

FIG-SEED PREDATION BY 2 SPECIES OF *CHIRODERMA*: DISCOVERY OF A NEW FEEDING STRATEGY IN BATS

MARCELO R. NOGUEIRA* AND ADRIANO L. PERACCHI

*Departamento de Biologia Animal, Universidade Federal Rural do Rio de Janeiro,
CEP 23851-970, Seropédica, Rio de Janeiro, Brazil*

The feeding ecology of most neotropical bat species is still poorly known, indicating that many complex ecological relationships may be obscured. During a study of bats and their potential role as seed dispersers at the Botanical Garden of Rio de Janeiro, southeastern Brazil, we obtained data on 2 species, *Chiroderma doriae* and *C. villosum*, that act as seed predators rather than as seed dispersers. Fecal sample analyses and captive-feeding experiments confirmed this previously undocumented feeding strategy in bats. Both species use a specialized strategy of fig-seed predation, ingesting the rich nutrient content of seeds and discarding most of the coat fragments as compact oral pellets. Evidence from the more abundant *C. doriae* showed that seeds were consumed in both drier and wetter seasons and by individuals of both sexes, all age classes, and all reproductive stages. Use of seeds, in addition to fruit pulp, probably represents an improvement in the acquisition of nutrients available in figs, showing that the degree of feeding specialization of *Chiroderma* on this resource may be higher than previous data have shown.

Key words: *Chiroderma doriae*, *Chiroderma villosum*, *Ficus*, predation, feeding behavior, southeastern Brazil

The diversity of feeding habits observed within Chiroptera surpasses that found in any other group of living mammals. Depending on the species, bat diets can include insects and other arthropods, vertebrates, blood, and a variety of plant material (Kunz and Pierson 1994). For plant material, the extensive list of known items includes ripe and unripe fruits (Fleming 1988; Gardner 1977; Mickleburgh et al. 1992; Nelson et al. 2000), a variety of floral resources, such as nectar, pollen, buds, petals, and bracts (Gardner 1977; Mickleburgh et al. 1992), young and mature leaves (Kunz and Diaz 1995; Nelson et al. 2000), bark, seed pods, cones, and twigs (Mickleburgh et al. 1992). A single record of seed predation is also available (Bonaccorso 1979), but specialized granivory has not been recorded in bats, which are often known for

their mutualistic relationships with food plants (Fleming 1988; Fleming and Sosa 1994).

The genus *Chiroderma* (Phyllostomidae, Stenodermatinae) ranges from Mexico to southern Brazil and Paraguay (Gregorin 1998; Koopman 1993; López-González et al. 1998) and includes 5 species (*C. doriae*, *C. improvisum*, *C. salvini*, *C. trinitatum*, *C. villosum*) whose general habits remain poorly known (Eisenberg and Redford 1999; Emmons 1990). *C. doriae* and *C. villosum* apparently specialize on wild figs (*Ficus*). Taddei (1973, 1980) reported that several attempts to maintain these species in captivity by providing them fruits regularly consumed by other frugivorous bats were unsuccessful. Positive results, with specimens being kept for a 30-day period, were only obtained when whole, native figs were offered to them. Figs constitute a key-

* Correspondent: mrnogueira@rionet.com.br

stone resource for many groups of frugivorous vertebrates (Janzen 1979; Terborgh 1986) that, generally, disperse seeds rather than prey upon them or excrete them in the parent tree (Janzen 1979). Several studies conducted in the Neotropics and Old World have demonstrated that bats fit into this general pattern (Entwistle and Corp 1997; Figueiredo and Perin 1995; Funakoshi et al. 1993; Kalko et al. 1996), but no consistent evidence about species of *Chiroderma* is available.

In October 1995 we began to study bats and their potential role as seed dispersers at the Botanical Garden of Rio de Janeiro. Through fecal sample analysis and seed germination experiments, we quickly identified the participation of several species in the dispersal processes of many plants. By February 1997, however, we had caught 25 specimens of *Chiroderma*, and all 6 fecal samples obtained from them were composed only of fruit pulp. At that time we were surprised because in the same netting sessions in which these fecal samples were obtained other frugivorous bats had defecated many seeds of *Ficus*, evincing fig availability. On 12 June 1997, we captured 14 specimens of *C. doriae* and 1 *C. villosum* on a single night. During this occasion we found a partially eaten green fig close to an entangled *C. doriae*, and we noticed that many apparently intact fig seeds were spread inside the bat's mouth. From this result, we proposed that species of *Chiroderma* were fig-seed dispersers. However, our preliminary analysis showed that fecal samples contained only reddish-brown fruit pulp. Intact seeds associated with this pulp material appeared in reduced numbers and in only 3 of the 13 fecal samples analyzed. A close examination of what we considered pulp fruit revealed that the unsuspected potential of *C. doriae* and *C. villosum* as fig-seed predators was notable because fragments of seed coat were scattered within the fruit pulp of all 13 fecal samples.

To better evaluate this evidence of seed predation in bats, we netted bats under fig

trees potentially visited by species of *Chiroderma* at the Botanical Garden of Rio de Janeiro and subjected some of the captured specimens to short-duration captive-feeding experiments, the results of which are presented in this article.

MATERIALS AND METHODS

The Botanical Garden of Rio de Janeiro (22°58'14"S, 43°13'18"W) encompasses a 137-ha area located on the southern slope of the Maciço da Tijuca mountain chain, in the state of Rio de Janeiro, southeastern Brazil. In addition to a highly diversified arboretum (about 8,000 native and exotic species of trees in 54 ha), the Botanical Garden includes 83 ha of a secondary Atlantic forest (Brasil 1983), which extends into the Tijuca National Park (3,300 ha), the largest urban natural park of the world (Bandeira 1993). A floristic survey of the hills of the Botanical Garden can be found in Silva et al. (1994). Altitudes inside the limits of the Botanical Garden range from 2 m at the arboretum to 400 m close to Tijuca National Park (Brasil 1983). The climate is tropical humid with total annual rainfall exceeding 1,550 mm (Souto-Maior 1954). Although there is not a defined dry season in the Maciço da Tijuca region (Souto-Maior 1954), precipitation is conspicuously reduced during winter (June–August), referred to as a “drier season” (Setzer 1954; Souto-Maior 1954).

From March 1999 to March 2001 we performed 10 netting sessions under individual *Ficus* trees bearing ripe fruit. Nine sessions were associated with *F. tomentella* trees and 1 with *F. cyclophylla*. The former species produces green figs that had been used by *Chiroderma* when we first noticed their potential as seed predators in 1997. Data from the 1997 netting session and from 4 others (4 June 1998, 18 July 1998, 20 February 1999, 20 December 1999) that subsequently resulted in *Chiroderma* captures were also included in our analyses. Three of these netting sessions, including the 1 in 1997 that resulted in a large number of captures, were performed in an alley at the border of the forest. The remaining 2 were conducted in the arboretum under the crown of flowering *Caryocar*. Nets were set at ground level and opened just before sunset. Time to net closure, however, depended on capture rates and varied from 1 h after sunset until sunrise. In our last year of field-

work we used the Audubon Bird Call (R. W. Eddy, Newington, Connecticut) to attract bats to the nets. This device produces high-pitched (but not ultrasonic) squeaks resembling stenoderma-tine distress calls and has been shown to be useful in attracting both stenodermatines and phyllostomines (Simmons and Voss 1998).

From each bat we recorded the following data: species, length of forearm (in mm), body mass (in g), sex, age, and reproductive status. Except for bats captured in June 1997, which were recognized only as young (opened phalangeal epiphyses detected through transillumination of the wings) or adults, all *Chiroderma* specimens were classified using an additional age category (subadult), as proposed by Fleming (1988) and Handley (1988). Criteria used in this more refined classification are as follows: juveniles—individuals with phalangeal epiphyses unclosed and usually a grayish pelage; subadults—epiphyses recently closed, pelage still grayish, and apparent sexual immaturity (indicated by presence of small testes in males and tiny nipples in females); and adults—closed epiphyses (knobby and truncated), brownish pelage, and signs of present or past sexual activity. Potential biases associated with this change in our protocol, however, were not a concern because quantitative comparisons among age groups were not made. Pregnancy and lactation were determined by palpation, and adult females showing no evidence of reproductive activity were classified as apparently inactive because early stages of pregnancy are difficult to detect by palpation.

To obtain fecal samples, bats were held in individually labeled cloth bags for at least 1 h after capture. In the laboratory, these fecal samples were kept in the same bags and dried in natural conditions for later analysis. Laboratory feeding experiments were conducted in September 1999 (*C. villosum*, 2 males), November 1999 (*C. doriae*, 1 female), and April 2000 (*C. doriae*, 2 males), always on the night after the bats were captured. Feeding experiments were performed in an adapted terrarium (40 by 19 by 24 cm) and only included adult bats. Ripe figs (*F. tomentella*) were offered to each individual, and feeding behavior was observed. The following times were recorded: fig ingestion time (min), time until 1st defecation (min), pulp mastication time (s), and seed mastication time (s). Only observations from entirely eaten figs were included in

the analysis of fig ingestion time. There was a difference in the mean mass of figs offered to *C. doriae* and *C. villosum*, due to variation in the size of figs available during the experiments. In addition to recording presence and quantity of apparently undamaged seeds, we examined pulp material to characterize its color and note the presence or absence of seed-coat fragments. Both fecal samples and oral pellets discarded by the bats were analyzed under a stereomicroscope.

To confirm predation of seeds of *F. cyclophylla*, all 7 bats captured under this tree were subjected to brief captive experimentation in the field. In this group there were 2 juveniles (1 male, 1 female) of *C. doriae*, 2 adult males of *C. doriae* and 1 of *C. villosum*, and 2 adult females of *C. doriae* (1 lactating and 1 apparently inactive). Two hours after capture, these specimens were transferred to clean bags and a mature fig of *F. cyclophylla* was offered to each bat. Bags were subsequently checked for the presence of oral pellets composed of seed-coat fragments. Voucher specimens of dry, preserved seed-coat pellets, as well as *C. doriae* and *C. villosum*, were deposited in the A. L. Peracchi collection, Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil.

Fisher's exact test was used to test the null hypotheses of no interspecific (*C. doriae* and *C. villosum*) and no intersexual (*C. doriae* adults) differences in the proportions of positive fecal samples (indicative of seed predation) obtained by season. Because few specimens were subjected to the captive feeding experiments and because values from behavioral parameters presented in Table 1 resulted from a kind of pseudoreplication (Hurlbert 1984), we did not use inferential statistics on these data.

RESULTS

We captured 54 individuals of *Chiroderma* (49 *C. doriae* and 5 *C. villosum*) in 8 of the 10 netting sessions conducted under fruiting fig trees. Additional individuals were captured in June 1997 (14 *C. doriae* and 1 *C. villosum*) and June–July 1998 (2 *C. doriae* and 1 *C. villosum*) at the border of the forest and in February–December 1999 (1 *C. doriae* and 1 *C. villosum*) under flowering trees, for a total of 74 bats. *C. doriae*, represented by 66 individuals (27

TABLE 1.—Times spent by captive *Chiroderma doriae* (2 males, 1 female) and *C. villosum* (2 males) feeding on mature figs (*Ficus tomentella*). Sample size (n) is number of feeding observations for each behavior.

Behavior	<i>C. doriae</i>			<i>C. villosum</i>		
	\bar{X}	SD	n	\bar{X}	SD	n
Ingesting fig ^a (min)	31.50	13.30	4	45.00	5.80	4
Time to 1st defecation (min)	14.00	5.58	7	14.25	7.09	4
Masticating pulp (s)	31.40	16.20	166	31.40	8.47	54
Masticating seed (s)	74.20	19.20	44	91.80	16.02	16

^a Figs offered to *C. doriae* and *C. villosum* had mean mass of $7 \text{ g} \pm 0.5 \text{ SD}$ and $10.6 \pm 1 \text{ g}$, respectively.

males, 39 females), was more abundant than *C. villosum* (6 males, 2 females). Fecal samples were obtained from 70% ($n = 46$) of the *C. doriae* and 62% ($n = 5$) of the *C. villosum* specimens. All samples obtained from *C. villosum* and 98% ($n = 45$) of those recorded for *C. doriae* contained seed-coat fragments attached to fruit pulp, indicating seed-predation. Undamaged seeds, also attached to fruit pulp, appeared in only 1 sample (20%) from *C. villosum* and in 6 (13%) from *C. doriae*. The sample from *C. villosum*, however, was the only 1 that included a relatively high number of apparently undamaged fig-seeds (88). In those obtained from *C. doriae*, number of seeds ranged from 1 to 15 ($4.8 \pm 5.2 \text{ SD}$).

Distribution of fecal samples containing seed-coat fragments obtained by season and species was as follows: wetter season—33 for *C. doriae* and 3 for *C. villosum*; drier season—12 for *C. doriae* and 2 for *C. villosum*. We found no interspecific difference in proportions of positive fecal samples obtained by season (Fisher's exact test, $P = 0.6098$). Although fecal samples from *C. villosum* were quantitatively limited, data from *C. doriae* consistently showed that fig-seed predation (as indicated by presence of seed-coat fragments in bat feces) was extensive in individuals of both sexes, all age classes, and all reproductive states. Samples from *C. doriae* were obtained from juvenile (4) and adult (8) males, subadult males (5) and females (4), and apparently inactive (15), pregnant (2), and lactating (7) females. When fecal samples from adult *C.*

doriae were analyzed by season, no evidence of intersexual difference was found (Fisher's exact test, $P = 0.9984$). Characters observed in most fecal samples obtained in the field (reddish-brown fruit pulp with seed-coat fragments) were the same as those found in feces of the captive bats that fed on figs of *F. tomentella*.

All 5 bats studied in the laboratory exhibited the same feeding behavior. After promptly biting figs of *F. tomentella* that were offered, bats manipulated them with their thumbs and began eating them. Each bite taken from the fig was slowly chewed (Table 1), and, thereafter, a compact pellet composed primarily of fibrous material and parasitized seeds (with conspicuous holes) was ejected from the mouth. *C. doriae* and *C. villosum* did not swallow intact seeds. Instead, they demonstrated the ability of detaching them from each fig bite and stocking them in their mouth. After processing a variable number of bites ($5 \pm 2.6 \text{ SD}$ in *C. doriae*; $n = 30$), they performed a specific mastication over the accumulated seed mass, producing a conspicuous crunching sound. A compact pellet containing seed-coat fragments (Fig. 1) was then ejected, indicating that the seed content had been ingested. Data recorded during laboratory feeding experiments are presented in Table 1. These species spent twice the time in the seed mastication process as they spent with the pulp and fibrous material. All 6 individuals who accepted figs of *F. cyclophylla* during the field captive experiments predated seeds, indicated by presence of compact

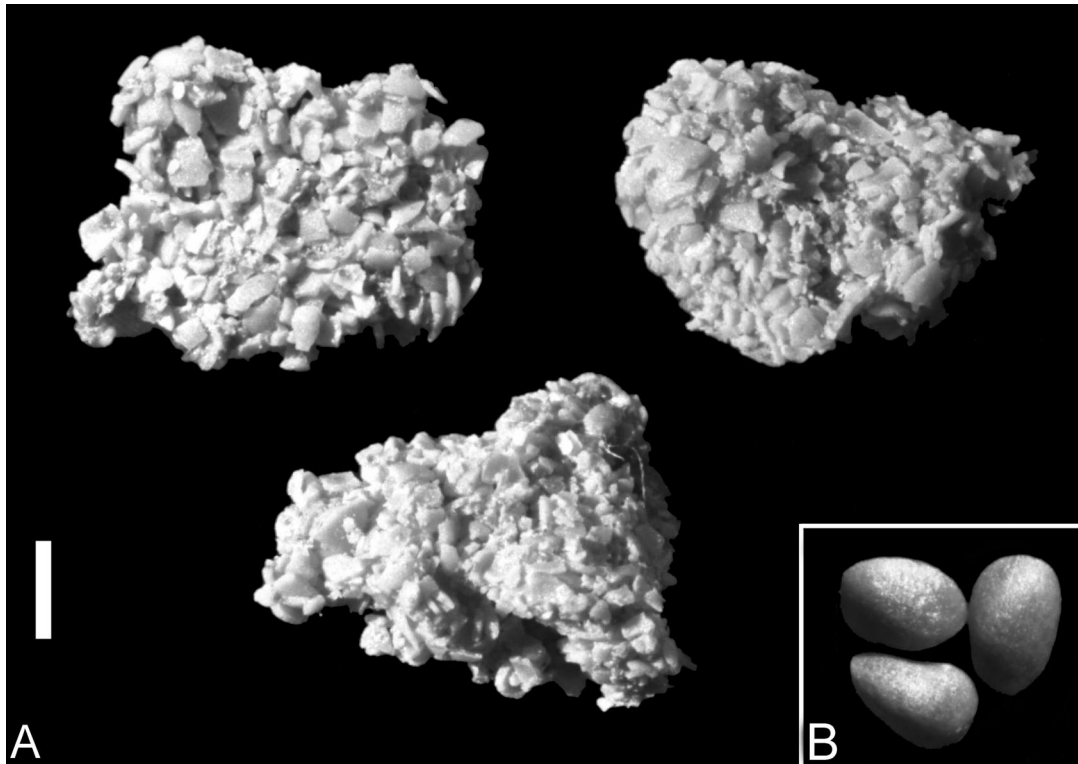


FIG. 1.—A) Oral pellets of seed coat fragments ejected by a captive *Chiroderma doriae* during feeding on a fig (*Ficus tomentella*) and B) undamaged seeds of *Ficus tomentella*; scale bar = 1 mm (pellets and seeds on the same scale).

seed-coat fragment pellets in the bags in which they were held.

DISCUSSION

Contrasting with several frugivorous bat species studied in the Neotropics (Figueiredo and Perin 1995; Fleming 1988; Kalko et al. 1996) and in the Old World (Entwistle and Corp 1997; Funakoshi et al. 1993; Marshall 1985; Utzurrum and Heideman 1991), data presented in this study show that *C. doriae* and *C. villosum* can act as predispersal predators of small (about 1.5 mm) seeds of *Ficus*. Even among plants with medium- to large-sized seeds, the only other record of seed predation by bats was reported by Bonaccorso (1979), who documented the use of *Anacardium excelsum* seeds (Anacardiaceae) by *Carollia perspicillata* (Phyllostomidae). In other frugivo-

rous vertebrate groups, fig-seed predation also appears to be uncommon. Janzen (1979) reported that small parrots (e.g., *Brotogeris gularis*) and very small rodents may extract seeds directly from the fig and crack them. Fruit pigeons (e.g., *Treron*), and some primates (e.g., *Alouatta*), may also act as seed predators to some degree (Janzen 1979).

While discussing the counterpoints between opportunism and specialization in frugivorous bats, Fleming (1986) pointed out a strong association between *Artibeus* (Phyllostomidae, Stenodermatinae) and *Ficus*. According to Fleming (1986), specialization on figs, which are nutritionally poor, directly influences foraging and feeding behavior of *Artibeus*. To compensate for the deficiency of nutrients in figs, *Artibeus* needs to ingest a relatively large amount of

fruit, which is handled over a much longer time period (5–10 times) than that observed when non-fig specialists, such as *Carollia*, consume the same type of fruit (Bonaccorso and Gush 1987). In *Artibeus*, each piece of fruit is slowly chewed and then the pulp mass is pressed with the tongue against the palate, squeezing out the juice that is then swallowed before a dry fibrous pellet is expelled (Fleming 1986). This complex and specialized feeding behavior observed in *Artibeus*, as well as in other stenodermatines (Kalko et al. 1996) and in Old World fruit-bats (Pteropodidae; Funakoshi et al. 1993; Marshall 1983), makes it possible for these bats to efficiently extract nutrients available in figs (Fleming 1986). However, 25–33% of the total energy content in the matter ingested by *Artibeus* is contained in the seeds, most of which pass intact through the bat's digestive tract; seeds also contain 30% of the protein present in figs (Morrison 1980). Therefore, by not taking advantage of the fig-seed contents, frugivorous bats do not retain all available nutrients.

Our data indicate that *C. doriae* and *C. villosum* are more specialized in the use of figs than any other frugivorous bats studied. Their feeding behavior is, in part, similar to that observed in other fruit bats but includes an additional strategy that makes it possible for them to optimize nutrient gain. Steps involved in this particular feeding mode appear to include the separation of the undamaged seeds from each fig bite, retention of these seeds in the bat's mouth until a certain amount becomes available, crunching the accumulated seeds using molars, ingestion of the seed's contents, and ejection of seed coat fragments as compact oral pellets. This implies an exceptional ability for managing fig seeds, which are covered by a gelatinous coat that can make it difficult for bats to avoid swallowing them (Utzurum and Heideman 1991). As would be expected, seed predation considerably increased fig ingestion time. While consuming figs of *F. tomentella*, *C. villosum* spent, on average, more than 4 times (45 versus 10 min) the

amount of time spent by *A. jamaicensis* to eat figs of similar mass (Morrison 1980). Nutrient gain from seed predation may result in a reduction in number of figs ingested each night, which would reduce the number of visits to fruiting trees. Considering predation risks associated with foraging activities (Kalko et al. 1996; Morrison 1978), limiting the number of foraging trips may be advantageous to *C. doriae* and *C. villosum*.

Because fruits are usually low in protein (Kunz and Diaz 1995), frugivorous bats have adopted a variety of strategies to obtain their daily requirements of protein (Courts 1998). They can overconsume protein-poor fruits, ingest a variety of protein-rich food items (pollen, foliage, live birds, carrion, and insects), or perform a combination of these strategies (Courts 1998). Morrison (1980) verified that *A. jamaicensis* probably cannot obtain a sufficient amount of protein feeding on figs alone, which could explain the intensive leaf consumption documented in this species by Kunz and Diaz (1995). Wendeln et al. (2000) analyzed nutritional values of several neotropical figs and argued that by feeding on a combination of fig species bats could obtain a complete set of nutrients. Although emphasizing that their proposed protein value could be overestimated, Wendeln et al. (2000) also suggest that a sufficient amount of protein can be obtained from figs, even if seeds are not digested. Although some doubts still persist regarding the potential for figs to sustain strictly frugivorous bats, at least in the case of *C. doriae* and *C. villosum* they are minimized by the additional protein and energy intake, which is an expected result of fig-seed predation.

Kunz and Diaz (1995) argued that leaf consumption in *A. jamaicensis* could be associated with particular situations in which protein demand may be higher (e.g., males defending harems, pregnant or lactating females). From our data we suggest a different situation regarding seed consumption.

In only 1 of the 51 fecal samples obtained from *Chiroderma* was seed-coat fragments not found. As this sample is representative of all age categories, reproductive stages, and seasons, we assume that this behavior is widespread within the populations studied. Additional data are necessary to evaluate the prevalence of this conspicuous behavioral trait and whether it is expressed across the distribution of *C. doriae* and *C. villosum*, and whether seed predation is exhibited by other species in this currently accepted monophyletic genus (Baker et al. 1994).

Although *C. doriae* and *C. villosum* may occasionally act as potential dispersers for *Ficus*, because undamaged seeds were found in some fecal samples, data presented in this study put these species in an antagonistic relationship (sensu Fleming and Sosa 1994) with the food resource on which they are highly specialized to feed. While discussing the relationship between plants and animals that use them as food resources, Fleming (1988:37–38) made the following comment: “these benefits (pollination and dispersal), are not the result of a conscious effort by animals to cooperate with plants. . . . Animals are also under selective pressure to maximize their fitness, but they do this in a way that is independent of the evolutionary goals of their food plants.” Seed predation can now be considered an important way by which bats maximize nutritional intake, expanding our view of the trophic roles played by this group. Our capacity to understand factors responsible for the high bat diversity in tropical ecosystems as well as our ability to protect such diversity rely greatly on the clarification of these trophic roles (Fenton et al. 2001; Kalko 1997).

RESUMO

A ecologia alimentar da maioria das espécies de morcegos neotropicais é ainda pouco conhecida, indicando que muitas relações ecológicas complexas podem estar obscurecidas. Durante estudo sobre os mor-

cegos e seu potencial papel como dispersores de sementes no Jardim Botânico do Rio de Janeiro, sudeste do Brasil, nós obtivemos dados sobre duas espécies, *Chiroderma doriae* e *C. villosum*, que atuam como predadoras de sementes ao invés de dispersoras. Análise de amostras fecais e experimentos de alimentação em cativeiro confirmaram esta estratégia alimentar que até então era desconhecida em morcegos. Ambas as espécies empregam uma especializada estratégia de predação das sementes de *Ficus*, ingerindo seu conteúdo rico em nutrientes e descartando a maioria dos fragmentos da casca sob a forma de compactas pelotas orais. Evidências obtidas da espécie mais abundante, *C. doriae*, mostraram que as sementes foram consumidas tanto na estação mais seca quanto na mais chuvosa, e por indivíduos de ambos os sexos, todas as classes de idade, e todos os estados reprodutivos. O uso de sementes, em adição à polpa do fruto, provavelmente representa um incremento na aquisição de nutrientes disponíveis nos figos, mostrando que o grau de especialização alimentar de *Chiroderma* neste recurso pode ser ainda mais elevado do que dados prévios têm mostrado.

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