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Passage time of seeds through the guts of frugivorous birds, a first assessment in Brazil

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RESUMO: Tempo de passagem de sementes pelo trato digestório de aves frugívoras, uma primeira avaliação no Brasil. O tempo de passagem das sementes ingeridas por animais frugívoros tem importantes implicações para a distribuição espacial das sementes e sua distância de dispersão. Apesar disso, raramente este parâmetro é abordado em estudos de dispersão de sementes. Neste trabalho, fornecemos informações sobre o tempo de passagem de sementes de nove espécies de plantas ingeridas por indivíduos cativos de seis espécies de aves (*Turdus albicollis, T. amaurochalinus, T. leucomelas, T. rufiventris, Stephanophorus diadematus* e *Saltator similis*). Observamos que (1) sementes regurgitadas passam mais rapidamente pelo trato digestório das aves que sementes defecadas e (2) sementes grandes (*e.g.,* > 5 mm de diâmetro para *Turdus* spp.) são regurgitadas e não defecadas. Estes resultados corroboram outros estudos, porém a relação entre tamanho da semente e tempo de passagem parece ser bastante complexa e variável, necessitando de estudos mais detalhados sobre este importante aspecto da ecologia da dispersão de sementes e da fisiologia digestiva das aves frugívoras.

PALAVRAS-CHAVE: aves frugívoras, dispersão de sementes, frugivoria, tamanho das sementes, tempo de passagem das sementes, Turdidae.

ABSTRACT: Passage time of seeds through the guts of frugivorous birds, a first assessment in Brazil. The transit time of seeds ingested by frugivorous animals has important implications for the spatial distribution of seeds and their dispersal distance. Nevertheless, this parameter is rarely included in seed dispersal studies. In this paper, we provide information about the transit time of seeds of nine species of plants ingested by individuals of six species of captive birds (*Turdus albicollis, T. amaurochalinus, T. leucomelas, T. rufiventris, Stephanophorus diadematus* and *Saltator similis*). We found that (1) seeds are regurgitated quickly through the digestive tract of birds than defecated seeds, and (2) large seeds (*e.g.,* > 5 mm in diameter for *Turdus* spp.) are regurgitated rather than defecated. These results corroborate other studies, but the relationship between seed size and transit time seems to be quite complex and variable, requiring more detailed studies on this important aspect of the ecology of seed dispersal and digestive physiology of frugivorous birds.

KEY-WORDS: frugivory, GPT, seed dispersal, seed size, Turdidae.

The time elapsed between fruit ingestion and the regurgitation or defecation of the ingested seeds (gut passage time or GPT) by a frugivorous animal is an essential component of the effectiveness of seed dispersal (*sensu* Schupp 1993). Among birds, GPT alone may influence the spatial distribution of ingested seeds (Obeso *et al.* 2011), and combined with information on the movement of birds, GPT permit to infer the distance of seed dispersal (Westcott *et al.* 2005).

In birds GPT of seeds is influenced by body mass, diet (the degree of frugivory is positively associated with GPT), rate of fruit ingestion, seed size and seed load, fruit chemistry, and pulp texture (Herrera 1984, Levey 1986, Worthington 1989, Schabaker and Curio 2000). Seed size is especially important, because it determines in great part if the seed will be defecated or regurgitated. Such distinction is not trivial because defecated seeds usually have a longer GPT than regurgitated ones, which may influence the distance of seed dispersal and the mechanical and/or chemical scarification of the seed coat, thus influencing seed germination (Traveset and Verdú 2002).

Despite its importance to determine where the seeds will be deposited, GPT is rarely assessed. In Brazil, for instance, a literature survey revealed over 200 studies involving avian frugivory (a complete list of these studies may be requested from the senior author), but none present the GPT of ingested seeds. Many of such studies present information about the time spent by birds on the plants where they fed, a parameter related to the probability of the ingested seeds to be discarded beneath the parent plant or elsewhere. However, without the information on GPT of seeds, even the basic question of

TABLE 1: Number and size of seeds of the fruits offered to captive birds. Many refer to > 20 seeds. Plant species are arranged in alphabetical order.

Seed species (Plant families)[a]	Number of seeds	Seed measurements (mm)		
		N	Width	Length
Eugenia uniflora (Myrtaceae)	1	3	8.39 ± 1.40	9.60 ± 1.73
Ficus sp. (Moraceae)	many	2	0.79 ± 0.13	1.02 ± 0.04
Leandra sp. (Melastomataceae)	many	3	0.47 ± 0.08	0.93 ± 0.08
Morus nigra (Moraceae)	many	10	1.61 ± 0.16	2.06 ± 0.19
Murraya paniculata (Rutaceae)	1	9	5.12 ± 0.31	7.10 ± 0.45
Psychotria carthagenensis (Rubiaceae)	2	4	2.14 ± 0.11	3.76 ± 0.15
Rapanea coriacea (Myrsinaceae)	1	6	3.19 ± 0.15	3.22 ± 0.09
Rapanea umbellata (Myrsinaceae)	1	6	4.96 ± 0.18	5.34 ± 0.18
Schinus terebinthifolia (Anacardiaceae)	1	10	2.84 ± 0.20	4.35 ± 0.25

[a] Plant names are arranged in alphabetical order, and follow the APG II (2003) classification.

whether birds stay on plants time enough to allow the deposition of seeds beneath them or, alternatively, they effectively remove the seeds from the vicinity of parent plants, cannot be properly answered. To help fulfill this gap of knowledge, we present here information on GPT for seeds of nine plant species ingested by six captive frugivorous bird species (*Turdus albicollis, T. amaurochalinus, T. leucomelas, T. rufiventris, Stephanophorus diadematus,* and *Saltator similis*). In addition to presenting data that will eventually permit draw general patterns about the GPT of bird-ingested seeds, our intention is to stimulate future studies that deal with this important aspect of seed dispersal ecology and digestive physiology of frugivorous birds.

METHODS

We assessed the GPT of seeds ingested by captive birds that have been removed from the wild by illegal poachers. Birds were maintained with water, a commercial bird food plus an assortment of fresh commercial fruits (bananas, papayas). For the trials birds were kept in cages (38 × 22 × 40 cm) lined with white paper. The daily food was removed, while experimental fruits and water were offered *ad libitum.* Only one fruit species was used per trial. We then recorded the time elapsed between the ingestion of the first fruit and defecation of the first seed. Note that this procedure only permits the assessment of minimum GPT because seeds kept on passing after the first seed was defecated. However, in birds GPT of seeds is typically skewed to the right, *i.e.,* most of the ingested seeds are defecated a few minutes after the first seed appears in feces (Levey 1986), meaning that our GPT should not greatly differ from the GPT of the majority of the ingested seeds.

The bird species tested reflect the availability of frugivorous birds in captivity. The width and length of the seeds eaten by birds were measured with calipers to the next 0.01 mm.

RESULTS

The fruit species used had seed sizes, as denoted by seed widths, ranging from 0.47 to 8.39 mm (Table 1). Overall, mean time for defecation of seeds (22.9 ± 14.3 min, range 6-60 min, n = 27) was longer than the time needed for seed regurgitation (11.3 ± 7.0 min, range 3.8-22.8 min, n = 10; Table 2). Restricting the comparison to the genus *Turdus,* the difference remains: defecated seeds have longer GPT than regurgitated seeds (24.0 ± 16.1 min *vs.* 11.3 ± 7.0 min; t test applied to log-transformed data: t = 2.92, df = 20, P = 0.008).

Focusing on the two bird species with greater sample sizes, we noted a general positive relationship between seed size and GPT, with the exception of *Leandra* sp. eaten by *T. amaurochalinus* (Figure 1). Note, however, that some of the bird-seed species combinations were tested only once, thus results presented in Figure 1 should be interpreted with caution.

For *Turdus* spp., seeds with 3.2-5 mm width represented by *Rapanea* species were either defecated or regurgitated, denoting that this seed size range is close to

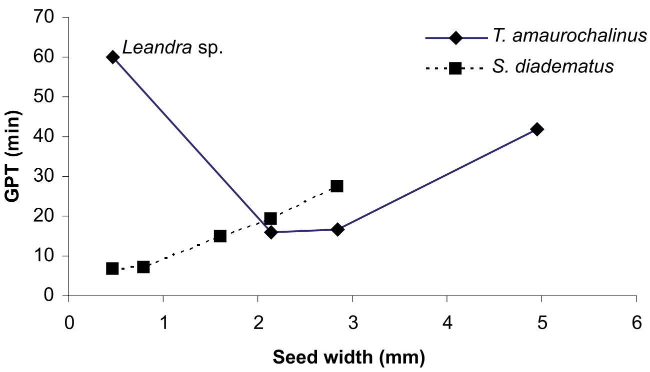

FIGURE 1: The relationship between seed width and gut passage time (GPT) for seeds defecated by *Turdus amaurochalinus* and *Stephanophorus diadematus.* GPT of *Leandra* sp. seeds ingested by *T. amaurochalinus* is highlighted (see text).

TABLE 2: Gut passage time (GPT) of seeds defecated or regurgitated by captive frugivorous birds. Values are means followed by standard deviations for seed species with more than three replicates with a given bird species. Dashes indicate that the seed was not tested with the respective bird. Between parentheses are sample sizes and data range. Body masses came from Dunning Jr. (2008).

Bird species	Body mass (g)	Seed species	GPT (min) Defecation	Regurgitation
Turdus albicollis	54.0	*Eugenia uniflora*	—	6.0 (1)
		Morus nigra	12.3 (1)	—
		Murraya paniculata	—	6.0 ± 3.4 (3; 3.8-10.0)
		Rapanea coriacea	—	7.3 (1)
Turdus amaurochalinus	57.9	*Leandra* sp.	60.0 (1)	—
		Murraya paniculata	—	22.8 (1)
		Psychotria carthagenensis	15.8 ± 3.9 (5; 11.0-21.0)	—
		Rapanea umbellata	42.0 (1)	9.5 (2; 9.0. 10.0)
		Schinus terebinthifolia	16.5 ± 6.6 (3; 11.7-24.0)	—
Turdus leucomelas	69.1	*Rapanea coriacea*	45.0 (1)	20.0 (1)
Turdus rufiventris	66.8	*Rapanea coriacea*	—	20.0 (1)
Stephanophorus diadematus	35.4	*Ficus* sp.	7.0 (1)	—
		Leandra sp.	6.5 (2; 6.0. 7.0)	—
		Morus nigra	14.7 (1)	—
		Psychotria carthagenensis	19.3 ± 6.0 (3; 13-25)	—
		Schinus terebinthifolia	27.5 (2; 15.0. 40.0)	—
Saltator similis	43.3	*Morus nigra*	27.5 (2; 25.0. 29.5)	—
		Psychotria carthagenensis	32 (1)	—
		Schinus terebinthifolia	32.5 ± 19.6 (3; 20.0. 55.0)	—

the limit for seed defecation. Above 5 mm width (*e.g., Eugenia uniflora, Murraya paniculata*) seeds were always regurgitated (Table 2)

The GPT of seeds ingested by *Saltator similis,* the bird with the most diverse diet (see below), were always longer than the other bird species tested with the same seed species (Table 2).

DISCUSSION

Because our sample sizes were small for most bird-seed species combinations, our results should be interpreted with caution, but some of them parallel the trends observed in other studies: (1) defecated seeds take longer to be discarded than regurgitated seeds, and (2) large seeds are regurgitated rather than defecated (Levey 1986, Obeso *et al.* 2011). The exact seed size marking the boundary between defecation and regurgitation depends on bird size. In the case of thrushes, it seems that 5 mm is close to the maximum seed width for defecation. Seeds larger than that are regurgitated.

The relationship between seed size and GPT is highly variable (Levey 1986, Wothington 1989, Schabaker and Curio 2000), likely reflecting the complexity of the internal handling of seeds by birds, which is influenced by several factors related to the fruit (*e.g.,* fruit chemistry, pulp texture, seed load) and to the bird itself (*e.g.,* state of nutrition, state of stress; Schabaker and Curio 2000). For instance, GPT usually decreases with increasing seed load (*i.e.,* the ratio between seed and pulp masses), which in turn decreases with increasing seed number (Schabaker and Curio 2000). Therefore, there is a trend for longer GPT for seeds whose fruits have many small seeds, which may explain the large GPT of *Leandra* seeds eaten by *T. amaurochalinus.* The GPT of the same seeds eaten by *S. diadematus* was, however, much shorter than observed for *T. amaurochalinus* (6.5 vs. 60.0 min, respectively). Part of such difference may reflect the smaller body mass of *S. diadematus,* but other unknown factors could be involved.

GPT usually bears a negative relationship with the degree of frugivory, i. e. highly frugivorous birds rapidly pass the seeds through the guts as an adaptation to frugivory (Herrera 1984, Jordano 1987). The least frugivorous bird species tested was probably *Saltator similis,* which is best classified as an omnivorous species, feeding on fruits, seeds, insects, leaves, and honeydew (Moojen *et al.* 1941, Orenstein and Brewer 2011). Therefore, there is no surprise that the GPT of the seeds ingested by *S. similis* were higher than the GPT recorded for the other bird species tested with the same seed species. If long GPT has the advantage of promoting longer dispersal distances, it has also the potential disadvantage of injuring seeds, especially soft seeds, due to long exposition to mechanic or chemical abrasion in the gut (Traveset and Verdú 2002).

We hope that this study help to stimulate researchers in Brazil and elsewhere to investigate the intricate interplay between bird and fruit characteristics that ultimately influence GPT. GPT has important implications for the viability, spatial distribution and dispersal distances of seeds. It is also an important feature of the digestive physiology of frugivorous birds, which represent a frontier in our understanding of the seed dispersal process.

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