

## Frugivory and Seed Dispersal by the Lowland Tapir (*Tapirus terrestris*) in Southeast Brazil<sup>1</sup>

*Key words:* Atlantic Forest; frugivory; seed dispersal; Syagrus; Tapirus.

SEED DISPERSAL REPRESENTS THE LAST PHASE of a plant's reproductive cycle, and is therefore critical for regeneration (Janzen 1970, Chapman & Chapman 1995). Birds and mammals are the most important vertebrate seed dispersers in the Neotropics (Jordano 2001). This relationship between vertebrates and fruiting plants is so important that in some tropical areas *ca* 90 percent of tree species are dispersed by vertebrates (Opler *et al.* 1980, Galetti 1996, Jordano 2001). Among mammalian dispersers, ungulates are particularly important because they can distribute great quantities of seeds (Janzen 1981, Bodmer 1991, Miller 1996, Olmos 1997, Fragoso & Huffman 2000) and move them long distances (Fragoso 1997).

Tapirs (*Tapirus* spp., Perissodactyla, Tapiridae) are the only remaining species of Pleistocene megafauna in South and Central America (Simpson 1980, Eisenberg 1981). Studies on frugivory and seed dispersal by tapirs have been conducted at several Neotropical sites (Bodmer 1990, Rodrigues *et al.* 1993, Salas & Fuller 1996, Fragoso 1997, Olmos 1997, Fragoso & Huffman 2000, Henry *et al.* 2000) but are lacking from semi-deciduous forests of South America.

Tapirs disperse large-seeded species, especially palms (Bodmer 1990, 1991; Fragoso 1997); yet they may not be efficient seed dispersers (*sensu* Schupp 1993). In fact, they digest many seeds and generally defecate in areas not favorable for the establishment of seedlings (*e.g.*, water channels; Janzen 1981a, Salas & Fuller 1996). In addition, they typically defecate large quantities of seeds in a single place, thus causing high competition among seedlings (Howe 1990) or facilitating location by seed predators (Chapman 1989, Fragoso 1997).

In the semi-deciduous forests of São Paulo, Brazil, few areas support viable tapir populations (Morro do Diabo State Park and Ecological Station of Caetetus; Cullen *et al.* 2000). Although not considered threatened, the lowland tapir *Tapirus terrestris* is vulnerable to hunting and habitat fragmentation and often faces local extinction in small or overhunted forest patches (Chiarello 1999, Cullen *et al.* 2000). For this reason, it is essential to understand the role of tapirs as seed dispersers (especially for large-seeded species) in maintaining plant species diversity (Fragoso & Huffman 2000).

We evaluated the use of fruits by the lowland tapir and its role as a seed disperser in a semi-deciduous forest fragment in southeast Brazil.

The Estação Ecológica de Caetetus (E. E. Caetetus; 22°27'S, 49°43'W) is a 2,100 ha forest fragment located between Gália and Alvinlândia, São Paulo, Brazil. This area is considered a semi-deciduous tropical forest and was once an extension of the coastal Atlantic Forest. During the dry season there is a partial leaf fall in some tree species (Leitão-Filho & Morellato 1997). Annual rainfall is *ca* 1480 mm.

Vegetation in the area constitutes a mosaic of at least four different habitats: primary forest (49%); second growth (edge and bamboo; 13%); palmito (*Euterpe edulis*) stands (1%); and swamp areas (2%; Keuroghlian, pers. obs.). The arboreal flora is rich with Lauraceae, Myrtaceae, and Rubiaceae species (Durigan *et al.* 2000).

The non-volant, medium-sized mammal fauna is relatively well preserved. It includes three primates species (*Leontopithecus chrysopygus*, *Cebus apella*, and *Alouatta fusca*), two peccary species (*Tajacu pecari* and *T. tajacu*), tayra (*Eira barbara*), coati (*Nasua nasua*), paca (*Agouti paca*), and deer (*Mazama* spp.; Keuroghlian 1990).

The frugivorous diet of the tapirs was sampled by collecting feces encountered during mammal censuses in the area. Different trails, ranging from 1 to 8 km, were walked 13 days each month between January 1994 and April 1999. Fecal samples were found in numerous piles together (latrines), individually in dry areas, or near the forest edge and in streams.

Each fecal sample was collected, placed in a paper bag, numbered, and dried in an oven at 55°C.

<sup>1</sup> Received 10 October 2000; accepted 10 June 2001.

TABLE 1. Fruit species consumed by *Tapirus terrestris* at E. E. Caetetus and the number of seeds found.

Family	Species	Season	No. of seeds
Palmae	<i>Euterpe edulis</i>	dry	1
	<i>Syagrus romanzoffiana</i>	dry/wet	1002
	<i>S. oleracea</i>	wet	7
Leguminosae	<i>Copaifera langsdorffii</i>	wet	7
	<i>Enterolobium contortisiliquum</i>	dry	12
	<i>Inga</i> sp.	dry	6
Moraceae	<i>Ficus</i> sp.	wet	not counted
Myrtaceae	<i>Psidium guajava</i>	wet	2914
	<i>Mangifera indica</i>	wet	25

After the sample was dried, it was washed in a  $5 \times 5$  mm mesh sieve. Seeds were then separated, counted, weighed, and identified. Seed identification was facilitated by comparing them to seeds found in the Herbarium at Rio Claro's State University of São Paulo (UNESP).

We collected and analyzed 46 scat samples, 33 from the dry season and 13 from the wet season (Table 1). Twelve samples did not contain seeds; 10 of these samples were from the dry season and 2 were from the wet season.

We found nine seed species in tapir scat (Table 1), including two exotics (mango [*Mangifera indica*] and guava [*Psidium guajava*]) from orchards outside the reserve. The native species most commonly consumed (54% of samples; 25% of the seeds) was "jeriva," *Syagrus romanzoffiana*. During the dry season, 91 percent of seeds in tapir scats were of this species.

Tapirs consumed both large seeds, such as "guariroba" (*Syagrus oleracea*; 3–4 cm diam.) and mango, and small seeds such as figs (*Ficus* spp.). Tapirs are the only extant mammal that can disperse *S. oleracea* and *Enterolobium contortisiliquum* through the gut. Agoutis (*Dasyprocta* spp.) may disperse *S. oleracea* seeds by caching them in the soil, but they were absent in the study area (Cullen *et al.* 2000).

Numbers of seeds in the feces did not differ between the two seasons (Mann-Whitney test:  $U = 109.5$ ,  $P = 0.98$ ), even when the exotic species were removed ( $U = 76$ ,  $P = 0.690$ ; Table 2). The maximum number of seeds (>3 mm diam.) found in scats was 2103 (including 1992 guava seeds). Even seeds of large-seeded species were defecated with numerous other types of seeds (Table 1). For example, one defecation contained 647 *S. romanzoffiana* seeds and 7 *E. contortisiliquum* seeds. We did not estimate the number of *Ficus* seeds found in the scat samples because these seeds were too small to count effectively.

Compared to other studies on tapirs, we documented a low diversity of consumed fruit species (Table 2). The high frequency of palm fruits in the diet of lowland tapirs also has been observed in other regions. In our study area, tapirs dispersed *ca* 22 *S. romanzoffiana* seeds per scat. In the Amazon, *T. terrestris* disperses *ca* 78 "buriti" (*Maximiliana maripa*) seeds per scat pile (Fragoso 1997). Seeds of this species were recorded in 70 percent of all feces (Fragoso & Huffman 2000). Bodmer (1990) found a 76 percent occurrence of *Mauritia flexuosa* seeds in the Peruvian Amazon. *Syagrus romanzoffiana* palms were very abundant in our study site and produced many fruits during the dry season (Keuroghlian, pers. obs.). In addition, this palm fruit is rich in carbohydrates and is widely consumed by a great diversity

TABLE 2. Diet of three tapir species in different regions.

Tapir species	Site	No. of scats analyzed	No. of species eaten	Reference
<i>T. bairdii</i>	México	62	21**	Piñera & Aldán (1998)
<i>T. bairdii</i>	Costa Rica	136	10	Piñera (1995)
<i>T. pinchaque</i>	Colombia	37	86	Downer (1996)
<i>T. terrestris</i>	Peru (Amazon)	44**	6	Bodmer (1991)
<i>T. terrestris</i>	Venezuela	206	33	Salas & Fuller (1996)
<i>T. terrestris</i>	Brazil (Amazon)	356	39	Fragoso & Huffman (2000)
<i>T. terrestris</i>	Brazil	46	8	this study

\*\* Scat and stomach analysis.

of birds and mammals, including peccaries, pacas, capuchins, lion tamarins, coatis, tayras, foxes, and guans (Keuroghlian 1990; M. Galetti, pers. obs.).

The number of seeds dispersed by the lowland tapir in our site was higher ( $147 \pm 417$  seeds/scat;  $N = 32$  scats) than that found by Fragoso and Huffman (2000) in the Amazon ( $101.6 \pm 378.3$ ;  $N = 356$  scats). In both areas, small seeds (e.g., *Ficus* spp.; Moraceae) were not included in analyses.

Among the native species we found in tapir scat, only *E. edulis* and *Copaifera langsdorffii* are dispersed primarily by birds (Galetti & Pizo 1996, Galetti *et al.* 1999). The tapir is the main disperser of *S. oleracea* and *E. contortisiliquum* at our site because fruits of these species are too large to be disseminated by primates and other frugivores. White-lipped peccaries also eat *E. contortisiliquum* but typically destroy the seed. Two peccary species at our site eat *S. oleracea* but they chew and discard the seeds close to the parent plant, representing poor seed dispersal. Janzen (1981b) noted that 78 percent of the *E. contortisiliquum* and all *Cassia grandis* seeds were preyed on by *Tapirus bairdii* in Costa Rica.

*Syagrus romanzoffiana* is by far the most important fruit resource eaten by tapirs at Caetetus, particularly during the dry season when fruit is least available (Passos 1997). In fact, several large mammals seem to rely on *S. romanzoffiana* fruits during the dry season. For example, the two peccary species consume from 40 to 80 percent of *Syagrus* fruits during the dry season (Keuroghlian, pers. obs.), and black lion tamarins eat from 40 to 75 percent (Keuroghlian 1990, Passos 1997). This palm species is the most abundant and widespread in the semi-deciduous forest of the Atlantic Forest interior, and may play a key role in maintaining medium and large mammals during the dry season.

Tapir populations are declining throughout their range, and their long-distance dispersal and use of large-seeded species is unique among Neotropical frugivores. Although effects of seed disperser extinction on plant regeneration remain unclear (Galetti 2001), we predict that populations of large-seeded species, (e.g., *S. oleracea*; seeds > 25 mm wide) will be more affected, especially in areas where even agoutis are absent (M. Galetti, pers. obs.). In the whole Atlantic Forest, from a list of 1380 species (Siqueira 1994), we estimate that at least 50 plant species with large seeds will be deleteriously affected by tapir extinction.

We would like to thank to the Instituto Florestal for permission to work at Caetetus. José Carvalho and Don Eaton helped in the field. M. A. Pizo, D. Levey, and two anonymous reviewers provided comments on the manuscript. This project received financial support of FAPESP (proc. 96/10464-7) and Earthwatch Institute. M. Galetti thanks CNPq (proc. 300025/97-1).

- BODMER, R. E. 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *J. Zool.* 222: 121–128.
- . 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23: 255–261.
- CHAPMAN, C. A. 1989. Primate seed dispersal: the fate of dispersed seeds. *Biotropica* 21: 148–154.
- , AND L. J. CHAPMAN. 1995. Survival without dispersers: seedling recruitment under parents. *Conserv. Biol.* 9: 675–678.
- CHIARELLO, A. G. 1999. Effects of fragmentation of the Atlantic Forest on mammal communities in south-eastern Brazil. *Biol. Conserv.* 89: 71–82.
- CULLEN L. JR., L. R. E. BODMER, AND C. V. PADUA. 2000. Effects of hunting in habitat fragments of the Atlantic forests, Brazil. *Biol. Conserv.* 95: 49–56.
- DOWNER, R. C. 1996. The mountain tapir, endangered 'flagship' species of high Andes. *Oryx* 30: 45–58.
- DURIGAN, G., G. A. CORRÊA, M. SAITO, AND J. B. BAITELLO. 2000. Estrutura e diversidade do componente arbóreo da floresta na Estação Ecológica dos Caetetus, Gália, SP. *Rev. Brasil. de Bot.* 23: 371–383.
- EISENBERG, J. F. 1981. *The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior.* University of Chicago Press, Chicago, Illinois.
- FRAGOSO, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J. Ecol.* 85: 519–529.
- , AND J. M. HUFFMAN. 2000. Seed-dispersal and seedling recruitment patterns by the last Neotropical mega-faunal element in Amazonia, the tapir. *J. Trop. Ecol.* 16: 369–385.
- GALETTI, M. 1996. *Fruits and frugivores in a Brazilian Atlantic forest.* Ph.D. dissertation. University of Cambridge, Cambridge, England.
- . 2001. The future of the Atlantic Forest. *Conserv. Biol.* 14: 4.
- , AND M. A. PIZO. 1996. Fruit eating birds in a forest fragment in southeastern Brazil. *Ararajuba* 4: 71–79.
- , V. ZIPPARRO, AND L. P. MORELLATO. 1999. Fruit phenology and frugivory on the palm *Euterpe edulis* in a lowland Atlantic forest of Brazil. *Ecotropica* 5: 115–122.
- HENRY, O., F. FEER, AND D. SABATIER. 2000. Diet of the lowland tapir (*Tapirus terrestris* L.) in French Guiana. *Biotropica* 32: 364–368.
- HOWE, H. 1990. Seed dispersal by birds and mammals: implications for seedling demography. In K. S. Bawa and M. Hadley (Eds.). *Reproductive ecology of tropical forest plants*, pp. 191–218. Parthenon Publishing Group, Paris, France.

- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- . 1981a. Digestive seed predation by a Costa Rican Baird's tapir. *Biotropica* 13: 59–63.
- . 1981b. *Enterolobium cyclocarpum* seed passage rate and survival in horses, Costa Rican Pleistocene seed dispersal agents. *Ecology* 62: 593–601.
- JORDANO, P. 2001. Fruits and frugivory. In M. Fenner (Ed.). *Seeds: the ecology of regeneration in plant communities*, 2nd edition, pp. 125–165. CAB, Wallingford, England.
- KEUROGHLIAN, A. 1990. Observations on the behavioral ecology of the black lion tamarin (*Leontopithecus chrysopygus*) at Caetetus Reserve, São Paulo, Brasil. M.S. thesis, University of West Virginia, West Virginia.
- LEITÃO-FILHO, E., AND L. P. MORELLATO. 1997. Semi-deciduous forests of Southeastern Brazil—Serra do Japi. In S. D. Davis, V. H. Heywood, O. Herrera-MacBride, J. Villa-Lobos, and A. C. Hamilton (Eds.). *Centers for Plant Diversity: a guide and strategy for their conservation*. Vol. 3—The Americas, pp. IUCN/WWF, Washington, DC.
- MILLER, M. X. 1996. Dispersal of *Acacia* seeds by ungulates and ostriches in an African savanna. *J. Trop. Ecol.* 12: 345–356.
- OLMOS, F. 1997. Tapirs as seed dispersers and predators. In D. M. Brooks, R. E. Bodmer, and S. Matola (Eds.). *Tapirs—Status survey and conservation action plan*, pp. 3–9. IUCN/SSC Tapir Specialist Group, Gland, Switzerland.
- OPLER, P. A., G. W. FRANKIE, AND H. G. BAKER. 1980. Comparative phenological studies of treelet and shrub species in tropical wet and dry forests of Costa Rica. *J. Ecol.* 68: 167–188.
- PASSOS, F. C. 1997. Padrão de atividades, dieta e uso do espaço em um grupo de mico-leão preto (*Leontopithecus chrysopygus*) na Estação Ecológica de Caetetus, SP. Ph.D. dissertation. Universidade Federal de São Carlos, São Paulo, Brasil.
- PIÑERA, E. J. N. 1995. Hábitos de alimentación del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silv. Neotrop.* 4: 32–37.
- , AND E. C. ALDÁN. 1998. Ecología del tapir (*Tapirus bairdii*) en la reserva de la biosfera la sepultura, Chiapas, Mexico. *Acta Zool. Mex.* 73: 111–125.
- RODRIGUES, M., F. OLMO, AND M. GALETTI. 1993. Seed dispersal by tapir in southeastern Brazil. *Mammalia* 57: 460–461.
- SALAS, L. S., AND T. K. FULLER. 1996. Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela. *Can. J. Zool.* 74: 1444–1451.
- SCHUPP, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. In T. H. Fleming and A. Estrada (Eds.). *Frugivory and seed dispersal: ecological and evolutionary aspects*, pp. 15–29. Kluwer Academic, Dordrecht, The Netherlands.
- SIMPSON, G. G. 1980. *Splendid isolation: the curious history of South American mammals*. Yale University, Westford.
- SIQUEIRA, M. F. 1994. Análise florística e ordenação es espécies arbóreas da Mata Atlântica através de dados binários. M.S. thesis. UNICAMP, Campinas, São Paulo, Brasil.

#### Mauro Galetti<sup>2</sup>

Plant Phenology and Seed Dispersal Research Group, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), C.P. 199, 13506-900 Rio Claro São Paulo, Brazil

#### Alexine Keuroghlian

University of Nevada, Reno, EECB, Reno, Nevada 89957, U.S.A.

#### Lais Hanada and Maria Inez Morato

Plant Phenology and Seed Dispersal Research Group, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), C.P. 199, 13506-900 Rio Claro São Paulo, Brazil

---

<sup>2</sup> E-mail: mgaletti@rc.unesp.br