia farnesiana* (14.04%). Females consumed high proportions of *Vismia glaziovii* (23.40%) followed by

Table 1. Seed morphotypes found in the diet of males and females of *Carollia perspicillata* between June 2012 and July 2013 at the Macaregua cave. The abbreviation of the biological collection, the encounter frequency in the faeces (n), and the proportion of each item (%) within the total sample is included..

Tabla 1. Morfotipos de semilla encontrados en la dieta de los machos y las hembras de *Carollia perspicillata* entre junio de 2012 y junio de 2013 en la cueva de Macaregua. Se incluyen la abreviación de la colección biológica, la frecuencia de encuentro en las heces (n) y la proporción de cada elemento (%) en la muestra total.

Morphotypes	Abbreviation	Males		Females	
		n	(%)	n	(%)
<i>Ficus gigantocyce</i>	F2	34	29.82	16	17.02
<i>Vismia glaziovii</i>	V1	19	16.67	22	23.40
<i>Acacia farnesiana</i>	A3	16	14.04	18	19.15
<i>Piper aduncum</i>	O1	9	7.89	4	4.26
<i>Myrcia popayanensis</i>	M1	8	7.02	4	4.26
<i>Myrcia</i> sp. 1	M2	7	6.14	9	9.57
<i>Ficus</i> sp. 1	F1	4	3.51	3	3.19
<i>Acacia</i> sp. 1	A2	3	2.63	5	5.32
Undetermined 1	Indv.1	2	1.75	3	3.19
Undetermined 2	Indv.2	2	1.75	1	1.06
<i>Solanum mauritianum</i>	S1	2	1.75	1	1.06
<i>Piper nigrum</i>	P3	2	1.75	0	0
<i>Piper</i> sp. 1	P4	1	0.88	0	0
<i>Vismia</i> sp. 2	V2	1	0.88	0	0
Undetermined 3	Indv.3	1	0.88	1	1.06
<i>Vismia</i> sp. 3	V3	1	0.88	1	1.06
Asteraceae	Ast.	1	0.88	0	0
<i>Piper</i> sp. 2	P2	1	0.88	0	0
<i>Acacia</i> sp. 2	A1	0	0	1	1.06
<i>Solanum</i> sp. 1	S2	0	0	1	1.06
Undetermined 4	Indv.4	0	0	4	4.26

Acacia farnesiana (19.15%) and *Ficus gigantocyce* (17.02%). The remaining morphotypes showed similar frequencies. In addition, males were more likely to consume more *Ficus*, *Piper* and *Myrcia*, while females had higher probabilities of consuming *Vismia*, *Acacia* and *Myrcia*. The remaining identified morphotypes had similar probabilities of being consumed by both sexes (fig. 2).

Structure and composition indexes were calculated to compare the assembly of plants species (table 2). Overall, males and females had similar dietary compositions. There was, however, variation across the sampling months. The major differences occurred during the wet season when rainfall and fructification were at their highest. During the wet season (June and August), dietary richness between males and females differed significantly (June: α males = 0.79, α

females = 14.12, n = 26, d.f. = 25, $p = 0.02$; August: α males = 8.86, α females = 0, n = 54, d.f. = 53, $p = 0.03$). Males consumed *Ficus gigantocyce* more frequently, while females consumed more *Vismia glaziovii*. Females ate a wide variety of items in June (14 spp.) but consumed only a few items in August (2 spp.) despite the high resource availability. This finding may indicate a level of resource selection by females. In contrast, males consumed one food item in June, but expanded their diet considerably in August (1 to 4). No significant difference in dietary richness was observed in the dry season (December) (α males = 2.63, 1.78 ± 2.63 ; α females = 2.39, 1.05 ± 2.39 ; n = 53, d.f. = 52, $p = 0.3$). However, males presented a wider dietary breadth than females during the other sampling months. Females had a wider diet breadth during April and October (wet season). The diets of

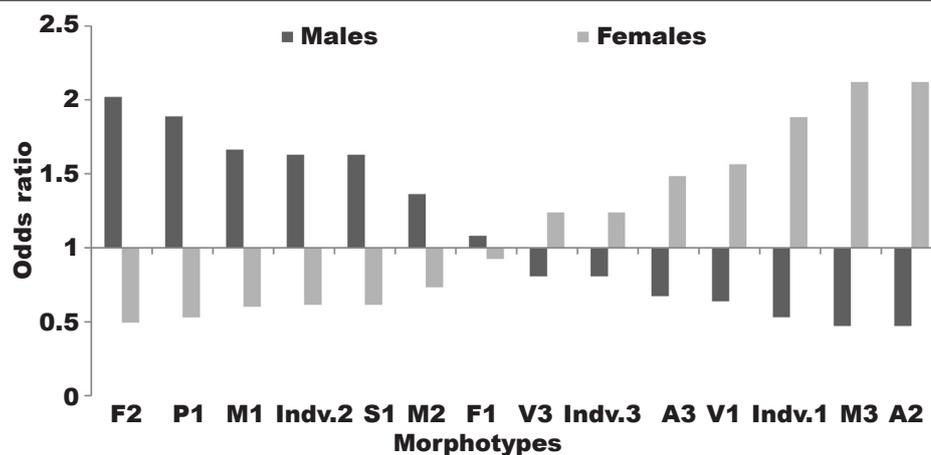


Fig. 2. Odds ratio of the items consumed by male and female *Carollia perspicillata* at the Macaregua cave. Table 1 shows the morphotypes. The proportion is the number of times an item is present in the total samples per bat species. In this case, females and males are taken as two different species. (For abbreviations of morphotypes, see table 1).

Fig. 2. Oportunidad relativa de los elementos consumidos por los machos y las hembras de Carollia perspicillata en la cueva de Macaregua. En la tabla 1 se muestran los morfotipos. La proporción es el número de veces que un elemento está presente en todas las muestras por especie de murciélago. En este caso, las hembras y los machos se consideran como si fueran dos especies diferentes. (Para las abreviaturas de los morfotipos, véase tabla 1).

Table 2. Structure and composition indices calculated for the ensemble of plants consumed by male and female *Carollia perspicillata* at the Macaregua cave.

Tabla 2. Índices de estructura y composición calculados para el conjunto de plantas consumidas por los machos y las hembras de Carollia perspicillata en la cueva de Macaregua.

Indices	Sex	Sampling months						Total
		Jun	Aug	Oct	Dec	Feb	Apr	
Equitability (J')	Male	0.00	0.89	0.95	0.68	0.84	0.57	0.78
	Female	0.97	1.00	0.92	0.69	0.86	0.55	0.81
	<i>p</i>	0.02	0.22	0.37	0.84	0.78	0.82	0.2
Dominance (λ)	Male	1.00	0.21	0.23	0.52	0.24	0.52	0.15
	Female	0.22	0.25	0.39	0.47	0.23	0.62	0.14
	<i>p</i>	0.02	0.66	0.11	0.97	0.92	0.28	0.4
Diversity (D)	Male	0.00	0.79	0.77	0.48	0.77	0.48	0.85
	Female	0.78	0.75	0.61	0.53	0.77	0.38	0.86
	<i>P</i>	0.02	0.62	0.05	0.97	0.92	0.28	0.4
Richness (α)	Male	0.80	8.86	2.63	2.47	3.09	2.03	6.48
	Female	14.12	0.00	2.39	1.55	3.01	1.59	6.1
	<i>P</i>	0.02	0.03	1.00	0.3	0.99	0.72	0.99
Breadth (B)	Male	1.00	2.33	4.46	5.78	2.5	4.46	7.58
	Female	4.17	2.34	3.2	2.63	2.52	5.14	8.19
Overlap (C _H)	M and F	0.16	0.91	0.89	0.91	0.46	0.95	0.92

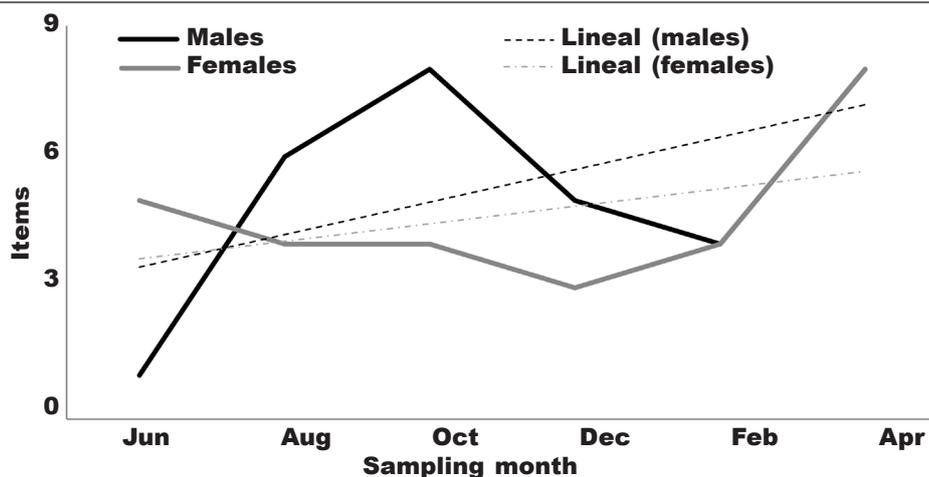


Fig. 3. Temporal series of the items consumed by male and female *Carollia perspicillata* in each sampling month at the Macaregua cave. The series shows important peaks of consumption of items in October and April for males, and a peak in April for females.

Fig. 3. Serie cronológica de los elementos consumidos por los machos y las hembras de *Carollia perspicillata* en cada mes del muestreo en la cueva de Macaregua. En la serie se muestran picos importantes de consumo de elementos en octubre y abril para los machos y un pico en abril para las hembras.

males and females showed a high degree of similarity for much of the year (C_H : Aug = 0.91, Oct = 0.89, Dec = 0.91, Apr = 0.95), with the exception of June (wet season; C_H = 0.16) and February (dry season; C_H = 0.46), when they exhibited a differential intake of resources (fig. 3).

In general, the plant communities that constitute the diets of male and female Seba's short-tailed fruit bat were highly rich and diverse because there was no clear dominance among the most frequently consumed species and their distributions were highly equitable. Even so, the diet of the males was richer, with a slightly more pronounced dominance of some species, contrasting with the diet of females that was more equitable and more diverse. This indicates that the males consume more items, but that the diet of the females is more varied.

This variation may be a response to high energy demands by females during reproductive stages, especially during pregnancy and lactation (Angell et al., 2013; Pfeiffer and Mayer, 2013). Unlike males, females must invest more time foraging to obtain food with a different nutritional composition to satisfy energy demands and pre- and post-natal growth (Angell et al., 2013). For this reason, variation can be related to the nutritional quality of plants (Barclay and Jacobs, 2011).

Females exhibited a high consumption of fruits of *Ficus* during August and October, when lactation occurs. The fruits of *Ficus* contain low levels of nitrogen, which is an essential component during lactation (Herbst, 1986; Shanahan et al., 2001). However, females can meet their nitrogen demands by consuming fruits of *Acacia* (Hackett et al., 2013).

Fruits of *Vismia* and *Myrcia* also contain some calcium content (Charles-Dominique, 1991; López and Vaughan, 2007), so calcium-rich *Ficus* fruits can be supplementary (Shanahan et al., 2001; Angell et al., 2013). Barclay and Jacobs (2011) reported that calcium is a limiting resource for pregnant bats because their diets are relatively low in calcium. Bat may thus supplement their diet with *Ficus* fruits due to their high calcium content (Shanahan et al., 2001). This is consistent with other studies that have evaluated the nutritional content of the fruits of *Ficus* because of their high frequency in the diet of some frugivorous bats (Herbst, 1986; Charles-Dominique, 1991; Korine et al., 2000; Angell et al., 2013; Saldaña-Vásquez et al., 2013).

Ficus fruits may be key resources for replenishing energy requirements of females, which may explain their high consumption during reproductive season. Males have a high richness in consumed items so are not as limited as females because their energetic costs are less than those of pregnant and lactating females (Cryan and Wolf, 2003; Encarnação and Dietz, 2006; Almenar et al., 2011). In other geographical regions, males have richer diets than females (Cryan and Wolf, 2003; Angell et al., 2013). However, males of *C. perspicillata* at the Macaregua cave appeared to have additional energetic demands due to the harem maintenance (McCracken and Wilkinson, 2000; Ortega et al., 2008). If energetic costs increase by maintaining harems, males may need to increase consumption of items and adapt their diet to meet their nutritional demands. In addition, males showed increased consumption of items between August and October, which coincided with reproductive inactivity (inguinal testicles),

and again between February and April when males were reproductively active (scrotal testicles).

In general, there was a temporary variation in the diet components between males and females, taking into account the differences that have been reported in terms of energy cost related to reproductive times and resources availability. Unlike what was predicted, there was an increase in the consumption of food items among males during reproductive times, and higher dietary differences with respect to females, possibly due to the fact that they are social males and harem defenders. On the other hand, females were expected to exhibit higher consumption rates of food items during breastfeeding and during periods of higher availability. This means that the consumption that is being presented in the cave differs in time and space due to the additional variations in foraging strategies and social behavior.

Knowing the variations that occur in the diet of males and females allows us to more specifically address the differences in the foraging strategies applied regarding movement patterns, differential habitat use, nutritional requirements and energy demands. Diet knowledge is essential to understand all the processes that organisms must carry out for their survival and maintenance. This information is extremely important in order to develop conservation plans for threatened species and ecosystems based on the potential in the resources availability and how organisms adapt and respond to environmental disturbances.

Conclusion

The diet of *Carollia perspicillata* was composed of 26 morphotypes, the most representative items being species of the genus *Ficus*, *Vismia*, *Acacia* and *Myrcia*. This is the first record of *Myrcia popayanensis* in the diet of *Carollia perspicillata*. The bats' diet was rich and diverse throughout the year, suggesting that *Carollia perspicillata* is a generalist species. Males exhibited high consumption of *Ficus gigantocyce*, while females consumed more *Vismia glaziovii* fruits. The consumption of resources differed between sexes, as reflected in both foraging strategies and reproductive times of the year.

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