

## Consistency in fruit preferences across the geographical range of the frugivorous bats *Artibeus*, *Carollia* and *Sturnira* (Chiroptera)

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**ABSTRACT.** The frugivorous phyllostomid bat genera *Artibeus*, *Carollia* and *Sturnira* are important seed dispersers in the Neotropics, and exhibit supposed preferences for fruits of the genus *Ficus*, *Piper* and *Solanum*, respectively. We performed a quantified literature review to test the hypothesis that interactions with plants are consistent throughout the bats' geographic ranges. Through an extensive literature review we obtained a total of 4,448 records of fruit consumption from 180 publications. To test which fruits were most frequently consumed across the Neotropical region and in each of its component countries these data were organized by bat species and country. In general, considering the 176 botanical genera eaten by these bats, the results showed a high consumption frequency of *Ficus* (24.0%) by *Artibeus*, *Piper* (38.7%) by *Carollia* and *Solanum* (31.0%) by *Sturnira*. Additionally, our findings support the hypothesis of diet consistency throughout the geographic range of these genera. We suggest that this consistency is related to the wide distribution of the study groups (both bats and plants), the phenology of the zoochoric species consumed, the spatial fidelity of bats and the foraging patterns of the different bat species.

**KEYWORDS.** Diet, frugivory, fruit phenology, geographic distribution, Phyllostomidae.

**RESUMO.** Consistência na preferência de frutos na extensão geográfica de morcegos frugívoros *Artibeus*, *Carollia* and *Sturnira* (Chiroptera). Os filostomídeos frugívoros *Artibeus*, *Carollia* e *Sturnira* são importantes dispersores de sementes na região Neotropical, se destacando por possuírem uma suposta preferência por frutos dos gêneros *Ficus*, *Piper* e *Solanum*, respectivamente. Nós realizamos uma metanálise para testar a hipótese de que as interações entre esses morcegos e plantas são consistentes ao longo de toda sua distribuição geográfica. Por meio de uma extensa revisão bibliográfica, foram compilados 4.448 registros de consumo de frutos provenientes de 180 publicações. Estes dados foram organizados por espécie de morcego e país, testando quais gêneros de frutos foram mais frequentes na região neotropical como um todo e em cada um dos seus países componentes. Num panorama geral, os resultados demonstraram alta frequência no consumo de *Ficus* (24,0%) por *Artibeus*, *Piper* (38,7%) por *Carollia* e *Solanum* (31,0%) por *Sturnira*, considerando 176 gêneros botânicos citados. O estudo corrobora, assim, a hipótese da consistência da dieta desses morcegos ao longo de toda a sua distribuição geográfica, sendo esta relacionada à ampla distribuição dos grupos (morcegos e plantas) envolvidos, à fenologia das espécies zoocóricas consumidas e à fidelidade espacial dos morcegos, esta, por sua vez, moldada pela capacidade de voo das diferentes espécies.

**PALAVRAS-CHAVE.** Dieta, distribuição geográfica, fenologia, frugivoria, Phyllostomidae.

The family Phyllostomidae comprises 160 species that are widely distributed in the Neotropics, with 34 genera and approximately 120 species recorded as frugivorous and/or nectivorous (SIMMONS, 2005; GARDNER, 2008). Members of this family are noted for their ecological functions, acting as controllers of insect populations, predators of small vertebrates and especially pollinators and seed dispersers (e.g. FLEMING, 1988).

Since the 1930s frugivorous phyllostomids have been recognized as one of the most efficient mammalian seed dispersers in tropical forests (RIDLEY, 1930). These animals feed on ripe fruit and do not generally destroy the seeds, passing them intact through the digestive system, defecating

in flight (CHARLES-DOMINIQUE, 1991; DUMONT, 2003), which results in a widely spread seed dispersal.

*Artibeus* Leach, 1821, *Carollia* Gray, 1838 and *Sturnira* Gray, 1842, are among the most abundant and diverse bat genera in the Americas (KALKO & HANDLEY, 2001; GARDNER, 2008). They have great ecological importance due to their dispersal of pioneer plants (FLEMING, 1988; HENRY & JOUARD, 2007) and according to several authors (e.g. FLEMING, 1988; KALKO *et al.*, 1996; WENDELN *et al.*, 2000; MIKICH, 2002; MELLO *et al.*, 2008; ANDRADE *et al.*, 2013) predominantly consume fruits of *Ficus* L. (Moraceae), *Piper* L. (Piperaceae) and *Solanum* L. (Solanaceae), respectively.

Along this same line of reasoning, studies by MIKICH

*et al.* (2003) and BIANCONI *et al.* (2007) addressed the use of smell in finding food, and showed positive results in the attraction of the genera *Carollia* and *Artibeus* with the provision of essential oils extracted from *Piper* and *Ficus* fruits. The results proved so effective that it was possible to propose such essential oils as a tool for the recovery of degraded areas, due to the associated increase in seed rain in these locations. However, monitoring the recruitment of seedlings is needed to evaluate the efficiency of the method (see REID & HOLL, 2013).

The preference of *Artibeus*, *Carollia* and *Sturnira* for *Ficus*, *Piper* and *Solanum* fruits, respectively, is commonly cited and a recent study (ANDRADE *et al.*, 2013) has demonstrated these preferences by combining a literature database with field experiments. Nevertheless, how bat-plant relationships behave across the spatial distribution of these three bat genera has not been investigated. It is known, however, that the phyllostomids in question are exclusively Neotropical (GARDNER, 2008) and that the three fruit genera are spread across much of the world, with *Ficus* (800 species) and *Piper* (approximately 1000 species) being pantropical and *Solanum* (approximately 1500 species) distributed in all continents of the globe (JARAMILLO & MANOS, 2001; SHANAHAN *et al.*, 2001; KNAPP *et al.*, 2004). *Ficus* is intraspecifically asynchronous, producing an abundance of ripe fruit in the same individual, which is generally available for only a few weeks (MORRISON, 1978). In contrast, *Piper* and *Solanum* are synchronous and provide lower amounts of fruit per night, but over a longer period (DUMONT, 2003).

The objective of the present study is to fill this gap through a quantified literature review of the interactions between these bat and plant genera throughout the Neotropics. We use these widely distributed genera to test the hypothesis of consistency of diet across the geographic range, which is associated with the broad distribution of the groups (bats and plants), the phenology of the species consumed and also the spatial fidelity of the phyllostomids.

## MATERIAL AND METHODS

The study consisted of a literature review and data compilation of fruit consumption by representatives of the genera *Artibeus*, *Carollia* and *Sturnira* throughout their distributional range. Therefore, we performed a search in Web of Science (<http://apps.webofknowledge.com>) with the following keywords and combinations thereof: “*Artibeus*”, “*Carollia*”, “*Sturnira*”, “Chiroptera”, “bat”, “diet”, “fruit”, “frugivory” and “plant”. We also used information obtained from the DATABASE OF NEOTROPICAL BAT/PLANT INTERACTIONS (2013), a database created in 2001 with information on dispersal and pollination by Neotropical bats.

The collected information was organized in a spreadsheet with the following entries: bat (species and/or genus), fruit consumed (species, genus and/or family), location, country, recording method and source. Each entry of a plant species (or genus/family when species unknown) accounted for one record. Records could be based on direct

observations, analysis of stomach contents and/or analysis of fecal samples.

To identify the fruit genera with a significantly greater number of consumption records for each bat genus a chi-square test was used, with a  $\alpha$  significance probability of  $P < 0.05$ . The same procedure was used to compare the number of records among countries. Prior analyses, all duplicate information, derived from compilations of primary data sources (i.e. review articles, studies referring to data collected and published in other sources), were excluded.

The data were first tabulated as cited in the source and the taxonomy subsequently standardized according to SIMMONS (2005) for bats, and following FORZZA *et al.* (2013) for native Brazilian plant species and THE PLANT LIST (2013) for other plant species included in the spreadsheet.

Maps were made using the political boundaries of the countries of the Neotropical region, with the distribution of the fruit genera consumed (*cf.* JARAMILLO & MANOS, 2001 – *Piper*, KNAPP *et al.*, 2004 – *Solanum*, LOBOVA *et al.*, 2003 – *Cecropia*, SHANAHAN *et al.*, 2001 – *Ficus*), which was then overlaid on that of the bat genera, following GARDNER (2008). The maps show the Wallaceana configuration of the Neotropical region (COX, 2001). The distribution of both fruits and bats was presented at the scale of the whole country, regardless of whether their documented coverage included all or only a portion of that territory. This decision was made due to the lack of detailed information presented in most of the sources consulted. We selected only the most common fruit genera consumed by each bat genera for mapping.

## RESULTS

The literature review resulted in 180 studies and 4,448 records of fruit consumption by the three bat genera. Of these, 3,243 were used in analyzes and 1,205 were excluded as they were duplicate records reported by different sources. Altogether, 176 genera from 62 botanical families were reported. A total of 22 bat species were recorded for *Artibeus* (N=11), *Carollia* (N= 5) and *Sturnira* (N= 6).

All three studied bats were found to consume a wide range of fruit genera and families: *Artibeus* consumed fruit from 51 families, 135 genera and 268 species, *Carollia* from 44 families, 78 genera and 220 species, and *Sturnira* from 32 families, 54 genera and 165 species. Nevertheless, almost 24.0% (n= 376) of all records for *Artibeus* were represented by *Ficus* ( $\chi^2= 292.41$ ,  $P < 0.00001$ ). The same was true for 38.7% (n= 425) of all records for *Carollia*, which belonged to *Piper* ( $\chi^2= 1183.63$ ,  $P < 0.00001$ ) and 31.0% (n=162) of all records for *Sturnira*, which were represented by *Solanum* ( $\chi^2= 247.17$ ,  $P < 0.00001$ ). *Cecropia* Loebl. (Urticaceae) was the second (*Artibeus*) or third (*Carollia* and *Sturnira*) most frequently consumed fruit genus by these bats (Fig. 1).

When the geographic distribution of these four fruit genera was superimposed on that of the three bat general (Fig. 2), considerable overlap was found, although bats do not occupy all Neotropical areas where these fruit are available.

When the data were analyzed by country, *Ficus* was

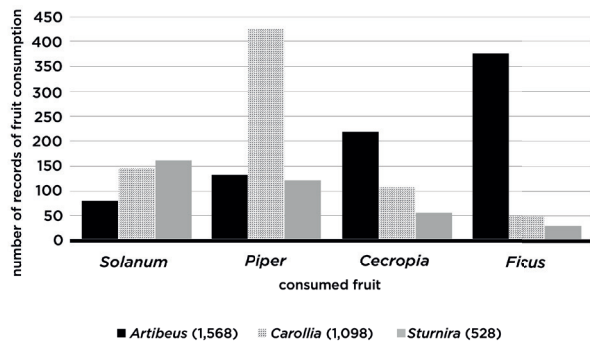


Fig. 1. Number of records for the four fruit genera most frequently consumed by *Artibeus*, *Carollia* and *Sturnira* (total number of records for each bat species) based on literature review.



Fig. 2. Distribution of three bat genera (*Artibeus*, *Carollia* and *Sturnira* – solid gray) and the four most frequent plant genera (*Cecropia*, *Ficus*, *Piper* and *Solanum* – dotted pattern) in their diet in the Neotropical region. Sources: bat distribution follows GARDNER (2008); plant distribution follows JARAMILLO & MANOS (2001) for *Piper*; KNAPP *et al.* (2004) for *Solanum*, LOBOVA *et al.* (2003) for *Cecropia*; SHANAHAN *et al.* (2001) for *Ficus*.

the most consumed fruit species by *Artibeus* in Bolivia, Brazil, Costa Rica, Cuba, Guatemala, Mexico and Panama. However, when compared to the other fruit genera consumed the difference was significant only in countries with a large total number of fruit consumption records. This was true for Brazil ( $n=924$ ), Costa Rica ( $n=638$ ), Panama ( $n=304$ ) and Mexico ( $n=205$ ), but not for French Guiana ( $n=556$ ), where the consumption of fruits from the genus *Cecropia* predominated (Tab. I).

*Piper* was the genus most consumed by *Carollia* in Brazil, Costa Rica, Guatemala, Guyana, Mexico, Panama, Peru, Bolivia and Mexico, with the latter two only being non-significant (Tab. I). *Solanum* was the most consumed fruit genus by *Sturnira* in Argentina, Bolivia, Brazil, French Guiana, Mexico and Peru, whereas *Piper* was more frequently consumed in Costa Rica and Guatemala (Tab. I).

The majority of the most intensively sampled countries showed more records of the preferred plant genera, while those countries with fewer records and publications did not show the pattern observed for the Neotropics (Fig. 1 and Tab. I). Among the latter (all with  $<5$  studies) were the French Antilles, Colombia, El Salvador, Guyana, Jamaica, Puerto Rico, Trinidad and Tobago, Uruguay and Venezuela (Tab. I).

## DISCUSSION

Our findings confirm consistency in the consumption of *Ficus*, *Piper* and *Solanum* fruits throughout the Neotropical range of *Artibeus*, *Carollia* and *Sturnira*, respectively. However, in some countries, this pattern was not evident, probably due to the small number of studies on the diet of bats conducted there, as in most regions with a large sampling effort (with the exception of French Guiana) the pattern was consistent.

The exclusively Neotropical pioneer genus *Cecropia* (LOBOVA *et al.*, 2003) was among the four most commonly consumed genera by the bats, particularly *Artibeus*. This is probably related to its phylogenetic proximity with the family Moraceae (ZHANG *et al.*, 2011), the family that includes *Ficus*. Other genera appeared to be more frequently consumed within certain regions, such as *Vismia* Vand. (Hypericaceae) in Brazil and Panama, *Spondias* L. (Anacardiaceae) in Cuba, El Salvador and Panama, and *Philodendron* Schott (Araceae) in French Guiana.

Some of the species (*Carica papaya* L. and *Syzygium jambos* (L.) Alston, for example) consumed by these bats are exotic and their consumption and subsequent dispersion may impact native flora (MINOR & GARDNER, 2011; VOIGT *et al.*, 2011). Bats seem to respond positively to fruit availability (LOBOVA *et al.*, 2009), reinforcing the need for planning in both urban and rural areas to protect native flora from invasions (BARROS *et al.*, 2006).

Frugivory is a facultative mutualistic interaction as it benefits the consumer (which gains energy and nutrients) and the plant, which has its propagules transported far from the parent plant (BOUCHER *et al.*, 1982). According to some authors, species with broad geographic ranges experience different pressures depending on their location, thereby establishing different interactions and developing geographically distinct specializations (THOMPSON, 2005; MELLO *et al.*, 2011). However, in the case of the bats studied, it is clear that regardless of the climatic, geomorphologic, and floristic differences found throughout the Neotropics and all the plant diversity available (90,000 Neotropical plant species according to GENTRY, 1982), the consumption of some fruit genera remained relatively unchanged. In equatorial Mexico, for example, these bats fed mainly on *Ficus*, *Piper* and *Solanum* (OLEA-WAGNER *et al.*, 2007), the same pattern observed in Argentina, a country with a subtropical climate (SÁNCHEZ *et al.*, 2012).

The consistency found in the diet of the studied phyllostomids throughout their distribution suggests a strong interaction with some food plants. One of the factors

Tab. I. Consumption of fruit from different plant genera by *Artibeus*, *Carollia* and *Sturnira* in different countries of the Neotropical region, based on literature review [N<sub>stu</sub>, number of studies revised for each country; N<sub>rec</sub>, total number of records to that particular genus; \*, indicates that the number of records for a given genus (shown in parentheses) is significantly greater than the others obtained for the same country (P<0.05)].

Country	N <sub>stu</sub>	N <sub>rec</sub>	<i>Artibeus</i>	<i>Carollia</i>	<i>Sturnira</i>
French Antilles	1	3	<i>Manilkara</i> (1) <i>Solanum</i> (1) <i>Terminalia</i> (1)	-	-
Argentina	5	14	-	-	<i>Celtis</i> (2) <i>Piper</i> (4) <i>Solanum</i> (8)*
Bolivia	2	8	<i>Cecropia</i> (1) <i>Brosimum</i> (2) <i>Ficus</i> (2)	<i>Piper</i> (2)	<i>Solanum</i> (1)
Brazil	78	924	<i>Piper</i> (44) <i>Cecropia</i> (74) <i>Ficus</i> (116)*	<i>Vismia</i> (20) <i>Solanum</i> (49) <i>Piper</i> (88)*	<i>Ficus</i> (20) <i>Piper</i> (56) <i>Solanum</i> (76)*
Colombia	1	1	<i>Pilocereus</i> (1)	-	-
Costa Rica	26	638	<i>Cecropia</i> (25) <i>Piper</i> (36) <i>Ficus</i> (51)*	<i>Cecropia</i> (26) <i>Solanum</i> (35) <i>Piper</i> (171)*	<i>Cecropia</i> (8) <i>Solanum</i> (20) <i>Piper</i> (34)*
Cuba	1	33	<i>Spondias</i> (2) <i>Syzygium</i> (2) <i>Ficus</i> (3)	-	-
El Salvador	1	4	<i>Ficus</i> (2) <i>Spondias</i> (2)	-	-
Ecuador	1	6	-	<i>Ficus</i> (1) <i>Cecropia</i> (2) <i>Piper</i> (2)	-
Guatemala	1	61	<i>Cecropia</i> (4) <i>Piper</i> (8) <i>Ficus</i> (9)	<i>Cecropia</i> (3) <i>Solanum</i> (6) <i>Piper</i> (16)*	<i>Cecropia</i> (1) <i>Solanum</i> (4) <i>Piper</i> (6)
Guyana	1	4	-	<i>Solanum</i> (1) <i>Vismia</i> (1)	<i>Solanum</i> (1) <i>Vismia</i> (1)
French Guiana	17	556	<i>Andira</i> (10) <i>Ficus</i> (41) <i>Cecropia</i> (66)*	<i>Cecropia</i> (28) <i>Solanum</i> (37) <i>Piper</i> (57)*	<i>Cecropia</i> (20) <i>Philodendron</i> (21) <i>Solanum</i> (31)*
Jamaica	1	2	<i>Andira</i> (1) <i>Brosimum</i> (1)	-	-
Mexico	17	205	<i>Cecropia</i> (12) <i>Piper</i> (23) <i>Ficus</i> (35)*	<i>Ficus</i> (3) <i>Cecropia</i> (5) <i>Piper</i> (7)	<i>Cecropia</i> (4) <i>Piper</i> (6) <i>Solanum</i> (7)
Panama	13	304	<i>Cecropia</i> (12) <i>Spondias</i> (22) <i>Ficus</i> (51)*	<i>Vismia</i> (7) <i>Solanum</i> (8) <i>Piper</i> (59)*	<i>Cecropia</i> (1)
Peru	5	139	<i>Piper</i> (7) <i>Cecropia</i> (15)*	<i>Solanum</i> (7) <i>Cecropia</i> (17) <i>Piper</i> (21)*	<i>Piper</i> (1) <i>Cecropia</i> (2) <i>Solanum</i> (3)
Porto Rico	3	15	<i>Manilkara</i> (2) <i>Cecropia</i> (2)	-	-
Trinidad and Tobago	3	237	<i>Manilkara</i> (8) <i>Syzygium</i> (12)	<i>Manilkara</i> (4) <i>Syzygium</i> (6)	-
Uruguay	1	2	-	-	<i>Eugenia</i> (1) <i>Passiflora</i> (1)
Venezuela	4	42	<i>Anacardium</i> (4) <i>Syzygium</i> (4)	<i>Vismia</i> (1)	<i>Solanum</i> (1) <i>Saurauia</i> (1) <i>Calycolpus</i> (1)

contributing to this interaction may be the seed dispersal syndrome. In fact, the three most consumed fruit genera all have several species that fall into the bat-dispersal syndrome (*cf.* VAN DER PIJL, 1957) as their attributes are believed to facilitate the location and consumption by bats (LASKA & SCHMIDT, 1986; THIES *et al.*, 1998). Nevertheless, as shown by this study and ANDRADE *et al.* (2013), diet segregation at genus and species level suggests that other factors (chemical, behavioural, etc.) are acting as well.

A rarely discussed but interesting and relevant factor is the spatial fidelity of bats, which is shaped by the

phenology and occurrence of their most consumed fruits (BIANCONI *et al.*, 2006; FARIA & BAUMGARTEN, 2007). For example, *Carollia* spp. exhibit greater constancy in the use of certain habitats compared with *Artibeus*, supposedly due to the spatial and temporal predictability of the *Piper* fruits (see above). Bat morphology may also be related to these foraging patterns, as due to the relatively small size of *Carollia* spp. (14-25 g) their flight capacity is more restricted to closed environments (STOCKWELL, 2001). The opposite occurs with *Artibeus* spp., which does not remain long in the same environment, probably due to the low abundance



and asynchronous behavior of *Ficus* (BIANCONI *et al.*, 2006). This pattern may also be related to their larger size (55-70 g) and greater potential for flight, which enables them to travel great distances in a single night in search of food (STOCKWELL, 2001; DUMONT, 2003).

The significant consumption of Moraceae fruits - mainly figs - by *Artibeus* spp. is widely supported by previous studies (*e.g.* MORRISON, 1978; BONACCORSO, 1979; HANDLEY *et al.*, 1991). *Ficus* is a genus of canopy trees, widely distributed in the Neotropics from Mexico to Paraguay (BANACK *et al.*, 2002), whose representatives are intraspecifically asynchronous, but present a “boom” of syconia maturation within the canopy, which generally contains thousands of fruits (MORRISON, 1978). Such an abundance of resources attracts consumers from various groups, including birds, primates and other mammals (see SHANAHAN *et al.*, 2001 for a review). For this reason, figs are considered keystone species for frugivores (TERBORGH, 1986). Some authors relate the elevated consumption of *Ficus* by bats to: position occupied by these trees in the forest stratum (BONACCORSO, 1979), nutritional composition (WENDELN *et al.*, 2000; DUMONT, 2003), or opportunistic behavior related to the abundance of this resource (HEITHAUS *et al.*, 1975; BONACCORSO, 1979; MELLO & PASSOS, 2008). Although this last factor should contribute to the maintenance of the *Artibeus-Ficus* relationship, selection for fruit of this genus occurs even when their abundance is lower than that of other fruits (MORRISON, 1978; PAROLIN *et al.*, 2015).

Piperaceae and bats of the genus *Carollia* possess a high affinity and the literature abounds with records of *Piper* fruit consumption by these phyllostomids (*e.g.* BONACCORSO, 1979; FLEMING, 1988; THIES & KALKO, 2004; SÁNCHEZ *et al.*, 2012; the present study), with studies even proposing co-evolution between these genera (THIES & KALKO, 2004). The genus *Piper* comprises pioneer plants, common to degraded areas in the Neotropics (LOBOVA *et al.*, 2009). Their green smelly spike-shaped infructescences are typical examples of bat fruits (VAN DER PIJL, 1957). Each individual plant produces few ripe fruits per night (DUMONT, 2003, steady state pattern according to SNOW, 1965), over relatively extended periods (usually two or three months) (FLEMING, 1988). Nevertheless, different *Piper* species exhibit low phenological overlap allowing them to share dispersers and feed them all year round (FLEMING, 1985). All these traits are believed to be important in maintaining *Carollia* spp. as the main consumers and dispersers of *Piper* spp. (THIES & KALKO, 2004).

The genus *Sturnira* also appears to primarily consume steady state fruits. Although several studies show their preferential consumption of *Solanum* (*e.g.* GIANNINI, 1999; MELLO *et al.*, 2008; LOBOVA *et al.*, 2009; but see MIKICH, 2002), there are also several reports of interactions with the fruits of *Piper* (*e.g.* GIANNINI, 1999; SÁNCHEZ *et al.*, 2012). In fact, although we found that the *Solanum* was the genus most frequently consumed by *Sturnira*, the consumption of *Piper* fruits was also significant.

In the most intensively sampled localities the majority of fruit consumption by *Artibeus*, *Carollia* and *Sturnira* was recorded in the genera *Ficus*, *Piper* and *Solanum*. This finding confirms the spatial consistency of these supposed preferences. There are several non-mutually exclusive explanations for this phenomenon, including the broad distribution of the groups, the way these resources are offered and the spatial and temporal patterns in habitat use by bats, all of which favor these mutualistic encounters. Our results also indicate the need for a greater effort to fill knowledge gaps in countries where the diet of these frugivorous bats remains poorly sampled.

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