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Short Communication

Differential ingestion of fig seeds by a Neotropical bat, Platyrrhinus lineatus

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ABSTRACT

It has been suggested that bats selectively ingest viable rather than wasp-parasitized fig seeds, but such a differential ingestion has not been demonstrated for Neotropical bats yet. We ask whether the fruit bat *Platyrrhinus lineatus* selectively ingests viable rather than parasitized *Ficus citrifolia* and *F. crocata* seeds, based on the proportion of parasitized seeds in three types of samples: ripe syconia, dry oral pellets and faeces. The proportion of parasitized seeds per *F. citrifolia* and *F. crocata* syconium ranged from 56 to 80% and from 66 to 93%, respectively. Most of the pellet samples presented more than 90% of parasitized seeds, and most of the faecal samples presented less than 5% of parasitized seeds. Results show that *P. lineatus* exhibits differential ingestion of *F. citrifolia* and *F. crocata* seeds, representing the first direct evidence of this phenomenon for Neotropical bats.

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Pollination of figs (*Ficus* species; Moraceae) by fig wasps (Agaonidae) involves two types of female flowers, short-styled flowers whose ovules generally feed wasp larvae and long-styled flowers that can develop viable seeds through pollination by adult wasps (Weiblen, 2002; Dumont et al., 2004). Ripe syconia ("fruits" of figs) of monoecious fig species present wasp-parasitized seeds originated from short-styled flowers mixed with viable seeds produced in long-styled flowers (Weiblen, 2002). However, the ingestion of parasitized seeds by the fig-eating fauna is likely disadvantageous for fig species because it can reduce the amount of viable seeds available for long-distance dispersal through faecal deposition (Utzurrum and Heideman, 1991; Reiter, 2002).

Most New and Old World fig-eating bats do not swallow figs wholly; they press fig parts with the tongue against the palate, swallowing the juice and soft parts and discarding the solid matter into dry oral pellets (Janzen, 1978; Fleming, 1986; Kalko et al., 1996; Nogueira and Peracchi, 2003; Heer et al., 2010). Based on this feeding behaviour and on records that fig seeds in the bat's faeces are predominantly viable rather than wasp-parasitized, it has been suggested that bats selectively ingest viable seeds and discard wasp-parasitized ones in the pellets (Janzen, 1978; Utzurrum and Heideman, 1991; Kalko et al., 1996; Hodgkison et al., 2003; but see Nogueira and Peracchi, 2003). However, such a differential ingestion of fig seeds by the bats was not clearly demonstrated yet, except for captive individuals of the Old World bat *Ptenochirus*

* Corresponding author. Tel.: +55 67 33457338; fax: +55 67 33457342. *E-mail address*: robertomunin@yahoo.com.br (R.L. Munin). *jagori* (Pteropodidae) fed with unidentified figs (Reiter, 2002). Thus multiple studies are still needed to demonstrate the occurrence of differential ingestion of fig seeds and to know variable patterns of seed ingestion by different bat species feeding on variable fig species.

Here we asked whether the bat *Platyrrhinus lineatus* (Phyllostomidae) shows differential ingestion of seeds of two strangler figs, *Ficus citrifolia* and *F. crocata*. Since this bat species exhibits the behaviour of ingesting fruit juice and discarding pellets, we hypothesized that it predominantly swallows viable and discards unviable seeds of these two plant species. This is the first study addressing differential ingestion of fig seeds by a Neotropical bat, and the first controlled for both bat and plant species. In addition, the present study was designed in nature without bat or fruit manipulations which avoid bias on behaviour of bats or fig conditions.

The study was carried out in two semideciduous riparian forests along Formoso and Taquaruçu rivers, South-western Brazil (21°07′S, 56°23′W and 20°31′S, 55°46′W; respectively). The Formoso basin is in the karstic region of Serra da Bodoquena and the Taquaruçu river crosses Cerrado areas in the Serra de Maracaju; *P. lineatus, F. citrifolia* and *F. crocata* naturally inhabit these forests (Baptista-Maria et al., 2009; Camargo et al., 2009; Cunha et al., 2009).

In the Formoso region we selected a previously known colony of *P. lineatus* composed of 12 adult individuals roosted underneath the roof of a 2×3 m terrace constructed inside the riparian forest. The terrace was exclusively used by this colony during the study. On November 29 and 30, 2009, we found these bat individuals feeding on a fruiting *F. citrifolia* tree, 7 m distant from the roost. We then cleaned the paved floor under the terrace and hap-

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Fig. 1. *Platyrrhinus lineatus* (Phyllostomidae) perched on a *Pachira aquatica* (Malvaceae) tree, and feeding on a ripe *Ficus crocata* (Moraceae) fig, in South-western Brazil.

hazardly collected faecal and pellet samples deposited throughout two subsequent nights.

In the Taquaruçu region we found a *Pachira aquatica* (Malvaceae) tree used as feeding roost by *P. lineatus* (Fig. 1), which were visiting a fruiting *F. crocata* tree, 20 m apart. We observed up to three bats simultaneously perched on the roost tree while other individuals were visiting the fruit source. For samplings, we put plastic covers on forest soil just below the bat's perching branches and collected faecal and pellet samples deposited during two subsequent nights, in July 16 and 17, 2010. Time spent by bats for manipulating an entire *F. crocata* fig, the number of oral pellets discarded per fig, and the numbers of defecations while feeding on a fig were also registered in the Taquaruçu region.

In the Formoso and Taquarucu regions, we additionally collected intact mature figs from the source F. citrifolia and F. crocata trees in order to sample viable and unviable seeds per fig, and to identify seeds of these species in faecal and pellet samples. Viable seeds of strangler figs present a gelatinous coating resistant to gut passage, contrasting with parasitized seeds which are hollowed and lack this coating. Bat identifications in both regions were based on direct observations (1-2 m close) of individuals and the knowledge of bat species at the study sites (Camargo et al., 2009). Plants were identified by specialists and voucher material was deposited in the herbarium of the Universidade Federal de Mato Grosso do Sul (CGMS). In laboratory, samples from both study sites were individually inspected under stereomicroscope for counting viable and wasp-parasitized fig seeds per faecal sample, per pellet sample, and per mature figs of each species. We also measured fig mass with an electronic balance (0.01 g accuracy), and fig and seed length and width with a caliper (0.05 mm accuracy).

To address our hypothesis, we tested for differences in the percentage of wasp-parasitized seeds per sample (dependent variable) among the three sample types (independent variable) – faeces, pellets and figs. We used faecal or pellet samples as independent units of replication as it represents a same event of dispersal. Because we were not able to identify bat individuals throughout the night, our procedure includes a certain level of pseudo-replication since some samples were likely provided by a same bat individual. The percentage of wasp-parasitized seeds per sample was normally distributed and presented homocedasticity among sample types, thus we used it in one-way analysis of variance (ANOVA) without transformation; post hoc comparisons among samples were carried out using

Table 1	1
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Fig and seed traits of *Ficus crocata* and *F. citrifolia*, and number of seeds discarded in pellets and faeces of *Platyrrhinus lineatus* bats, in South-western Brazil.

	Ficus citrifolia mean \pm SD (n)	Ficus crocata mean \pm SD (n)
Fig mass (g)	$2.4 \pm 0.6(10)$	$5.4 \pm 0.9 (25)$
Fig length (mm)	$18 \pm 1.1 (10)$	$25 \pm 1.7 (25)$
Fig width (mm)	$19 \pm 1.5 (10)$	$24 \pm 1.6 (25)$
Viable plus parasitized seeds per fig	$611 \pm 47.8(10)$	$1104 \pm 172.9(25)$
Length of parasitized seeds (mm)	$1.35\pm0.09(20)$	$1.38 \pm 0.05 (20)$
Width of parasitized seeds (mm)	$1.01\pm0.09(20)$	$1.01\pm0.06(20)$
Length of viable seeds (mm)	$1.37 \pm 0.11 (20)$	$1.36 \pm 0.06 (20)$
Width of viable seeds (mm)	$1.00\pm0.11(20)$	$0.98\pm0.06(20)$
Viable plus parasitized seeds per pellet	$20 \pm 7.3(50)$	$16 \pm 5.2 (80)$
Viable plus parasitized seeds per faeces	$63 \pm 23.3 (15)$	$61\pm14.6(27)$

Tukey's HSD. Size differences between viable and wasp-parasitized seeds for each plant species were tested using two-tailed *T*-test.

Syconia of *F. crocata* and *F. citrifolia* are roughly spherical (Table 1). Viable seeds did not differ from wasp-parasitized ones in length or width, for *F. crocata* (p = 0.16 and 0.19, respectively) and *F. citrifolia* (p = 0.54 and 0.76, respectively).

Of the 71 oral pellets collected in Formoso region, 50 presented only *F. citrifolia* seeds (Table 1), except one sample with one additional seed of *Cecropia pachystachya* (Urticaceae). The remaining 21 pellet samples produced by the 12 *P. lineatus* bats in Formoso region showed no seeds of *F. citrifolia*; 19 exclusively showed leaves of *Solanum riparium* (Solanaceae), and two samples contained only *C. pachystachya* seeds (*n*=5 and 35, respectively). In *P. lineatus*' faeces, in Formoso region, other seeds mixed with *F. citrifolia* were *C. pachystachya* and *Maclura tinctoria* (Moraceae). In Taquaruçu region, pellet and faecal samples presented only *F. cro*-

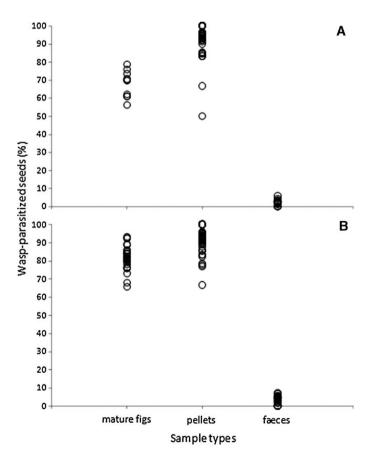


Fig. 2. Percentage of wasp-parasitized seeds of *Ficus citrifolia* (A) and *F. crocata* (B) found in mature figs, and among pellet and faecal samples of *Platyrrhinus lineatus* bats in South-western Brazil.

cata seeds (Table 1). In both regions no faecal samples presented either pollen or invertebrate pieces. *Platyrrhinus lineatus* individuals spent 20 ± 1.8 min (mean \pm SD; n = 12 figs) to eat pulp and discard pellets of each *F. crocata* fig. Bats discarded 43.6 ± 3.9 (n = 12 figs) dry oral pellets and defecated one to three times during consumption of one *F. crocata* fig.

Percentage of wasp-parasitized seeds per fig ranged from 56 to 80% for *F. citrifolia* (68 ± 7.4%, *n* = 10) and from 66 to 93% for *F. crocata* (82 ± 7.0%, *n* = 25) (Fig. 2). Most of the pellet samples in both regions, Formoso and Taquaruçu, presented more than 90% of parasitized seeds (*F. citrifolia*: 94 ± 9.4%, *n* = 50; *F. crocata*: 95 ± 6.8%, *n* = 80), whereas most faecal samples presented less than 5% of parasitized seeds (*F. citrifolia*: 2 ± 1.6%, *n* = 15; *F. crocata*: 3 ± 2.4%, *n* = 27). The percentage of wasp-parasitized seeds was higher in the pellets than in faeces or figs, and higher in figs than in feaces, for *F. citrifolia* (*F*_{2,72} = 727.2, *p* < 0.0001, ANOVA and Tukey tests) and *F. crocata* (*F*_{2,129} = 838.3, *p* < 0.0001, ANOVA and Tukey tests).

Our results support that P. lineatus bats feeding on F. citrifolia and F. crocata figs selectively ingest viable seeds and discard the wasp-parasitized ones in oral pellets. Results for both Ficus species were very similar, in spite they come from two bat groups at sites widely apart (\sim 110 km). As could be expected if differential ingestion is occurring, figs presented intermediate percentage of wasp-parasitized seeds when compared to pellet and faecal samples. Disadvantages of seeds being dispersed in oral pellets rather than in faeces include reduced distance of dispersal, increased susceptibility to predation, fungal attack, and low germination rates (Tang et al., 2008; Marques and Fischer, 2009). Therefore, P. lineatus can be considered a suitable fig disperser, in part, due to the differential ingestion of fig seeds (this study). It indicates that other bats (e.g. Morrison, 1980; Fleming, 1986; Kalko et al., 1996; Nogueira and Peracchi, 2003) which present the same behaviour as P. lineatus are expected to selectively ingest viable rather than wasp-parasitized fig seeds. Other fig-eating fauna which does not press the fruit to swallow the juice are not expected to present differential seed ingestion, thus they can be regarded as less efficient fig dispersers. Studies addressing the feeding behaviour of different fig-eating taxa are important to know their relative importance as fig dispersers.

On one hand, the presence of a slippery gelatinous coating might favour viable fig seeds to be ingested (Utzurrum and Heideman, 1991; Reiter, 2002; Heer et al., 2010) and, on the other hand, the attachment to fig tissues likely impels wasp-parasitized seeds to be discarded in the pellets (pers. obs.). Different traits between viable and parasitized fig seeds, therefore, appear to be adjusted to the bats' feeding behaviour in order to attain dispersal in faeces and to escape dispersal in oral pellets (Fleming, 1986; Utzurrum and Heideman, 1991; Kalko et al., 1996). However, although stenodermatine bats swallow the juice and discard dry matter, *Chiroderma doriae* and *C. villosum* are able to retain viable fig seeds in the mouth and to feed on them (Nogueira and Peracchi, 2003). These two species apparently accumulate viable fig seeds in the mouth, crunch them with molars and discard seed coat fragments in oral pellets. Such a typical coat fragments (see Nogueira and Peracchi, 2003) were not found among *P. lineatus*' pellets at the study sites, which indicates that it does not feed on fig seeds like *Chiroderma* species do. Further data on swallowing behaviour of multiple bat species are still needed to identify the different roles that they might play on fig seeds.

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