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Feeding specialization of two species of bats and the fruit quality of *Piper arboreum* in a Central Brazilian gallery forest.

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Abstract: Two widespread bats *Carollia perspicillata* and *Glossophaga soricina* were the main consumers of *Piper arboreum* fruits in a gallery forest near Brasilia. The success of their specialization relates with the bats' hih efficiency to locate ripe fruits, which occur at low densities. The relatively long fruiting season enabled the bats to specialize on the fruit for about one month. Bat activity apparently reduces the availability of *P. arboreum* fruits to other frugivores. The fruit food value is low but the nutritional content and volume consumed are enough to supply the metabolic requirements of *C. perspicillata.*

Key words: Bat, *Carollia*, frugivory, gallery forest, *Glossophaga*, *Piper*.

Plants produce fleshy fruits to attract frugivores which can disperse their seeds adequately (McKey 1975, Gauntier-Hion *et al* 1985). The factors usually considered relevant in this attraction are the morphological characteristics and nutritional content of the fruit, the period of presentation and sometimes seed size and the number of seeds each fruit contains (McKey 1975, Howe 1982).

The fruits (actually infructescences) of *Piper* (Piperaceae) are common constituents of the diets of neotropical bats (Heithaus *et al* 1975, Heithaus and Fleming 1978, Herbst 1986) and some species of *Carollia* and *Glossophaga* (Phyllostomidae) demonstrate distinct preferences for them (Fleming 1981, Palmeirim *et al* 1989, Charles-Dominique 1991). Nonetheless, few authors (Fleming *et al* 1977, Fleming 1981, Marinho-Filho 1991) have studied aspects of this specialization in any detail, and nothing is known about this bat-plant interaction in the gallery forests of Central Brazil.

The present study relates the characteristics of the fruits of a central Brazilian species, *Piper arboreum* Aubl. and the plants' temporal fruiting pattern to fruit selection by bats.

MATERIALS AND METHODS

The study was conducted in a disturbed gallery forest at Fazenda Água Limpa (15°, 57' S and 47°, 56' W; elevation about 1000 m), the experimental station of the University of Brasília which is located 18 km southwest of

the center of Brasília. The gallery forest is an evergreen mesophytic forest found along the valley bottoms and surrounded by cerrado; the savanna vegetation of central Brazil (Eiten 1972, Ratter 1991). The study area also included species typically found in altered areas like the grasses *Melinis minutiflora* and *Panicum ovulliferum* and the fern *Pteridium aquilinum*. The climate is tropical with distinct wet and dry seasons. The dry season occurs between June and September with monthly precipitation averaging 24.3 mm, and the wet season between October and May, with monthly precipitation averaging 212.4 mm (Gribel & Hay 1993). The field data were collected in March and April 1994 and in April and May 1995, the two periods when *P. arboreum* was in fruit in those years.

The density and spatial distribution of the plant was obtained for an area of 5000m^2 divided in 100 quadrats of 50m^2 each. The height, number of stems and number of fruits were recorded for 50 individuals.

We conducted 14 sessions to capture the bats, using two or three mist-nets on each occasion, comprising a total effort of 130 net-hours. The captured bats were identified and, in order to collect samples of their faeces, they were kept separately in cloth bags for approximately one hour. The faecal samples were examined in the laboratory for seeds.

In order to determine the rate of fruit consumption and the fates of fruits, 200 fruits were tagged at random on nine plants at the beginning of the 1994 fruiting season. These fruits were checked every two or three days until the end of the fruiting period. In 1995 we again marked 200 fruits for daily observation. The number of fruits which had ripened each day were counted and the numbers of fruits which the bats had fed on each night were recorded. In addition, twelve ripe fruits were removed from the trees and attached to other plant species at distances of at least 5 m from the nearest individual of *P. arboreum*. This method was used by Fleming *et al* (1977) and Fleming (1981) to test the bats' ability to locate fruits.

Chemical contents of fruits of *P. arboreum* were analyzed to ascertain percentages of water, carbohydrate, lipid and protein. The energy content of the fruit was calculated using the factors of conversion of 3.36 calories being equivalent to 1 g of protein, 8.37 calories to 1 g of lipid and 3.60 calories to 1 g of carbohydrate (Aguiar *et al* 1980).

RESULTS

The adult *P. arboreum* is a multiple-stemmed understory shrub, 2 m to 6 m tall and a crown 1.5 m to 3 m wide. The dispersion of the plants in the study area was clumped ($s^2/\bar{x} = 1.94$; $t = 6.71$; $df = 99$; $p < 0.01$) and the density in the study area was equivalent to 132 plants per hectare. Total fruit crop per plant of *P. arboreum* is significantly correlated to plant height ($r_s = 0.575$; $t = 4.87$; $df = 48$; $p < 0.01$) and to the number of stems per plant ($r_s = 0.396$; $t = 2.98$; $df = 48$; $p < 0.01$). The number of seeds per infructescence is also correlated to infructescence length ($r_s = 0.719$; $t = 4.39$; $df = 18$; $p < 0.01$). Each plant produced an average of 40 fruits per year giving an estimated annual total of 2,640 fruits which weighed 24.8 kg in the study area. Data on fruits (actually infructescences) and plant characteristics are given in Table 1.

A small number of fruits ripened on each plant every night, with a peak in fruit production during the middle of the season (Fig. 1). Observations on 200 marked fruits during the fruiting season of 1995, indicated an average of 6.8 ± 4.8 fruits ripening per night (about 3.4 % of total annual production). The duration of the fruiting season and the rate of fruit consumption were similar in the two years (Fig. 2), though there was a delay of 40 days in the start of ripening in 1995 (starting on 16 April) when compared to 1994 (starting on 7 March). This shift in the fruiting period between the two years is thought to be related a delay in the start of the spring rains. Normally, around Brasília, the annual rains begin in late September (as they did in 1993), but in 1994 they began in late November.

TABLE 1

Characteristics of Piper arboreum *fruits and plants in a Central Brazilian gallery forest.*

	Average (SD)	Range	N
Infructescences			
Length (mm)	169.1 (35.2)	75.0 - 223.0	35
Width (mm)	8.6 (0.7)	7.0 - 11.0	35
Fresh weight (g)	9.4 (2.3)	3.0 - 14.0	20
Number of seeds	472.9(117.2)	246 - 681	20
Plants *			
Height (m)	3.8 (1.0)	2.2 - 5.5	50
Number of stems	8.0 (5.5)	1 - 24	50
Number of fruits	42.0 (39.7)	0 - 213	50

* We considered only potentially reproductive plants, that is, taller than 2.2 m, which is the height of the shortest individual which bore fruits during this study.

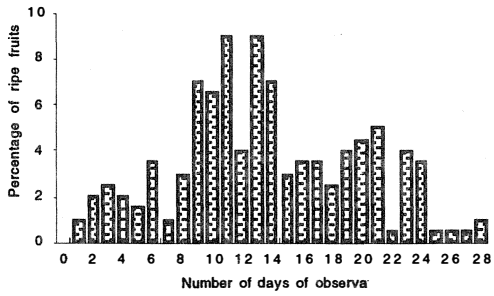

Fig. 1: Daily availability of ripe *Piper arboreum* fruits. Data are expressed in percentages of 200 marked fruits which were checked daily during the entire fruiting season. Counting started 16 April 1995.

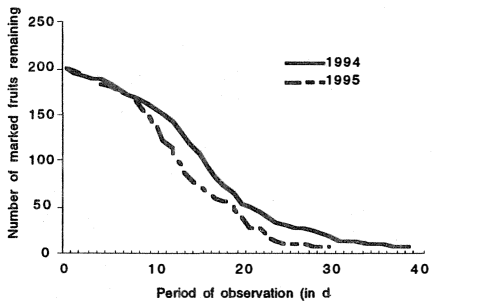

Fig 2. The removal of fruits of *Piper arboreum* from plants in a gallery forest in Central Brazil, in each fruiting season (1994 and 1995).

The fruit of *P. arboreum* has 77.6 % water (range 74.2 % to 80.6 %; n = 10). The chemical analysis of the dried pulp indicated a high percentage of carbohydrates (34.2 %) and low percentages of proteins (5.45 %) and lipids (1.63 %) in the fruits. The energy estimate indicated that 100 g of *P. arboreum* dry pulp contained 155 kcal which gave 38 440 kcal available in the study area.

A total of 115 bats of seven species was captured; all members of the family Phyllostomidae (Table 2). The capture success was 0.9 bat/ net-hour. The three species captured most often were *Artibeus lituratus*, *Carollia perspicillata* and *Glossophaga soricina* which comprised 77 % of the total captures. In addition to the five frugivorous species, one individual each of *Desmodus rotundus* and *Anoura caudifer* was captured.

The faeces of five of the species contained seeds which ranged from 10 % to 76 % of the total sample of each species (Table 2). The faeces of four of the species contained seeds of *P. arboreum* which ranged from 17% to 60 % of the samples. Seeds of *P. arboreum* were encountered most often in the faecal samples of *C. perspicillata* (60 % of the samples), followed by *G. soricina* (48 % of the samples). The seeds were also found in the faeces of *Sturnira lilium* and *A. lituratus*, but in fewer of the samples. Seeds of *P. arboreum* were not found in samples of one of the frugivorous species, *Platyrrhinus lineatus*.

Of the 200 fruits tagged in 1995 four did not ripen during the observation period. Bats encountered the remaining 196 at the same night they ripened. In addition, all the twelve ripe fruits which were attached to other plant species were located and eaten by bats; eleven on the first night that they were offered and the other on the second night.

TABLE 2

Numbers of captures, faecal samples and presence of Piper arboreum *seeds of the principal fruit-bat species captured at the Fazenda Água Limpa, Brasília.*

Bat species	Number of captures	Number of fecal samples taken	Number (%) of samples with seeds	Number (%) of samples with seeds of *P. arboreum*
Artibeus lituratus	36	18	4 (22)	3 (17)
Carollia perspicillata	26	25	19 (76)	15 (60)
Glossophaga soricina	26	21	10 (48)	10 (48)
Platyrrhinus lineatus	16	10	1 (10)	-
Sturnira lilium	9	8	4 (50)	2 (25)

TABLE 3

Daily energy and nitrogen requirements for a bat (Carollia perspicillata) *weighing 20 g. The aproximate number of* Piper arboreum *fruits and the amount dry pulp (g) needed to meet these requirements are estimated.*

Reproductive state of bat	Nitrogen requirement *	Weight (and number) of dry pulp for nitrogen requirement **	Energy requirement	Weight (and number) of dry pulp for energy requirement **
Non-reproductive	14 mg	2.2 g (1)	9.2 Kcal	5.9 g (3)
Lactating	60 mg	9.5 g (5)	19.2 Kcal	12.4 g (6)

* Values calculated by Herbst (1986).
** For our calculations for *Piper arboreum* we used the means of *Chlorophora tinctoria* and *Muntingia calabura* fruit digestibilities by bats, after Herbst (1986).

DISCUSSION

Apparently, four major factors have led to the specialized inter-relationship between *Piper arboreum* and the two bat species. These are: (1) the low number of fruits which ripen each night, (2) the rapid ripening of the fruits, (3) the high efficiency of these bats in locating ripe fruits, and (4) the apparent difficulty of other frugivores in detecting the ripe fruits.

Like other members of the genus, *P. arboreum* is chiropterochorous (van der Pijl 1982). The ripe fruit remains green but, when mature, it is soft and smells of sugar cane. It is difficult for a human observer to distinguish between the ripe and the unripe fruit visually and this may be so for visually oriented frugivores. This suggests that the plants' attraction may be more olfactory than visual which would be expected when the frugivores are nocturnal.

Piper arboreum produced a nutritionally poor fruit, with many small seeds and a few species of bats consumed most of the crop. This is contrary to the suggestion made by McKey (1975) and reinforced through the observations of Howe (1982) that soft, nutritionally poor fruits are normally eaten by a large number of opportunistic frugivores whereas nutritious fruits (with a high content of lipids) are consumed by a restricted number of specialized frugivores. Furthermore, other *Piper* species, whose fruits are consumed elsewhere by the same two species of bats which we studied (*Carollia perspicillata* and *Glossophaga soricina*), also have fruits which are similar to those of *P. arboreum* in being nutritionally poor (Fleming *et al* 1977, Fleming, 1981, Palmeirim *et al* 1989, Charles-Dominique 1991, Marinho-Filho 1991). In addition, *Piper amalago* is similar to *P. arboreum* in producing few ripe fruits each night (Fleming 1981). This pattern of ripening increases the length of the fruiting season and, coupled with the quick ripening of the fruits, it reduces the possibility that the fruits will be eaten by opportunistic frugivores.

This fruiting strategy facilitates the discovery of the ripe fruits by specialized frugivores because those species are more efficient searchers and they return regularly to the plant to look for newly ripened fruits. Four of the species captured are primarily frugivorous, whereas *G. soricina* is largely nectarivorous, but takes some fruits and insects (Gardner 1977).

Apparently, C. *perspicillata* and G. *soricina* have developed sensitive search images for *Piper* fruits (Fleming *et al* 1977). The speed with which the bats discovered the fruits of *P. arboreum* which were attached to other plants adds support to this suggestion.

Data presented in the present study lend support to Fleming's suggestion that bats such as *Carollia* and *Glossophaga* select *Piper* fruits only partly for their nutritional content and more for their spatio-temporal predictability during a prolonged period (Fleming 1981). However, in spite of the relatively poor nutritional quality, there are some positive aspects for the bats which specialize on *P. arboreum* fruits. Generally, small, volant mammals have high metabolic rates and relatively high energetic demands (Fleming 1979) so it may be advantageous for the bats to consume a juicy, sugary fruit as an energy source which is quickly and easily assimilated, specially by a primarily nectarivorous species like *G. soricina.* Secondly, the high water content of the fruits may be used by the bats to compensate for losses in the maintenance of body temperature.

The nitrogen concentration in the fruit is also an important aspect because diet affects the elemental composition of the milk of bats (Studier *et al* 1995) and because most births generally occur during periods of maximum fruit production (Fleming *et al* 1972, Bonaccorso 1979, Humphrey and Bonaccorso 1979). Concentrations of nitrogen in milk of *Carollia* are nearly identical to the nitrogen levels in *Piper*, and those concentrations are markedly lower than levels in the milk of the insectivorous bat *Tadarida brasiliensis* (Studier *et al* 1995). Herbst (1986) studied the proportion of nitrogen in five fruit species eaten by *C. perspicillata* and suggested that *Piper* fruits had the highest percentage of nitrogen and were the only fruits which contained an adequate source of nitrogen for the maintenance of metabolism even of lactating bats.

The nutritional analysis indicates that the pulp of *P. arboreum* contains a proportion of 5.5 % protein of the total dry weight which is close to the value of 6.0 % found in *P. amalago* fruits which were consumed by C. *perspicillata* in central America (Herbst 1986). We used Herbst's estimates to demonstrate that fruit of *P. arboreum* also comprise an adequate nitrogen source for the maintenance of normal metabolism of *C. perspicillata* and also for lactating mothers (Table 3). Although the fruits of *P. arboreum* is considered to be nutritionally poor, they supply the nutritional and energetic requirements of a bat which ingest adequate quantities of these fruits. In this respect, even a lactating mother of *C. perspicillata* would need to consume about six entire fruits of *P. arboreum* per night in order to obtain her nitrogen and energy requirements.

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RESUMEN

Dos especies de murciélagos de amplia distribución (*Carollia perspicillata* y *Glossophaga soricina*) fueron los principales frugívoros consumidores de los frutos de la especie local, *Piper arboreum* (Piperaceae), en un bosque de galeria próximo a Brasilia. El éxito de esta especialización se debe en parte a la alta eficiencia de estos murciélagos en localizar los pocos frutos maduros disponibles en la noche. El periodo de fructificación relativamente grande favorece la especializacíon de los murciélagos en estos frutos por cerca de un mes. La eficiencia con la cual localizan y consumen los frutos debe reducir la disponibilidad de estos a otros frugívoros. A pesar de no ser considerado rico, el volumen consumido y el contenido nutricional del fruto de *P. arboreum* presentó características que lo califican como un recurso bastante eficaz en suprir las necesidades nutricionales y energéticas de *C. perspicillata.*

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