Journal of Tropical Ecology (2000) 16:369–385. With 4 figures

Seed-dispersal and seedling recruitment patterns by the last Neotropical megafaunal element in Amazonia, the tapir

JOSÉ M. V. FRAGOSO[1] *and* JEAN M. HUFFMAN[2]

Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL 32611, USA

(Accepted 1st December 1999)

ABSTRACT. Tapirs (Tapiridae) are the last representatives of the Pleistocene megafauna of South and Central America. How they affect the ecology of plants was examined by studying the diversity, abundance, and condition of seeds defecatedd by the lowland tapir (*Tapirus terrestris*) in Amazonian Brazil. Additionally, the spatio-temporal pattern of the seed-rain and seed-shadows generated by tapirs was recorded. Three hundred and fifty-six tapir faeces were examined. Eleven per cent were found in water (n = 41), while 88% were located on dry land (n = 315). Of those found on dry land, 84% were located at sites that flood seasonally, while 14% of the total were encountered at forest sites that do not flood. In 127 faeces checked in the laboratory over 12 906 seeds of at least 39 species were found. Seed viability ranged from 65% for *Maximiliana maripa* to 98% for *Enterolobium schomburgkii*. Of nine seed species planted in the laboratory, seven germinated within 4 wk, with one species achieving an 89% germination rate. For many species recruitment to the seedling stage was also high under natural conditions, with 13 plant species occurring as seedlings in older faeces. Tapir generated seed-rain occurred throughout the year, with seeds defecated in all months. Two temporal patterns in species seed rain occurred: (1) contiguous monthly occurrence with peaks in abundance, and (2) discontinuous occurrence (time clumped) with small (a few months) to large (many months to more than a year) temporal gaps. The highest diversity of seeds appeared in April, at the end of the dry season. As the last of the Pleistocene megafauna of the region, tapirs may have particular importance as dispersers of large seeds and generators of unique seed dispersion patterns.

KEY WORDS: megafauna, palms, seed dispersal, secondary dispersal, seed rain, seed shadows, tapir, *Tapirus terrestris*, tropical forest structure, Maraca Island

---

[1] Present address: Department of Biological Sciences, Florida Atlantic University, Boca Raton, FL, 33431-0991 USA. E-mail: jfragoso@fau.edu.

[2] Present address: Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, 70803 USA.

INTRODUCTION

Seed dispersal processes play a critical role in structuring plant communities (Connell 1971, Estrada & Fleming 1986, Fleming & Estrada 1993, Fragoso 1997, Hubbell 1979, Janzen 1970). In the Neotropics, research has focused on how small-bodied vertebrates, and invertebrates, affect seeds and seedlings, under the assumption that these were the key structuring processes for this region (see Estrada & Fleming 1986, Fleming & Estrada 1993, Wheelwright 1988). Little attention has been paid to how medium (> 10 kg) and large-bodied (> 50 kg) vertebrates affect ecological processes, even though Janzen & Martin (1982) had suggested that megafaunal species extant (but now extinct) in Central America during the Pleistocene, may have maintained unique biological relationships with the plants they fed upon. This hypothesis has been supported by work with 'megaherbivores' in African savannas, which indicates that large mammals maintain unique ecological relationships with savanna plants and generate unique patterns in vegetation distributions (e.g. Dublin 1995, Owen-Smith 1992, Sinclair 1995). However, not all of the neotropical megafauna went extinct. Tapirs survived the Pleistocene and, at 150–300 kg, are the largest native terrestrial vertebrates in the neotropics (Eisenberg 1981, 1989). There are three neotropical species, the Baird's or Central American tapir (*Tapirus bairdii* Gill 1865), the mountain tapir (*Tapirus pinchaque* Roulin 1829), and the Brazilian or lowland tapir (*Tapirus terrestris* Linnaeus 1758). All are considered to be browsers and frugivores.

There is debate as to whether tapirs enhance or reduce the fitness of their food plants. Janzen (1981) demonstrated that a domesticated Central American tapir destroyed 78% of *Enterolobium cyclocarpum*, and 100 % of *Cassia grandis* seeds that it ingested and concluded that tapirs may be trivial dispersal agents. Similarly, Salas & Fuller (1996) described the lowland tapir as mainly a seed predator because they destroyed the seeds of some species. Janzen (1981) also described the Central American tapir as defaecating exclusively in water or dry areas that flood seasonally. Salas & Fuller (1996) following Janzen's (1981, 1982) and Fragoso's (1991a, b) studies noted that the lowland tapir also defecatedd exclusively in flooded or seasonally flooded areas. Salas & Fuller (1996) along with Janzen (1981, 1982) argued that by defaecating viable seeds in these unsafe/unsuitable sites (*sensu* Harper 1977) tapirs played limited roles as seed dispersers for upland plant species. However, Janzen (1982) also stated that their importance as a seed disperser will be contingent on the plant species in question.

In contrast, Bodmer (1990, 1991), Fragoso (1994, 1997) and Rodrigues *et al.* (1993) found high rates of seed survivorship for seeds defecated by lowland tapirs. Fragoso (1997) described lowland tapirs as defaecating large numbers of viable *Maximiliana maripa* seeds at upland forest sites (latrines), and found that latrines (defined as sites with many faeces) and their surrounding areas supported higher densities of *Maximiliana* seedlings and saplings than did areas around parent trees or far from latrines. Fragoso (1997) posited that as the largest bodied frugivore in the Neotropics, and the only one that ingests large numbers of very large seeds, and defecateds repeatedly at certain sites, tapirs play a critical role in the structuring of tropical forests.

The timing of seed fall can be critical to the germination and recruitment success for many plants (Harper 1977). Additionally, temporal patterns of recruitment can influence plant dispersion patterns (Harper 1977). To date, studies of tapir seed dispersal have produced only partial temporal descriptions of tapir generated seed rain. For example, Salas & Fuller (1996) presented data covering two dry seasons (5 mo), and although Naranjo (1995) covered both the dry and wet seasons, his work extended only for 9 mo.

We examined the fruit eating habits of the lowland tapir in an undisturbed, old-growth forest region of the Brazilian Amazon. We focused on their role as a disperser of large seeds by examining the diversity, abundance and viability of seeds defecated over 13 mo. We tested the hypothesis that tapirs are good dispersers by evaluating their interactions with seeds and fruits and determining the outcomes of these interactions. Specifically we tested the hypotheses that (1) tapirs defecated whole and viable seeds, (2) seeds are dispersed to 'safe sites', (3) defecated seeds germinate, and (4) seeds in faeces recruit into the seedling class. We also examined the temporal pattern of the tapir-generated seed rain to understand the temporal variation in plant recruitment patterns.

STUDY SITE

Maracá Island Ecological Reserve is a 110 000-ha riverine island formed by the splitting of the Urariquera River (Amazon drainage), in Roraima, Brazil (latitude 3° 22″ N, longitude 61°26″ W). The dominant vegetation is old-growth tropical evergreen lowland rain forest (Moskovits 1985), contiguous with the Amazon rain forest (Milliken & Ratter 1989). The eastern tip of Maracá sits at the junction of the Amazonian forest and the large Ruppuni–Roraima savannas. In addition to lowland tapirs, Maracá supports populations of collared peccaries (*Tayassu tajacu* Linnaeus 1758), white-lipped peccaries (*Tayassu pecari* Link 1795), pumas (*Puma concolor* Linnaeus 1771), jaguars (*Panthera onca* Linnaeus 1758) and other animals typical of Neotropical areas undisturbed by Europeans and their descendants (Fragoso 1998a, Moskovits 1985). There have been no permanent human settlements on the island within historical time (though an Indian village may have existed on Maracá in the mid 1800s, Proctor & Miller 1998), and it has never been logged. Approximately eight isolated families lived at different times along the riverbanks of the eastern tip until 1977. A low human population density near Maracá results in minimal illegal hunting on the outskirts of the Reserve along navigable areas of the river; hunters avoid the area around the research station. Annual rainfall ranges from 1750 – 2400 mm (Muskovits 1985). Based on long-term averages, the wet

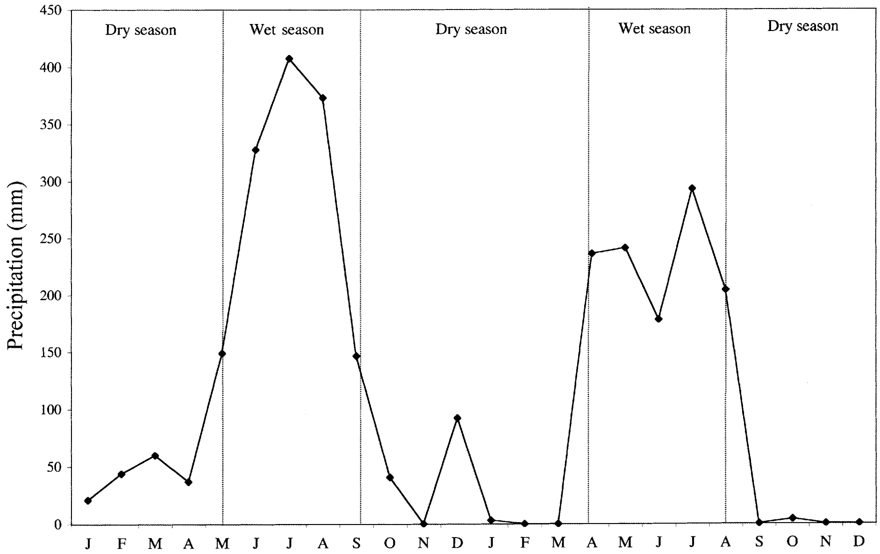

Figure 1. Monthly rainfall (mm) at eastern Maracá Island from January 1991 – December 1992.

season ($\geq$ 100 mm precipitation) is roughly April through August, with the greatest total rainfall usually occurring from May – July (Milliken & Ratter 1989). The dry season (< 100 mm precipitation) is November – March. During the study period, the dry season in eastern Maracá extended from October 1991 – March 1992, the wet season from April – August 1992, and the following dry season from September – December 1992 (Figure 1; precipitation recorded from a gauge in eastern Maracá).

Habitats

The specific study area included about 23 km^2 of eastern Maracá (Figure 2) accessed by 60 km of trails laid out in a grid pattern. We prepared a vegetation map of the region using a black and white aerial photograph and confirming vegetation patterns by a combination of aerial 'ground truthing' (during 150 h of low flight over the region in an ultralight aeroplane) and true ground truthing (conducted when walking in search of faeces). The ARC/INFO geographical information system software (ESRI Inc. 1987) was used to digitize the map and calculate habitat coverage. Major habitats consisted of terra firme forest (non-flooded upland forest), seasonal streams and wetlands dominated by *Mauritia flexuosa* (hereafter referred to as *Mauritia*) palms, low and riverine forest, and seasonally wet marshes dominated by grasses and sedges (Figure 2).

Seventy per cent of the study area consisted of terra firme forest (16.3 km^2). Seasonal marsh (including seasonally flooded savannas) was the next most extensive vegetation type covering 16% (3.8 km^2) of the region. The remaining three types, *Mauritia* wetlands (5%, 1.1 km^2), low forest (4%, 0.8 km^2) and

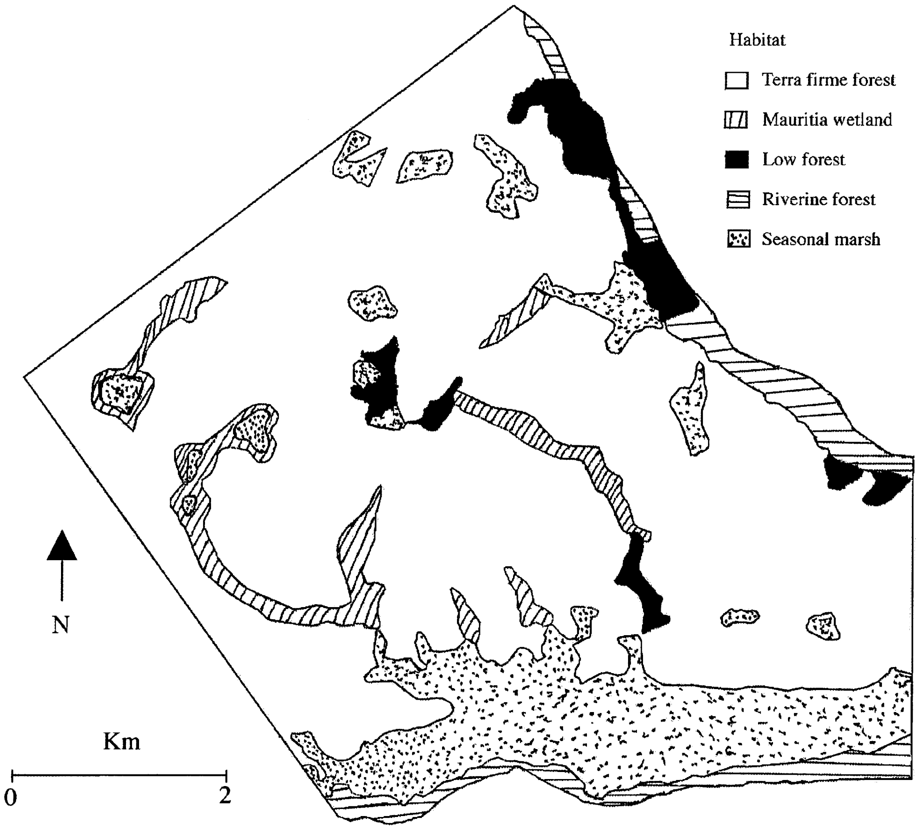

Figure 2. The study area and its habitats on Maracá Island Ecological Reserve, Roraima, Brazil.

riverine forest (5%, 1.2 km^2), covered less than 15% of the region. The riverine forest, found mostly on river levees, was rarely flooded; however, in exceptionally wet years most of this forest type floods when the river rises (Fragoso 1999).

METHODS

Tapir faeces were examined in the field opportunistically in September 1991 in western Maracá and systematically from October 1991 to November 1992, throughout the entire 23 km^2 area of eastern Maraca (Figure 2). We walked the entire trail system seven times each month in search of faeces. In addition, we haphazardly searched in the vegetation between and beyond trails (including water courses and upland areas) during the aforementioned trail-walks and during a concurrent study in the same region involving the ground-tracking of peccaries (Tayassuidae; see Fragoso 1998b). The tracking of peccaries occurred almost entirely off the trail system ensuring that intensive searches for faeces also occurred off the trail system. For each faeces, we noted location, position in or out of water, number of other faeces within 5 m, whether the site served as a latrine (presence of many faeces of different ages) and habitat type (terra firme forest, stream bed, pond or seasonally flooded wetland).

Only recently defecated, intact faeces (all boluses defecated at one time) less than 2–3 d old (very moist, reddish-brown in colour with intact boluses) were collected for laboratory analysis or searched for seeds in the field. We deviated from this method during the first week of March 1992, after a 2-mo absence from the site. During this period we sampled older dung piles defecatedd either in January or February 1992 (determination of month of defaecation was based on bolus condition, colour, moisture levels and presence of germinated seeds and seedlings).

All boluses of field-checked faeces were broken open by hand and seeds separated from faecal material. Seeds were classed as small ($\leq$ 5 mm in length), medium (5–14 mm), large (15–30 mm) or very large (31–80 mm). Faeces inspected in September 1991 were searched only for palm seeds. Those found in October and November 1991 were searched only for large seeds, with the incidental noting of some small seeds. From January 1992 onwards we noted the presence of all seeds regardless of size, and presence or absence of *Mauritia* exocarp scales. For field examined faeces we counted the number of *Anacardium giganteum*, *Mangifera indica*, *Spondias mombin*, *Maximiliana maripa*, *Mauritia flexuosa* and *Astrocaryum* seeds and noted occurrence in the hundreds or thousands for other species.

To obtain a more exact measurement of the diversity and abundance of very small seeds and seed fragments ($>$ 2.5 mm length) we examined 5 – 23 faeces per month in a laboratory. Entire faeces were collected while fresh, one per plastic bag from known upland and seasonally inundated latrines. They were air-dried for 2–5 d and the entire faeces filtered through a 5-mm^2 mesh screen. We noted the diversity and number of seeds of all types per faeces. Seeds were identified to as precise a taxonomic level as possible, using three sources: (1) van Roosmalen (1985), (2) a report on the vegetation of Maracá (Milliken & Ratter 1989) and a corresponding fruit and seed collection maintained at the Maracá research station, and (3) identifications by E. S. Silva, a botanist at the Roraima Museum.

We examined seed viability by opening and checking the endosperm of a subsample of *Spondias mombin*, *Maximiliana maripa*, *Enterolobium schomburgkii*, *Pradosia surinamensis* and *Mangifera indica* seeds. Conspecific seeds originated from a number of faeces. For a seed to be considered viable it had to have a minimum of one intact and firm endosperm. We also noted viability by the presence of germinated seeds and seedlings in older faeces. For some species we tested viability by planting seeds in a controlled laboratory situation in soil from the forest floor. Germination was recorded after 4 wk in May 1992. We also noted germination and recruitment success by recording the diversity and abundance of seedlings in older faeces from March – June 1992.

Table 1. The number of tapir faeces searched for seeds and fruit parts per month in the laboratory and field from September 1991 – November 1992, Maracá Island.

Month	Number faeces checked in laboratory	Number faeces checked in field	Total faeces
September	0	3	3
October	0	10	10
November	0	52	52
December	*	*	*
January†	13	16	29
February†	9	13	22
March	23	45	68
April	9	47	56
May	17	8	25
June	6	2	8
July	7	19	26
August	5	7	12
September	10	0	10
October	15	6	21
November	13	1	14
Total	127	229	356

*None collected.
†Information for these months derives from old to very old dung piles sampled in early March 1992.

Monthly per cent frequency of occurrence for each species was determined by dividing the number of occurrences per faeces for each species by the total number of samples for that month. Seed abundance per species was calculated for faeces analysed in the laboratory. Numerical or qualitative data on germination success for species planted during laboratory germination trials is presented. We also describe and analyse the temporal occurrence of the tapir generated seed rain.

RESULTS

Numbers of faeces and their locations

Three faeces were collected in September 1991, from western Maracá. During the focal sampling period (October 1991 – November 1991 and January – November 1992) we inspected an average of 27 faeces per month (SD = 19.5), finding 10 or more faeces in all but one month (Table 1). All but six faeces were found at latrines. Two hundred and twenty-nine faeces were examined in the field and 127 in the laboratory (total n = 356). Eighty-eight per cent of the faeces were defecatedd in areas that were dry at the time of sampling (n = 315); 84% of these locations (n = 265) were in seasonally dry palm swamps, marshes and stream beds that would eventually flood, and 16% (n = 50) were found in upland forest around the base of 13 emergent tauri trees (*Couratari multiflora* (J.E. Smith) Eyma); the latter sites were all latrines (Table 2).

Plant species diversity, growth forms, communities and faeces

We found viable seeds of 39 plant species in faeces. Twenty-six species were identified to at least the family level (Table 3). These were distributed over 12

Table 2. The number of tapir faeces found in and out of water in four habitats, Maracá, Island.

Habitat	Found in water	Not found in water	Total
Terra firme forest (dry year-round)	0	50	50
Palm swamp (seasonally flooded)	12	164	176
Marsh (seasonally flooded)	19	79	98
Stream bed (seasonally flooded)	10	22	32
Total	41	315	356

families, with the greatest number of species occurring in the Fabaceae, followed by the Araceae and Anacardiaceae. Fourteen types/species remained unidentified. Though we list only one unknown grass species this category may include up to five species. Most fruits originated from large forest trees (Table 3). At least seven of the 14 most abundantly encountered seed-species were from terra firme forest trees (Table 3). Adults trees of other species were common in either forest gaps, seasonal wetlands or forest/savanna edges (Milliken & Ratter 1989).

Seed abundance

We found 183 *Anacardium*, 33 *Mangifera*, 1788 *Spondias*, three *Mauritia*, and two *Astrocaryum* seeds in the 356 field and laboratory checked faeces. For this data-set *Maximiliana* with 4838 seeds in all faeces was the most abundant large to very large seed (31–80 mm in length). In the 127 faeces examined in the laboratory tapirs dispersed at least 12 906 (mean = 101.6, SD = 378.3) apparently viable seeds. This figure does not include the small seeds that were uncounted and classed instead as occurring in the hundreds or thousands per faeces (e.g. two species of Moraceae and a *Passiflora* species; Table 3). We found few (n = 218) *Maximiliana* seeds in laboratory-checked faeces because these were collected after the fruiting period (see Fragoso 1998a). For the 127 faeces sampled, *Enterolobium schomburgki* seeds were the most abundant of the medium to large-seeded species, followed by *Cassia moschata* and *Spondias* (Table 3). *Mauritia* palm fruit scales attained the highest frequency of occurrence (70%) of any fruit species (although we found only three seeds in faeces, one in the laboratory and two in the field), while *Cassia* was the most frequently encountered seed (27 %), followed by *Maximiliana* (25%), *Enterolobium* (22%), and *Spondias* (12%; Table 3). Other species occurred at frequencies of 10% or less.

Seasonality of fruit consumption and seed dispersal

The number of species consumed and dispersed varied through the study period. The greatest diversity of species (n = 14) was encountered in April, at the beginning of the wet season (Figures 3 & 4). Species diversity was also high in March (dry season), May (wet season) and July (mid-wet season). Seed diversity was lowest in November 1992 but did not drop below four species in any month checked for all fruit species (Figures 3 & 4).

Monthly patterns and peaks in occurrence varied between species (Figures

Table 3. The diversity and frequency of occurrence of plant species with seeds dispersed by the lowland tapir, plant community of origin, growth form and seed size. Seed size categories: small ≥ 5 mm in length; medium 5–14 mm; large 15–30 mm and very large 31–80 mm.

Family Genus, species	Habitat*	Growth form†	Seed size‡	Frequency of occurrence; field & laboratory faeces (n = 356)	Number of seeds in field and laboratory checked faeces (n = 356)	Number of seeds in laboratory faeces (n = 127)
Anacardiaceae						
Anacardium giganteum Hancock	F	LT	L, VL	6	183	50
Mangifera indica L.	F	LT	VL	2	33	26
Spondias mombin L.	F	LT	L	12	1788	1190
Araceae						
Maximiliana maripa (Correa de Serra) Drude	F	LP	VL	25	4838	218
Oenacarpus bacaba Mart.	F	LP	L	0.3		0
Mauritia flexuosa L.	FA	LP	VL	71[§]		1
Astrocaryum G.F.W. Mey. sp.	F	SP	L,VL	0.6		0
Bromeliaceae						
Aechmea rubiginosa Mez. or *Ananas ananassoides* (Baker) L.B. Smith	F	H	S	2		4
Burseraceae						
Tetragastris panamensis (Engl.) O. Kuntze	F	MT	M,L	2		3
Fabaceae						
Cassia moschata Kunth	F	MT	M	27		2057
Desmodium Desv. sp.		H	S	5		82
Enterolobium schomburgkii Benth.	F	LT	L	22		2099
Swartzia Schreb. sp.	F	MT	?	3		187
Unknown sp.			S	6		446
Moraceae						
Bagassa guianensis Aubl.	F	T	S	1		100s″
Ficus L. sp.	F	LT	S	7		1000s″
Unknown sp.	F	T	S	1		1000s″
Myrtaceae						
Psidium sp.	ME	ST	S	2		3773
Passifloraceae						
Passiflora L. sp.	FE	V	S	2		1000s″
Poaceae						
Unknown		G	S	10		314
Rubiaceae						
Genipa americana L.	FE,SF	SM	S	10		342
Duroia L.f. sp.	F, PS	SM	S	10		815
Unknown sp. nt			S	6		525
Sapindaceae						
Talisia Aubl. sp.	F	S or SM	M	1		16
Sapotaceae						
Pradosia surinamensis (Eyma) Penn.	F	T	L	3		21
Unknown sp. (14)	?	?	S to L			737
Total seeds						12,906

(14) = from morphology of seeds there were at least 14 unknown species

* F = forest; PS = palm swamp; SA = seasonally flooded areas; FE = forest edge; SF = secondary forest; ME = marsh edge.

† LT = large tree; MT = medium tree; SM = small tree; T = tree; LP = large palm; SM = small palm; S = shrub; H = herb; V = vine; G = grass.

‡ S = small; M = medium; L = large; VL = very large.

§ Seeds spat out, only fruit pulp is eaten.

″ Seeds very small and numerous but not counted, instead classed as occurring in the hundreds (100s) or thousands (1000s).

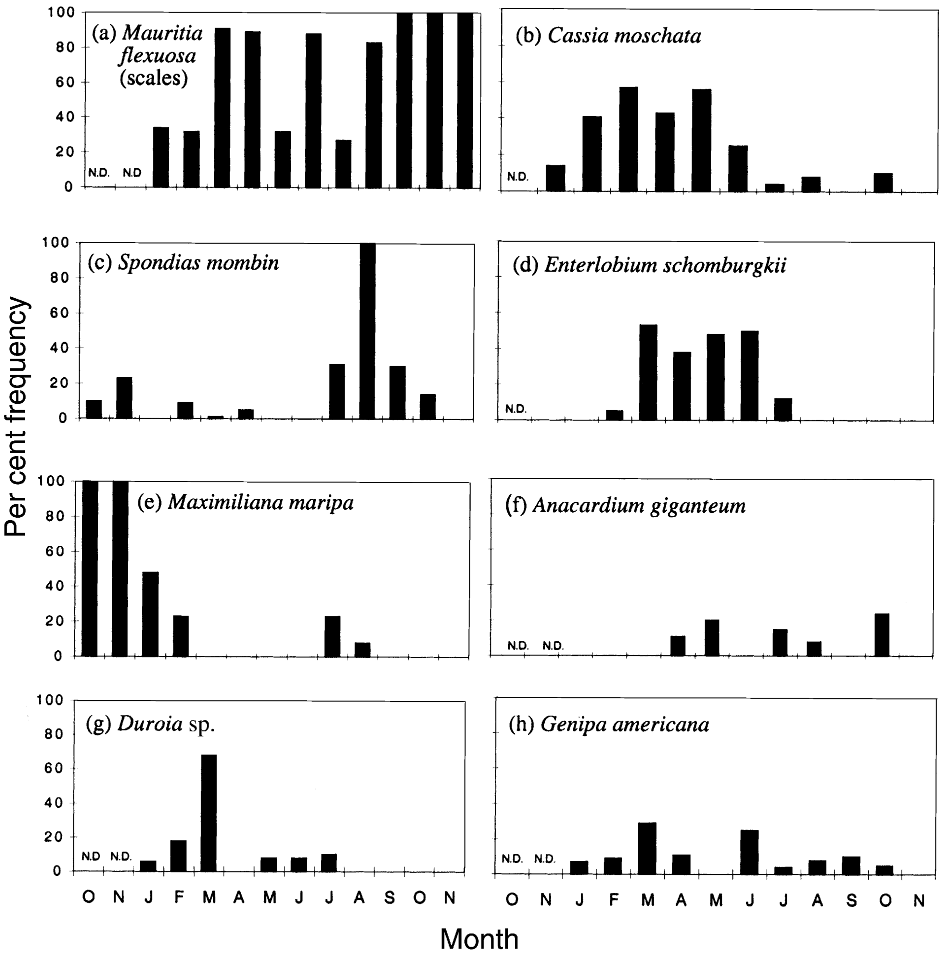

Figure 3. The per cent frequency of occurrence of the eight most commonly found seed species and, for *Mauritia flexuosa*, fruit scales in faeces (all samples) per month, from October 1991 – November 1992. No data was collected for December 1991 or for certain species for the months indicated N.D.

3 & 4). This is shown by examining the monthly frequency of occurrence for the most commonly encountered species, including the four most frequently encountered seeds and, for *Mauritia*, fruit scales (Figure 3).

Mauritia fruits were used in all months, but had an irregular pattern of occurrence (Figure 3a). Almost all faeces inspected from August – November contained fruit scales, while less than half of those searched in January, February, May and July contained scales. Frequency of *Mauritia* peaked from September – November, in the first few months of the dry season.

In contrast, *Maximiliana* seeds occurred discontinuously with large time gaps without seeds (Figure 3e). Faeces searched in October and November 1991 all contained seeds, while those from March – June did not. Seeds reappeared in faeces in July and August 1992, but at far lower frequencies than in 1991.

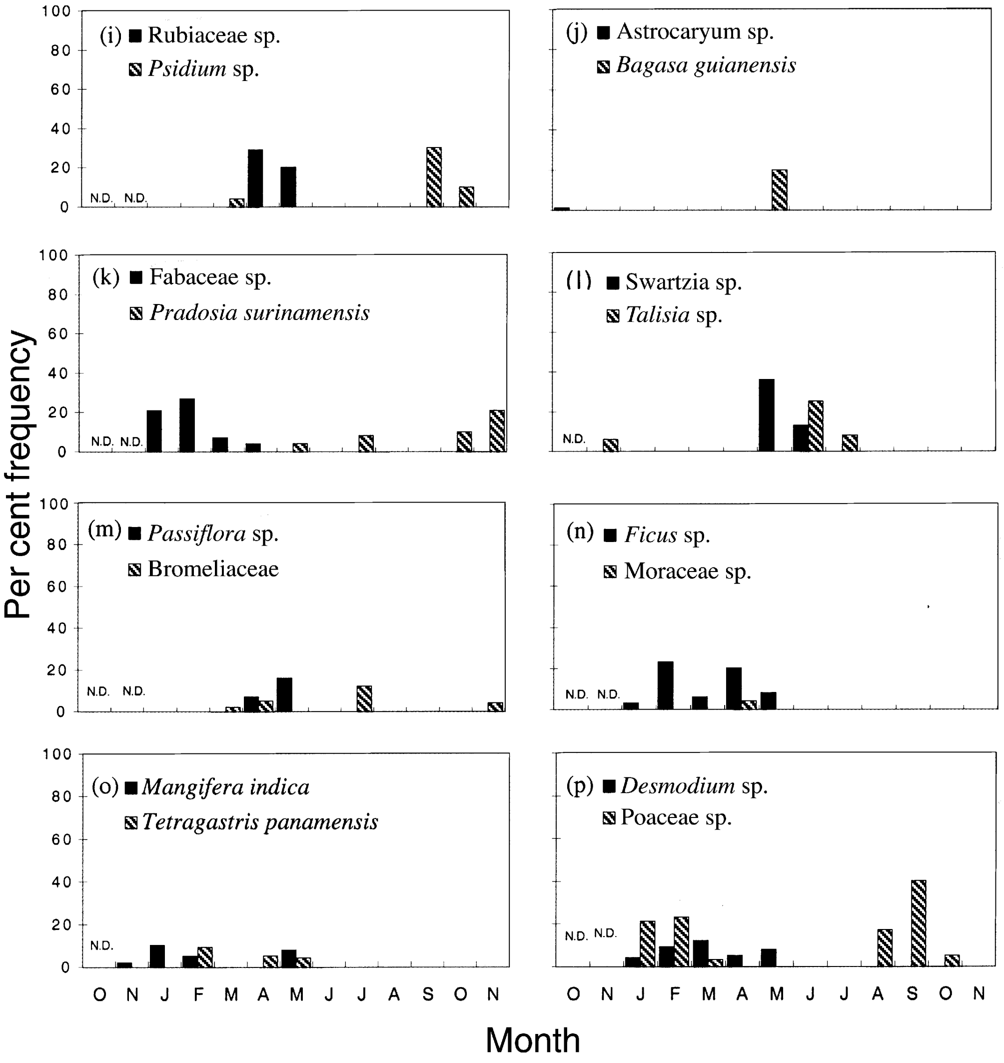

Figure 4. The per cent frequency of occurrence of 16 infrequently encountered seed species in faeces (all samples) per month, from October 1991 – November 1992. No data was collected for December 1991 or for certain species for the months indicated N.D.

Frequency of *Maximiliana* seeds peaked at the end of the wet and beginning of the dry season (October and November) in 1991 but not in 1992.

Enterolobium and *Cassia* had strong seasonal peaks in occurrence between March and June, a period that included the end of the dry season blending into the wet season (Figures 3b & 3d). However, *Enterolobium* seeds were not found from November 1991 – January 1992 (end of the wet season and into the dry season) or from August – November 1992 (dry season). This temporal pattern of occurrence differed from that of *Cassia* whose seeds were found in nine of the 11 mo sampled.

Table 4. The number of viable seeds for species whose seeds were opened to determine endosperm viability, Maracá Island

Species	Number of faeces sampled	Number of seeds opened	Mean (± SD) number per faeces	Number viable	Number dead
Spondias mombin	3	173	57.67 (± 69.79)	124	49
Maximiliana maripa	5	308	61.60 (± 52.46)	201	107
Enterolobium schomburgkii	4	432	108.50 (± 143.80)	425	7
Pradosia surinamensis	3	21	6.33 (± 2.52)	14	5
Mangifera indica	4	29	7.20 (± 7.93)	23	6

Like *Cassia* seeds and *Mauritia* scales, *Spondias* seeds were found in a few faeces almost throughout the sampling period, although rarely at high frequency levels (Figure 3c). *Spondias* occurred most frequently in August 1992, near the end of the wet season.

Seed germination and recruitment to seedling class

For the subset of species whose seeds were opened to confirm viability, survivorship was high; 72% of *Spondias*, 65% of *Maximiliana*, 98% of *Enterolobium*, 67% of *Pradosia* and 79% of *Mangifera* seeds contained viable endosperm (Table 4). Seeds of seven out of nine species (*Anacardium*, *Tetragastris panamensis*, *Enterolobium*, *Ficus* sp., *Passiflora* sp., *Genipa americana* and *Duroia* sp.) germinated under laboratory conditions. Seeds of *Spondias* and *Bagassa guianensis* did not germinate but this may have been related to the short duration of the experiment (4 wk). Germination frequency for two species were 89% (n = 319/360) for *Duroia*, and 0.04% for *Genipa* (n = 2/49). Sprouting seeds of *Duroia* were also frequently observed in collected samples with 263 counted in one faeces (Table 5).

Thirteen types of seedlings were observed growing in older faeces (Table 5).

Table 5. The species diversity and abundance of seedlings observed in field-checked tapir faeces in eastern Maracá.

Genus, species	Number of faeces with seedlings present	Number of faeces where seedlings were counted	Month of counts	Total number of seedlings	Mean number of seedlings per faeces (± SD)
Enterolobium schomburgkii	25	10	March, May	119	11.9 (8.9)
Anacardium giganteum	8	2	May, June	12	6 (7.07)
Desmodium	2	2	May	4	2 (1.41)
Duroia	8	1	May	263	
Leguminosae	5	1	May, June	27	
Spondias mombin	1	0	May		
Aechmea rubiginosa or *Ananas ananassoides*	6	0	May, June		
Tetragastris panamensis	3	0	May		
Cassia moschata	11	0	April, May		
Rubiaceae	12	0	May, June		
Ficus	6	0	May		
Passiflora	2	0	June		
Genipa americana	4	0	April, May		

Although seedlings were not systematically counted, they were common, with 119 *Enterolobium* seedlings counted in 10 faeces and 12 *Anacardium* seedlings found in two faeces.

DISCUSSION

As the only extant megafaunal fruit eater in the Neotropics tapirs may be the most important seed disperser in the ecosystem due to their maintenance of a set of interactions unique to large-bodied vertebrates and fruits/seeds. Tapirs created a large-scale (several km; Fragoso 1997), punctuated seed shadow, with thousands of seeds defecatedd at single sites (latrines). They are the only members of the terrestrial frugivore guild to disperse seeds in this manner (Fragoso 1997), although howler monkeys and spider monkeys may also defecated small, medium and some large seeds at latrines (Castellanos & Chanin 1996, Julliot 1997). Rodents, birds and smaller primates, the other members of the Neotropical seed-dispersing guild that move large and very large seeds, scatterhoard them as single units to sites separated by 1–100 m (e.g. Forget 1992, Hallwachs 1986, Izawa 1979, Munn 1988), or scatterhoard seeds in small numbers (e.g. Forget 1994, 1996; Hallwachs 1986). They do not disperse thousands of seeds long distances to single sites as do tapirs.

While some studies have described tapirs as ineffective seed dispersers, because they defecated in water or sites that flood seasonally (e.g. Janzen 1981, 1982; Salas & Fuller 1996), at Maracá they also defecatedd at upland sites that do not flood. Whether sites are 'safe' or 'unsafe' for seeds depends on the plant species under consideration, but even this categorization can be inappropriate because rodents secondarily dispersed seeds to upland sites from faeces located in seasonally dry wetland areas (see below). For species that can inhabit seasonally flooded areas, such as *Spondias*, a seasonally inundated site is a safe site. *Mauritia* palms also occur exclusively in seasonally flooded areas (Uhl & Dransfield 1987), indicating that seeds recruit into older age classes only within seasonally flooded zones. The presence of *Mauritia* fruit scales in almost all faeces but the near total absence of seeds indicates that tapirs spat out most of the seeds. Bodmer (1990) also found that tapirs spit out *Mauritia* seeds, almost exclusively within *Mauritia* swamps. The occasional dispersal of a few seeds (via tapir guts) to latrines in wetlands uninhabited by *Mauritia* may lead to the colonization of new areas.

Some studies have shown that high seed densities attract seed predators (e.g. Connell 1971, Janzen 1970) but this did not appear to occur with seeds defecatedd by tapirs. Survival was high for most species regardless of time of collection from faeces; for example, more than 60% of the seeds of the five species checked for viability were alive. Fragoso (1997) working concurrently at Maracá, found tapir dispersed *Maximiliana* seeds experienced higher rates of survivorship than seeds remaining near parent trees, or dispersed by rodents, primates and deer. High seed survivorship at tapir latrines suggests that there will be high intra- and interspecific competition in the seedling and sapling stages, due to a high number of seeds germinating in a small space. While this may be true to some degree, at Maracá rodents extended tapir generated seed-shadows by secondarily dispersing seeds away from latrines (Fragoso 1994, 1997). This would decrease competition between seedlings for space since rodents carry one to a few seeds at a time and deposit them at scattered sites (Forget 1994, Hallwachs 1986, Silvius 1999). Thus, while hypothetically the concentration of seeds at latrines could lead to intense intra- and interspecific competition for space between seedlings, other factors interact with seeds at latrines to reduce competition.

Tapirs can function as seed dispersers, as shown by the many seeds of several species that survived passage through the gut of lowland tapirs. These seeds germinated, and recruited into seedlings. Since we found few seed fragments in faeces, it appears that tapirs do not mechanically destroy the larger seeds surveyed here. Tapirs have also been indicated as seed dispersers in a number of other studies. Naranjo (1995) found intact seeds of eight species in faeces of the Central American tapir. Janzen (1982) found the same species in Costa Rica defecatedd viable seeds of 10 species. Williams (1984) found the Central American tapir defecatedd live seeds of 15 out of 20 species. Rodrigues *et al.* (1993) also found seeds of two species germinating in faeces of lowland tapirs in north-eastern Brazil. In another study with the lowland tapir and *Maximiliana*, high seed survivorship translated into higher rates of seedling and sapling survivorship (Fragoso 1997). This suggests that tapirs serve as an ecosystem level process, influencing the population and community dynamics of many tropical plants.

Salas & Fuller (1996) however, argued that tapirs may not be important seed dispersers for nine out of 33 species that they found in tapir faeces, because adult trees of these species were located in upland terra firme sites, while faeces occurred in water bodies. They did not base their conclusion on the viability of defecatedd seeds, thus excluding the possibility that faeces and seeds may be placed in upland sites and/or secondarily dispersed by rodents. In fact, they searched for faeces almost exclusively in and along water bodies, and only during the dry season.

Although tapirs dispersed seeds throughout the year there was temporal patterning in the tapir generated seed rain. Some species occurred in all months, some in only a few months and others appeared to skip years. The punctuated pattern in the tapir-generated seed rain per species reflected forest wide patterns in fruiting phenology; for example, *Mauritia* and *Maximiliana* palms produce fruit in different seasons and exhibit different mast styles (Fragoso 1998a). *Mauritia* drops relatively small quantities of fruit over a long period of time (Fragoso 1998a, Moskovits 1985). This fruit ripening pattern is reflected in the occurrence of *Mauritia* fruits scales in faeces year round, with the 4 mo of lowest occurrence corresponding to the 4 mo with the lowest availability of *Mauritia* fruit (this study and Fragoso 1998a). *Maximiliana* exhibits an irregular yearly cycle in fruiting, occasionally skipping years (Fragoso 1998a; J. M. V. Fragoso, unpubl. data). In good years *Maximiliana* produces an extremely large fruit crop and drops fruit over a relatively short period of time (Fragoso 1998a). In 1991, *Maximiliana* on Maracá produced a large crop of fruit that was eaten in large quantities by tapirs (Fragoso 1997, 1998a). In 1992 very little fruit was produced, in fact only 1 in 50 monitored trees produced fruit (J. M. V. Fragoso, unpubl. data). Even so, some *Maximiliana* seeds were present in tapir dung, indicating that tapirs sought out the few fruiting *Maximiliana* palms. Thus, in this region fruiting (per species) follows a punctuated pattern over time, with some species fruiting in every suitable season, some every 2 y and some with no discernible yearly pattern (Fragoso 1998a, Milliken & Ratter 1989, Moskovits 1985, Nuñes 1992). This implies that tapir influenced seed germination and plant recruitment patterns are unpredictable over months and amongst years, an important consideration when trying to understand the mechanisms structuring tropical forests.

In conclusion, tapirs provide a bulk seed dispersal service for very large, large and medium seeds, a form of dispersal unavailable from any other animal. They do not always disperse seeds into wetlands, as has been suggested by other researchers, and when they do, this is not necessarily a selective disadvantage. Some species do well in wetlands and secondary dispersal by rodents removes seeds to higher ground. All three Neotropical tapir species are in decline throughout their ranges, and the form of dispersal they provide is therefore also an endangered phenomenon. Tapirs are the last representatives of the Neotropical Pleistocene megafauna in the tropical ecosystems of South and Central America. Immediate studies are needed of these species so that we may determine how their extirpation would affect the larger ecosystem.

ACKNOWLEDGEMENTS

We thank K. Silvius for her editorial help, critical reviews and moral support; T. Benshoff, R. de Silva, G. Schwinden and R. de Santos for field assistance; G. de Oliviera for his enlightened administration of Maracá Island Ecological Reserve; and IBAMA for permission to work at Maracá. We also thank C.S. Holling and L. Gunderson, for their logistic and moral support throughout the writing of the manuscript and Sarah Blanchard for helping with the Arc/Info program and mapping. This research was supported by the Wildlife Conservation Society of the New York Zoological Society, World Wildlife Fund-USA, the Scott Neotropical Fund and the Royal Geographical Society.

LITERATURE CITED

BODMER, R. E. 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *Journal of Zoology (London)* 222:121–128.

BODMER, R. E. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23:255–261.

CASTELLANOS, H. G. & CHANIN, P. 1996. Seasonal differences in food choice and patch preference of long-haired spider monkeys (*Ateles belzebuth*). Pp. 451–466 in Norconk, M. A., Rosenberger, A. L. & Garber, P. A. (eds). *Adaptive radiations of Neotropical primates*. Plenum Press, New York.

CONNELL, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pp. 298–310 in de Boer, P. J. & Gradwell, G. R. (eds). *Dynamics of populations: proceedings of the advanced study institute on dynamics of numbers in populations*. Oosterbreak, Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.

DUBLIN, H. T. 1995. Vegetation dynamics in the Serengeti–Mara ecosystem: the role of elephants, fire, and other factors. Pp. 71–90 in Sinclair, A. R. E. & Arcese, P. (eds). *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, IL.

EISENBERG, J. F. 1981. *The mammalian radiations*. University of Chicago Press, Chicago, IL. 610 pp.

EISENBERG, J. F. 1989. *Mammals of the Neotropics: the northern Neotropics*. University of Chicago Press, Chicago, IL. 449 pp.

ESRI INC. 1987. *ARC/INFO users manual*. Environmental Systems Research Insititute Inc., Redlands, CA.

ESTRADA, A. & FLEMING, T. H. (eds). 1986. *Frugivores and seed dispersal*. Kluwer Academic Publishers, Boston. 329 pp.

FLEMING, T. H. & ESTRADA, A. (eds). 1993. Frugivory and seed dispersal: ecological and evolutionary aspects. *Vegetatio* 107/108.

FORGET, P. M. 1992. Seed removal and seed fate in *Gustavia superba* (Lecythidaceae). *Biotropica* 24:408–414.

FORGET, P. M. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpiiaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26:408–419.

FORGET, P. M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12:751–761.

FRAGOSO, J. M. V. 1991a. The effect of hunting on tapirs in Belize. Pp. 154–162 in Robinson, J. G. & Redford, K. H (eds). *Neotropical wildlife use and conservation*. University of Chicago Press, Chicago, IL.

FRAGOSO, J. M. V. 1991b. The effect of selective logging on Baird's tapir. Pp. 294–304 in Mares, M. A. & Schmidly, D. J. (eds). *Latin American mammalogy: history, biodiversity, and conservation*. University of Oklahoma Press, Norman, OK.

FRAGOSO, J. M. V. 1994. *Large mammals and the community dynamics of an Amazonian rain forest*. PhD thesis. University of Florida, Gainesville, FL. 210 pp.

FRAGOSO, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* 85:519–529.

FRAGOSO, J. M. V. 1998a. White–lipped peccaries and palms on the Ilha de Maracá. Pp. 151–164 in Milliken, W. & Ratter, J. A. (eds). *Maracá: the biodiversity and environment of an Amazonian rainforest*. J. Wiley & Sons, New York.

FRAGOSO, J. M. V. 1998b. Home range and movement patterns of white–lipped peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. *Biotropica* 30:458–469.

FRAGOSO, J. M. V. 1999. Habitat partitioning by rain forest peccary herds and species: behavioral causes and ecological implications. *Journal of Mammalogy* 80:993–1003.

HALLWACHS, W. 1986. Agoutis (*Dasyprocta punctata*): the inheritors of guapinol (*Hymenea courbaril*: Leguminosae). Pp. 285–304 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Kluwer Academic Publishers, Boston.

HARPER, J.L. 1977. *Population biology of plants*. Academic Press, New York. 892 pp.

HUBBELL, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203:1299–1309.

IZAWA, K. 1979. Foods and feeding behavior of wild black-capped capuchins (*Cebus apella*). *Primates* 20:57–76.

JANZEN, D. H. 1970. Herbivores and the number of tree species in a tropical forest. *American Naturalist* 104:501–528.

JANZEN, D. H. 1981. Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* 13:59–63.

JANZEN, D.H. 1982. Seeds in tapir dung in Santa Rosa National Park, Costa Rica. *Brenesia* 19/20:129–135.

JANZEN, D. H. & MARTIN, P. S. 1982. Neotropical anachronisms: the fruits the gomphotheres ate. *Science* 215:19–27.

JULLIOT, C. 1997. Impact of seed dispersal of red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *Journal of Ecology* 85:431–440.

MILLIKEN, W. & RATTER, J. A. 1989. *The vegetation of the Ilha de Maracá: first report of the vegetation survey of the Maracá Rain Forest Project*. Royal Botanical Garden, Edinburgh. 96 pp.

MOSKOVITS, D. K. 1985. *The behavior and ecology of two Amazonian tortoises,* Geochelone carbonaria *and* Geochelone denticulata, *in northwestern Brazil*. PhD thesis, University of Chicago, Chicago, IL. 328 pp.

MUNN, C. A. 1988. Macaw biology in Manu National Park, Peru. *Parrotletter* 1:18–21.

NARANJO, E. J. 1995. Habitos de alimentacion del tapir (*Tapirus bairdii*) en un bosque tropical humedo de Costa Rica. *Vida Silvestre Neotropical* 4:32–37.

NUÑES, A. P. 1992. *Uso do habitat, comportamento alimentar e organização social de* Ateles belzebuth belzebuth *(Primates: Cebidae)*. MSc thesis, Universidade Federal do Pará, Belém, Pará, Brazil. 194 pp.

OWEN-SMITH, R. N. 1992. *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, New York. 369 pp.

PROCTOR, J. & R. P. MILLER. 1998. Human occupation on the Ilha de Maracá: preliminary notes. Pp. 431–442 in Milliken, W. & Ratter, J. (eds). *Maracá: ecology and diversity of an Amazonian rainforest*. J. Wiley & Sons, New York.

RODRIGUES, M., OLMOS, F. & GALETTI, M. 1993. Seed dispersal by tapir in southeastern Brazil. *Mammalia* 57:460–461.

SALAS, L.A. & FULLER, T.K. 1996. Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela. *Canadian Journal of Zoology* 74:1444–1451.

SILVIUS, K. S. 1999. *Interactions among* Attalea *palms, bruchid beetles, and neotropical fruit-eating mammals: implications for the evolution of frugivory*. PhD thesis, University of Florida. 298 pp.

SINCLAIR, A. R. E. 1995. Equilibria in plant–herbivore interactions. Pp. 91–114 in Sinclair, A. R. E. & Arcese, P. (eds). *Serengeti II: dynamics, management, and conservation of an ecosystem*. University of Chicago Press, Chicago, IL.

UHL, N. W. & DRANSFIELD, J. 1987. *Genera Palmarum*. Allen Press, Lawrence, KS. 610 pp.

VAN ROOSMALEN, M. G. M. 1985. *Fruits of the Guianan flora*. Institute of Systematic Botany, Utrecht University, Netherlands. 483 pp.

WHEELWRIGHT, N. T. 1988. Fruit-eating birds and bird-dispersed plants in the tropics and temperate zone. *Trends in Ecology and Evolution* 3:270–274.

WILLIAMS, K. D. 1984. *The Central American tapir* (Tapirus bairdii) *in northwestern Costa Rica*. PhD thesis, Michigan State University. 109 pp.