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SHORT COMMUNICATION

Feeding behaviour of bats and the dispersal of *Piper arboreum* seeds in Brazil

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Phyllostomidae bats are the most important consumers of *Piper* fruits in the Neotropics (Heithaus *et al.* 1975) and, in particular, *Carollia perspicillata* and *Glossophaga soricina* are the species which demonstrate distinct preferences for these fruits (Charles-Dominique 1991, Fleming 1981, Fleming *et al.* 1977, Marinho-Filho 1991, Palmeirim *et al.* 1989). This is also true of *Piper arboreum* Aubl. (Piperaceae) in the gallery forests of Central Brazil (Bizerril & Raw 1997).

Several studies have been published on this bat-fruit interaction but few indicate the quantities of *Piper* fruits consumed by the bats or the fates of the fruits and seeds (Fleming 1981, Fleming & Heithaus 1981). The seed shadow can be strongly influenced by the foraging and defecatory behaviour of the dispersers, such as the time spent near the fruiting plant, distances moved, time that seeds are retained (Fleming & Heithaus 1981) and seed composition in animal droppings (Loiselle 1990). In this study, we present data on the feeding behaviour of the bats which consume *Piper arboreum* fruits, estimate the number of fruits consumed by each frugivore and make some inferences about the quality of seed dispersal.

The study was conducted in a gallery forest at Fazenda Água Limpa—FAL (15°57'S; 47°56'W) 18 km southwest of the centre of Brasília. The climate is tropical with a distinct wet season from October to April (mean monthly precipitation 210 mm) and a dry season (24 mm), from May to September (Gribel & Hay 1993) (See Ratter (1991) for details of the vegetation of FAL, and Eiten (1984) for a general description of cerrado vegetation).

Piper arboreum is a multiple-stemmed understorey plant in gallery forests of Central Brazil. Fruits weigh 9.4 g, and are 169 mm long and 9 mm wide. They contain a mean of 472 small seeds per fruit and each plant produces an average of 40 fruits y^{-1} , and bear a small number of ripe fruits each night in the late wet season (for more details in plant and fruit characteristics see Bizerril & Raw 1997).

We spent 20 h observing the feeding behaviour of the bats while they consumed the *P. arboreum* fruits, in order to identify their foraging techniques. In 9 h we observed the fruits to quantify the number of bat visits to each fruit. Bat identification was confirmed by capture in mist nets. The frugivores feeding modes on *P. arboreum* fruits were investigated by labelling 200 randomly-selected fruits on nine plants at the beginning of the 1994 fruiting season. We sketched the marked stems indicating the exact position of each fruit. These fruits were checked every 2 or 3 d until the end of the fruiting period. In 1995 we again marked 200 fruits and observed them daily.

The consumption of fruits which dropped under the parent-trees was investigated by depositing 25 fruits on the forest floor at previously marked places; each fruit under a fruiting *P. arboreum* plant. These fruits were checked daily for signs of animal activity, such as ants and small mammals, and also for possible fungal attack or rotting. In addition, we placed live-mammal (Young) traps baited with *P. arboreum* ripe fruits. Twenty five traps were set at the same places as in the first experiment in 1994 and 30 traps along two line-transects of 150 m each in 1995. These lines were parallel and 15 m apart with the traps set at 10 m intervals. The total effort in the 2 y was 220 trap-nights.

Germination experiments were conducted using two groups of *P. arboreum* seeds; one group taken from fresh, ripe fruits ($n = 136$), and the second removed from the faeces of the captured bats *C. perspicillata*, *G. soricina* and *Artibeus lituratus* ($n = 133$). The seeds were placed on moist filter paper in petri-dishes under natural light and at room temperature. The numbers of seeds which germinated were counted daily during 50 d.

Of the 200 fruits marked each year a small number aborted: 8 (4%) in 1994 and 4 (2%) in 1995. During a period of 34 d in 1994 and 28 d in 1995 the 388 (192 + 196) fruits ripened and the frugivores' feeding modes were assigned to three categories (Table 1). Most of the fruits (75%) were consumed on the

Table 1. Distribution of *Piper arboreum* marked fruits in three frugivore feeding modes categories (and principal frugivores) during two fruiting seasons in a gallery forest in central Brazil.

Feeding mode (principal consumer)	Fruiting seasons		
	1994 (%)	1995 (%)	Total (%)
Number eaten on plant by bats (<i>Carollia perspicillata</i> and <i>Glossophaga soricina</i>)	150 (78)	141 (72)	291 (75)
Number removed from plant by bats (<i>Artibeus lituratus</i>)	15 (8)	25 (13)	40 (10)
Number dropped and eaten under the tree (<i>Didelphis albiventris</i>)	27 (14)	30 (15)	57 (15)
Total number of ripe fruits marked	192	196	388

plant and only the core of the rachis remained the next morning. Fruits of the second category (10%) were removed from the plant and consumed elsewhere. The fruits of the third category (15% of the total) were dropped on the ground by bats which knocked them down when attempting to feed on them. A few of the fallen fruits are thought to have been knocked down by wind and rain. The distribution of the marked fruits in the three classes did not differ significantly between the two years ($\chi^2 = 4.27$, $df = 3$, $P > 0.05$).

Carollia perspicillata and *Glossophaga soricina* consumed the *P. arboreum* fruits by biting off parts of them while in flight. They made several visits to each fruit during the night and normally the next morning only the rachis of the infructescence remained attached to the plant. We defined as 'one visit' each flight of a bat to a ripe fruit, when part of the fruit was taken in one or more bites. Each visit to a fruit lasted few seconds, with a mean of $14.2 \pm (SD) 8.4$ visits h^{-1} (range 1–26, in 9 h of observations). *Carollia perspicillata* and *Glossophaga soricina* are believed to have consumed 75% of the labelled fruits (Table 1). The bats' activity was intense during the first hours of the night and then decreased. Up to three individuals were seen to fly together among the branches of the *P. arboreum* bushes, but each bat visited the fruits alone. *Artibeus lituratus* was the only bat which was seen to remove the entire fruit from the plant and some individuals were captured in mist nets carrying infructescences of *P. arboreum*. This bat plucked the fruits from the trees, and carried them to a feeding roost to eat. *Artibeus lituratus* is thought to be the transporter of the 10% of fruits which were taken away.

The foraging strategy of *C. perspicillata* and *G. soricina* towards *P. arboreum* fruits was different from when they fed on other species of *Piper* elsewhere. These bats generally take the infructescence to consume it at a feeding roost (Charles-Dominique 1991, Fleming 1981, Fleming *et al.* 1977). It is likely that this difference in the bats' behaviour lies in the differences of weights of the fruits of the *Piper* species. An adult *C. perspicillata* weighs 17 g while an adult of *G. soricina* weighs 10 g (Eisenberg 1989). In Costa Rica both species fed on the fruits of *Piper amalago* which averaged 1.6 g each (Fleming 1981). In contrast, the fruit of *P. arboreum* averaged 9 g, which represents *c.* 53 and 90% of the body-weights of the two species of bats respectively. The maximum size of fruit which a bat can carry is related to its body size (Heithaus *et al.* 1975). The fruit of *P. arboreum* is probably too heavy to be carried and handled efficiently by the small bats. It must be more efficient energetically for these bats to feed on the fruits at the plant than to carry them off. Other bat species, as *Artibeus jamaicensis*, have also been reported to bite off pieces of large fruits (Morrison 1980).

The foraging strategy employed by the two smaller species of bats under investigation has important consequences for the dispersal of *P. arboreum* seeds. The advantage for the plant is the reduced possibility that the seeds might accumulate beneath a feeding roost where the probability of attack by seed

predators and pathogens would be expected to be increased (Janzen 1970). Fleming (1981) observed that 40% of the seeds of *P. amalago* remained attached to the fruits which fell to the ground beneath the feeding roosts and were covered with fungal growth within 2 d.

The majority of the fruits which fell to the ground were eaten within 5 d and in each case the same pattern of consumption was observed: the entire fruit was consumed and only the stem of the infructescence (rachis) remained. Two species of ground mammals were captured in live-mammal traps; the opossum, *Didelphis albiventris* (six captures) and a rodent, *Proechimys roberti* (one capture). Mature fruits were offered to captive animals of these two species which confirmed their acceptance of these fruits and the pattern of consumption.

The fallen fruits were quickly eaten by nocturnal ground mammals (principally by *D. albiventris*) and it seems doubtful that any seeds would not be eaten in the forest. This opossum is a dietary generalist, feeding on worms, insects, small birds and a wide variety of ripening fruits (Redford & Eisenberg 1992). Nevertheless, preliminary data suggest that *D. albiventris* prefers the fruits of *P. arboreum* to those of other species which occurred in the study area whereas the remainder small mammals prefer the other fruits like *Renealmia alpinia* (Zingiberaceae) (Bizerril & Gastal 1997) and *Sacoglottis guianensis* (Humiriaceae) (M. L. Gastal and M. X. A. Bizerril, unpubl. data). Consumption of the fruits by the opossum prevented attack on the seeds by ants and fungi, but it is not known whether their rate of survival improved.

In the germination experiment, the great majority of the seeds germinated (Table 2). The seeds began to germinate from the 12th day onwards and 90% of them had germinated by the 45th day. There was no significant difference between the percentages which germinated of the seeds taken from mature fruits and those removed from the faeces of the bats ($\chi^2 = 0.075$, $df = 1$, $P > 0.05$) nor was there any difference between the two treatments of the rates of germination (Kolmogorov-Smirnov, $D_{\max} = 0.0107$, $\chi^2 = 0.714$, $df = 2$, $P = 0.70$). The analysis of the seed composition of *C. perspicillata* and *G. soricina* faecal samples indicated that the majority of samples contained one seed species (57%); 37% of samples did not contain seeds and only 6% of samples contained two or three seed species ($n = 46$ faecal samples).

Our data suggest that the bats probably provide a high quality of dispersal of *P. arboreum* seeds (*sensu* McKey 1975). Only two principal frugivores ingested and defaecated 75% of the seeds and, although we do not have information on

Table 2. Germination of *Piper arboreum* seeds from two sources in 50 d of observation.

Source	Total number of seeds	Number germinated (%)	Mean time (d) to germination ($\pm$ SD)
Ripe fruits	136	125 (92)	26.0 $\pm$ 5.6
Bat faecal samples	133	121 (91)	26.9 $\pm$ 7.3

the exact locations where seeds were deposited, several pieces of circumstantial evidence suggest that the seeds were scattered throughout the forest. A bat removes just a few seeds on each visit to a *P. arboreum* fruit, and the animal defaecates quickly (gut retention time is 15 to 20 min; Fleming & Heithaus 1981) and often and in flight (Fleming 1986). Furthermore, due to the foraging strategy of *C. perspicillata* and *G. soricina* at *P. arboreum* fruits, more than one individual can feed at the same fruit, leaving the seeds to different places in the forest. An additional factor is that the bats perform this service during the entire fruiting season of a month. Our laboratory tests revealed no significant differences in the rate of success or the period of germination of seeds of *P. arboreum* obtained from fruits or those from bats' faeces; a result also obtained for *P. amalago* (Fleming & Heithaus 1981). Finally, the seed composition of the bats faeces indicated that the probability of seedling interspecific competition is also reduced.

We estimated that the bat *A. lituratus* and two species of ground mammals consumed approximately a quarter of the ripe fruits although nothing is known about the fates of the seeds which they processed. However, *A. lituratus* may be an important disperser to *P. arboreum* seeds since this bat flies longer distances than the smaller bats, increasing the genetic flux and avoiding biparental inbreeding.

Other arboreal small mammal species and even birds might eat parts of fruits sporadically (M.X.A. Bizerril, *pers. obs.*). These animals are considered to have secondary roles in the dispersal of *P. arboreum* seeds compared to the activities of three of the bat species and the opossum.

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