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ORIGINAL ARTICLE

Viability of small seeds found in feces of the Central American tapir on Barro Colorado Island, Panama

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Abstract

Tapirs are known as effective dispersers of large-seeded tree species, but their role in dispersing small-seeded plant species has yet to be established. Tapir feces have been reported to contain large numbers of small seeds, but whether these are viable has rarely been evaluated. We determined the abundance and viability of small seeds in feces of Central American tapir (*Tapirus bairdii*) on Barro Colorado Island, Panama. A total of 72 fecal samples were collected opportunistically from 4 tapir latrine sites. Seeds were manually extracted from feces and classified by size. Seed viability was estimated by opening each seed and examining for the presence of at least 1 intact firm white endosperm. In total, we obtained 8166 seeds of at least 16 plant species. Small-seeded species dominated, with 96% of all seeds found measuring <5 mm. The canopy tree *Laetia procera* was the most abundant species in the samples. Of all small seeds found, 69% contained an intact endosperm and appeared viable. This suggests that small seeds, like large seeds, often pass through the digestive tract of *T. bairdii* intact. Thus, tapirs potentially serve as effective dispersers of a wide range of small-seeded plant species.

Key words: Central America, megafauna, seed dispersal, seed size, tapir

INTRODUCTION

Seed dispersal by tapirs (*Tapirus* spp.) is an important determinant of the spatial distribution of plants in Neotropical forests (Forget & Sabatier 1997; Fragoso *et al.* 2003). Tapirs are the largest extant terrestrial mammals in Neotropical forests, are able to swallow large seeds and can ingest a large quantity of seeds while feeding (Terwilliger 1978; Naranjo 1995). Tapirs possess a 'primitive' digestive tract characterized by incomplete digestion; therefore, many seeds can pass through the tapir gut intact (Janzen 1984; Bodmer 1991). Long seed retention times in the gut (Janzen 1981) and large home-range sizes (Foerster & Vaughan 2002) contribute to the tapir's ability to disperse seeds over long distances, in some cases to suitable sites beyond the range of seed-consuming larvae (Fragoso *et al.* 2003).

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Tapirs are considered effective dispersers of plant species with large, thick-walled seeds; that is, they tend to deposit seeds unharmed to suitable germination sites away from the parent plant (see Schupp 1993 and Jordano & Schupp 2000 for a detailed discussion of effective dispersal). For example, *Tapirus terrestris* (Linnaeus, 1758) is an effective disperser of large-seeded palms (Rodrigues *et al.* 1993; Fragoso & Huffman 2000; Quiroga-Castro & Roldan 2001; Tobler *et al*. 2010) and *Tapirus bairdii* (Gill, 1865) is an effective disperser of large-seeded tree species, including *Caesalpinia coriaria* (Janzen 1982), *Guazuma ulmifolia* (Janzen 1982) and *Manilkara zapota* (O'Farrill *et al.* 2006, 2012). However, tapirs also feed on fruits that contain many small seeds and are known to ingest small seeds while browsing (Janzen 1984). Fragoso and Huffman (2000) report that seeds of 4 small-seeded species germinated after they were extracted from *T. terrestris* feces. Small seeds have been found in *T. terrestris* stomach contents (Henry *et al*. 2000) and feces (Tófoli 2006; Zorzi 2009; Tobler *et al*. 2010), as well as in *T. bairdii* feces (Naranjo 1995). Whether tapirs are effective dispersers of these small seeds is partially determined by the degree to which small seeds survive passage through the digestive tract intact, which is largely unknown.

We examined the potential of the Central American tapir (*T. bairdii*) as a disperser of small-seeded plant species by estimating the viability of seeds found in tapir feces on Barro Colorado Island, Panama. We also recorded the abundance and diversity of small seeds in feces.

MATERIALS AND METHODS

Study site and species

Barro Colorado Island (BCI), Panama (9°9′N, 79°51′W) is a 16 km^2 island covered with tropical lowland moist forest. BCI has an average temperature of 27 °C, an average yearly rainfall of 2600 mm, a rainy season from May through December and a marked dry season from January through April. The island has a heterogeneous landscape with numerous creeks, most of which are seasonally dry (Leigh *et al.* 1996).

Tapirus bairdii is 1 of 4 species of the family Tapiridae of the order Perissodactyla and the only remaining Pleistocene megafauna in Central America (Janzen 1982). It is distributed intermittently from southern Mexico to northwestern Colombia in humid habitats from sea level to 3600 m (IUCN 2012). The diet of *T. bairdii* consists of a variety of plant species and plant parts, including leaves, stems and fruits (Terwilliger 1978; Naranjo 1995; Olmos 1997; Tobler 2002). *T. bairdii* is more active during nocturnal hours (Foerster & Vaughen 2002). It is known to use latrines or sites of repeated defecation (Flesher 1999; Naranjo 2009).

The diet of *T. bairdii* on BCI has been studied by Terwilliger (1978) through direct observation of the feeding behavior of individual tapirs. To our knowledge, no studies have examined fecal samples on BCI. Estimates of the tapir population on BCI have varied greatly over time (Enders 1935; Enders 1939; Eisenberg & Thorington 1973; Terwilliger 1978; Eisenberg 1980; Glanz 1996). More recent estimates of *T. bairdii* density on BCI obtained from diurnal and nocturnal census efforts are 0.19 and 0.36 individuals/km^2, respectively (Wright *et al*. 1994). The current population size of tapirs on BCI is unknown (R. W. Kays, pers. comm.).

Sampling

We collected fresh fecal samples (dung boluses <1 week old as judged by inspection of odor, color and integrity of fecal material) at 4 tapir latrine locations along the northern shore of BCI, near the terminal portions of the 'Standley' and 'Miller' trails, during May–Aug 2003. All 4 latrines were located within a straight-line distance of approximately 1.5 km (approximately 3 km ground distance), with 2 of the latrines in close proximity (approximately 50 m). Fecal samples were slowly dried in a dry closet for 3 days at approximately 35 °C and then spread out on trays in a dark air-conditioned laboratory for an additional 7 days until completely dry. Each fecal sample was packaged individually in a paper bag and assigned a number for identification, then stored in plastic with desiccant until processing, which was completed within 8 weeks. We extracted the seeds from dry feces manually. This proved more efficient than seed extraction using different-sized wire mesh screens (as in Naranjo 1995; Fragoso & Huffman 2000), because many small seeds passed directly through 5 mm^2 mesh sieves and could not be effectively separated from browse material with smaller-mesh sieves. We classified seeds as small (S < 5 mm), medium (M = 5–20 mm) or large (L > 20 mm) and identified seeds to 'morphospecies'. We attempted to identify morphospecies to species through comparison with BCI herbarium samples and with the assistance of Osvaldo Calderón and Andres Hernandez (BCI botanists). Viability was estimated by the cut test (Terry *et al*. 2003); opening each unimbibed seed and examining under magnification for the presence of at least 1 intact firm white endosperm (as in Fragoso & Huffman 2000). Although the cut test method is indirect and may vary by species, it has been used successfully to determine viability for tapir ingested seeds (Fragoso & Huffman 2000), for small seeds dispersed by frugivorous tortoises (Strong & Fragoso 2006) and for other small seeds (*Piper* spp.) where germination tests failed to distinguish between viability and dormancy (Daws *et al.* 2002) .

RESULTS

Of 72 fecal samples obtained, 52 from 3 tapir latrine locations in the early wet season comprised approximately 3900 cm^3 of fecal matter containing 1084 seeds (Table 1). A total of 20 samples from a fourth latrine location during the mid-wet season comprised approximately 1800 cm^3 of fecal matter containing 7082 seeds. The fecal collections from the 3 early wet season locations were deposited by tapirs in moist areas that were not flooded at the time of collection. Thirteen of the 20 mid-wet season samples were intact boluses collected from a flooded drainage and 7 were collected immediately adjacent to this drainage on dry soil.

In total, the feces contained 8166 seeds of at least 16 plant species. The size range of seeds encountered was approximately 1–30 mm in length, with 7864 small seeds, 193 medium seeds and 109 large seeds. The majority of the seeds (96%) and species (50%) were small-seeded. As much as 83% of all seeds came from the canopy tree *Laetia procera* (Flacourtiaceae); these 2–3 mm sized seeds were present in each of the 20 fecal samples collected in August. The next most abundant (group of) species was *Ficus*, which made up 11% of the seeds. Of all small seeds (<5 mm), the majority (69%) contained an intact endosperm.

DISCUSSION

Tapirs are important dispersers of large-seeded tree species (Bodmer 1991; Fragoso 1997; Quiroga-Castro & Roldan 2001; Fragoso *et al.* 2003; Giombini *et al.* 2009; O'Farrill *et al.* 2012). Previous studies reported that *T. terrestris* feces contain large numbers of small seeds (e.g. Fragoso & Huffman 2000; Tófoli 2006; Talamoni & Assis 2009; Zorzi 2009; Tobler *et al.* 2010). Our study provides similar data for *T. bairdii* and suggests that a large proportion of small seeds that pass through the digestive tract of *T. bairdii* are viable. Feces of the Central American tapir on Barro Colorado Island contained large numbers of small seeds, which by far outnumbered large seeds in the samples. The majority of these appeared viable in cut tests.

The most abundant seed in the fecal samples we collected was *L. procera*, an uncommon species in the old-growth forest of BCI, which produces 15–20 mm large berrylike capsules containing 10–20 seeds, in Aug–Sep (Croat 1978). These berrylike fruits are rich in crude fat and energy content (Castellanos & Chanin 1996) and are known to be eaten by a variety of birds and primates that collect the fruits directly from the trees (Snow 1971; Van Roosmalen *et al*. 1988; Castellanos & Chanin 1996; Wehncke *et al*. 2003). The tapirs producing the feces of this study must have fed on *L. procera* fruits that had fallen to the forest floor and deposited the seeds at latrines 79% intact.

As our study covered just 4 different latrines and possibly few individual tapirs, the abundances of various plant species we recorded in feces might not be representative of an unbiased sample. For example, *L. procera* appears to be overrepresented. This study did not address the relationship between abundance of seeds found in feces and the availability of the same species at the time of fecal sample collection. Year-round sampling in combination with large-scale inventory and monitoring of tree fruiting phenology would allow us to assess whether tapirs feed selectively, or rather on whatever is available.

Our results suggest that tapirs might act as dispersers not only of large-seeded plant species, as documented by previous studies (Bodmer 1991; Rodrigues *et al.* 1993; Fragoso 1997; Fragoso & Huffman 2000; Quiroga-Castro & Roldan 2001; Giombini *et al.* 2009; Tobler *et al*. 2010; O'Farrill *et al.* 2012), but also of plant species with relatively small seeds that are not presently considered 'tapir-dispersed'. To assess this role with more certainty, it would be worthwhile investigating the occurrence and viability rates of small seeds (<5 mm) in tapir dung at other locations and in all seasons. In addition, although cut tests provide acceptable estimates of viability (Terry *et al.* 2003; as in Fragoso & Huffman 2000, Daws *et al.* 2002 and Strong & Fragoso 2006), germination tests are recommended to determine viability with greater certainty.

Ultimately, the effectiveness of tapirs as dispersers of small seeds will also depend on the fate of the vi-

Table 1 Seeds found within 72 tapir feces of Central American tapir (*Tapirus bairdii*) on Barro Colorado Island, Panama

Species (family)	Life form	Seed size (length), size class[†]	Fresh mass (g)[‡]	Number	Number per feces (mean ± SD)	Number intact	Estimated viability (%)	Frequency (% of feces)[§]
Ficus sp. (Moraceae)	Tree/midstory	1 mm, S	NA	882	12.3 (± 21.5)	75	9	59.7
Casearia sp. (Flacourtiaceae)	Tree	1 mm, S	NA	6	0.08 (± 0.3)	2	33	6.9
Unknown sp_1		1 mm, S	NA	23	0.3 (± 0.8)	1	4	13.9
Unknown sp_2		1 mm, S	NA	100	1.4 (± 3.3)	3	3	19.4
Unknown sp_3		1 mm, S	NA	4	0.05 (± 0.2)	2	50	5.6
Unknown sp_4		2 mm, S	NA	32	0.4 (± 1.0)	25	78	25.0
Unknown sp_5		2 mm, S	NA	22	0.3 (± 0.7)	4	18	20.8
Laetia procera (Flacourtiaceae)	Tree	2–3 mm, S	0.007	6795	94.4 (± 195.2)	5336	79	27.8
Psychotria sp. (Rubiaceae)	Shrub	5 mm, M	0.01–0.03	176	2.4 (± 5.4)	0	0	25.0
Meibomia axillaris var. *Acutifolia* (Fabaceae)	Herbaceous	5 mm, M	NA	4	0.05 (± 0.2)	0	0	5.6
Unknown sp_6		5 mm, M	NA	1	0.01 (± 0.1)	0	0	1.4
Fabacea sp.	Shrub/tree	8 mm, M	NA	6	0.08 (± 0.3)	6	100	8.3
Cayaponia sp. (Cucurbitaceae)		8 mm, M	NA	3	0.04 (± 0.2)	0	0	4.2
Unknown sp_7		15 mm, M	NA	3	0.04 (± 0.2)	2	67	4.2
Spondias mombin (Anacardiaceae)	Tree	20–23 mm, L	1.9	108	1.5 (± 2.7)	102	94	27.8
Astrocaryum standleyanum (Arecaceae)	Tree (palm)	30 mm, L	9.7	1	0.01 (± 0.1)	1	100	1.4
Total				8166	113.4 (± 195.2)	5559	68.1	
Mean							39.7 (± 40.4)[¶]	

[†]Seed sizes are approximate. Size class (length): S < 5 mm, M = 5–20 mm, L > 20 mm. [‡]Fresh mass of *Laetia procera* obtained from Guariguata (2000); all other fresh mass records provided by J. Wright (pers. comm.). [§]Frequency = percentage of total fecal samples that contained the species. [¶]Mean estimated viability (%) across species. NA, not available.

able seeds in the feces in relation to the habitat. Tapirs are known to deposit feces in both dry and flooded sites (Fragoso & Huffman 2000; Tobler *et al.* 2010). For flooded sites, tapir-mediated dispersal might be especially effective for plant species associated with wet habitats (Salas & Fuller 1996), to which tapirs may provide directed dispersal (Wenny 2001). Dispersal by tapirs might also be effective for other small-seeded plant species when combined with secondary seed dispersal by dung beetles that move and bury dung in the soil (e.g. seeds in howler monkey feces [Estrada & Coates-Estrada 1991]).

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