

Diet of the Lowland Tapir (*Tapirus terrestris* L.) in French Guiana¹

Key words: diet; French Guiana; lowland tapir; seed dispersal; tropical rain forest.

LOWLAND TAPIR (*TAPIRUS TERRESTRIS*) ARE THE LARGEST NATIVE HERBIVORES in South American tropical forests (Eisenberg 1989, Emmons & Feer 1997). Foraging and energetic constraints explain why a 150-kg nonruminant herbivore such as tapir may consume large quantities of the more abundant low quality browse accompanied by smaller quantities of high quality fruits (Demment & Van Soest 1985, Bodmer 1990). For example, diet of Baird's tapir (*Tapirus bairdii*) in Costa Rica consists mainly of leaf and stem (79–91%), and fruit (9–19%; Naranjo 1995, C. Foerster, pers. comm.). These authors, and Terwilliger (1978), Janzen (1981, 1982), and Williams (1984) have documented that Baird's tapir browse >100 plant species in the tropical dry and humid forest of Costa Rica and Panama. Bodmer (1990) analyzed stomach, cecal, and fecal samples of lowland tapir in Amazonian Peru, and reported that it consumed 33 percent fruit and 66 percent leaf and fiber, a diet composition similar to that found in Brazil (Fragoso 1997). These authors explained the relative high frugivory of lowland tapir by the presence of abundant and clumped resources of palm fruits (e.g., *Mauritia flexuosa* in Peru and *Maximiliana maripa* in Brazil).

The presence of intact seeds in fecal deposits suggested that tapir were good potential seed dispersers (Janzen 1981, Bodmer 1991, Rodriguez *et al.* 1993, Fragoso 1997). Fragoso (1997) proposed that the distribution of *M. maripa* in the Amazon was due largely to tapir. Tapir also may affect forest composition by browsing selectively the vegetative parts of food plants (Salas & Fuller 1996). Tapir foraging habits and habitat use (Salas 1996) may have a deep effect on rain forest landscapes that is not yet fully understood.

This study investigated the diet of the lowland tapir during different seasons in the tropical rain forest of French Guiana (2–6°N, 52–54°W). The samples came from 18 different locations scattered over the area. The overall moist-tropical type weather pattern is characterized by a mean air temperature of 26°C and an average annual rainfall ranging 2000–4000 mm. The rainy season generally extends from December to July, with a maximum in May and a slight decrease in February or March. The forest canopy tree community is represented by a predominance of Caesalpinaceae, Chrysobalanaceae, Burseraceae, Lecythidaceae, and Sapotaceae in various proportions (Sabatier & Prevost 1990).

A total of 27 lowland tapir stomachs were collected from local hunters over the years 1989–1991 to study their diet *in situ*. No attempt was made to encourage hunting, and collectors were not paid. Stomachs were kept in 10 percent formaldehyde. Tooth eruption of the mandibles permitted distinction between adult and subadult individuals. Stomach contents were washed and filtered through sieves of 0.6- and 6-mm mesh sizes. All large particles (>6 mm) were categorized as fruit (seed, pulp), leaf, and fiber (stem, woody material, fibrous pericarp). The small particles were mixed and homogenized; then 100 g were removed randomly and categorized. Each category was dried and weighed, and the proportion extrapolated to the entire sample of small particles. Finally, the total percentage of the different food types was obtained by adding the corresponding figures for the small and large particles following guidelines by Bodmer (1989). Fruit and seed samples were measured and preserved for identification. Nomenclature of plants follows Boggan *et al.* (1997).

Based on previous studies of seasonal fruiting patterns in the Guianan forest (Sabatier 1985, Guillotin *et al.* 1994, Henry 1994, Pack *et al.* 1999), the data on diet categories ($N = 25$ samples) were grouped into three representative seasons: peak fruiting (February–May), minimum fruit production (June–September), and intermediate fruit production (October–January).

Lowland tapir in French Guiana consumed large proportions of fiber. On a dry matter basis, fruit material comprised 24.4 ± 4.4 SE, leaves 22.3 ± 5.2 , and fiber 53.2 ± 6.4 percent of 27 stomachs. Flowers constituted a small proportion with only 4 percent of forage weight. The proportion of fiber was greater than fruit and leaf (Wilcoxon's signed-ranks test: $z = 2.74$, $P = 0.006$ and $z = 2.69$, $P = 0.007$, respectively). The proportions were similar between leaf and fruit (Wilcoxon's signed-ranks test: $z = 0.77$, $P = 0.44$). Male ($N = 13$) and female ($N = 12$; 2 individuals were not sexed) tapir did not show dietary differences; they consumed similar proportions of fruit, leaf, and fiber (Friedman two-way

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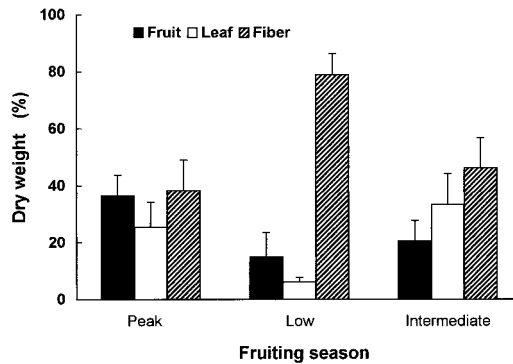


FIGURE 1. Seasonal composition of fruit, leaf, and fiber in stomach contents ($N = 25$, 2 samples have lost collection time) of lowland tapir in French Guiana (mean percent dry weight \pm SE). Fruiting seasons: peak (February–May), $N = 10$; low (June–September), $N = 6$; intermediate (October–January), $N = 9$.

ANOVA by ranks: $F_t = 2.1$, $df = 24$, $P > 0.05$). Sample sizes were too small to test for differences between adults ($N = 23$) and young ($N = 4$).

The proportions of leaf matter in the samples did not differ among peak fruiting, low fruiting, and intermediate fruiting seasons (Fig. 1; Kruskal-Wallis test: $H = 3.21$, $P > 0.05$). Proportions of fruit were only marginally different among seasons (Kruskal-Wallis test: $H = 5.65$, $P = 0.059$). During the peak fruiting, the proportions of fruit (36%) were greater than the following low fruiting season (15%; Mann-Whitney: $U = 49$, $P = 0.039$). The proportion of fiber in samples differed among seasons (Kruskal-Wallis test: $H = 7.83$, $P = 0.02$). Samples collected during low fruiting season had an increased proportion of fiber compared to peak and intermediate fruiting seasons (Mann-Whitney: $U = 7$, $P = 0.013$ and $U = 47$, $P = 0.018$, respectively).

A minimum of 42 species of fruit were found in the stomach samples, with a mean of 4.7 ± 0.5 SE (range = 0–11) species per stomach. All samples but one contained fruit items. *Spondias mombin* (Anacardiaceae) was the most important in percent total dry weight of large items (Table 1). This species may represent up to 92 percent of the dry weight, with a maximum of 382 fruits. *Pacouria guianensis* (Apocynaceae) and *Bagassa guianensis* (Moraceae) also were consumed frequently, but in smaller quantities. Inversely, species like *Sacoglottis cydonioides* (Humiriaceae), *Mouriri collocarpa*, and *Bellucia grossalarioides* (Melastomataceae) were abundant in only one or two samples.

The largest fruit consumed by lowland tapir was 6.0–8.5 cm in diameter (*P. guianensis*). Of 27 fruit species, 63 percent were < 3 cm in diameter. All species, except *Vosychia* sp., had fruit with fleshy/juicy pulp. The largest seed consumed was 4.7×2.5 cm (*Elephantomene eburnea*, Menispermaceae), but 67 percent ($N = 40$) of seed species were < 1.0 cm in diameter (diameter of short axis for elongated seeds). Intact seeds occurred in 81 percent of stomach samples. Of 68 seed samples extracted from the large items, 60 percent had intact seeds. Of 34 seed species found intact in stomachs, 7 species that were well protected by a hard ligneous endocarp (e.g., *S. mombin*) were never broken by tapir. Large quantities of *M. flexuosa* (Arecaceae) pulp were consumed, suggesting that tapir spit out the hard seeds ca 2.8 cm in diameter. Stomach samples contained 10 species of intact seeds < 5 mm (e.g., *Ficus* spp., *Cecropia* spp. [Moraceae], and *Psychotria* sp. [Rubiaceae]).

Pieces of leaves from monocotyledons and dicotyledons were present in all samples. Items of monocot leaves were more abundant than those of dicots in only 2 of 17 stomachs examined for leaf composition.

Lowland tapir eat a smaller proportion of leaf and fruit and a greater proportion of fiber in French Guiana than in Peru (Bodmer 1990). Habitat characteristics likely account for the differences in diet. In the drier forests of French Guiana, tapir forage on a majority of dicot species in the understory. The browsing behavior of tapir on shrubs and tree saplings (Salas & Fuller 1996) may explain the higher consumption of fiber from ingested twigs and stems. Salas (1996) and Salas and Fuller (1996) docu-

TABLE 1. *Fruits consumed by lowland tapir in French Guiana with percent occurrence in stomachs (N = 27) and percent dry weight of large particles (total).*

Species (Family)	Biological type ^a	Percent occurrence	Percent dry weight
<i>Pacouria guianensis</i> Aubl. (Apo.)	L	25.9	2.9
<i>Spondias mombin</i> L. (Anac.) ^b	Tt	22.2	30.1
<i>Bagassa guianensis</i> Aubl. (Mora.)	Tt	22.2	2.3
<i>Astrocaryum</i> sp. (Arec.)	St	14.8	0.3
<i>Symphonia globulifera</i> L.f. (Clus.)	Tt	11.1	0.8
<i>Strychnos</i> sp. (Logan.)	L	11.1	0.5
<i>Mouriri collocarpa</i> Ducke (Melast.) ^b	Mt	7.4	3.1
<i>Mauritia flexuosa</i> L.f. (Arec.)	Mt	7.4	1.7
<i>Bellucia grossalarioides</i> (L.) Triana (Melast.)	Mt/St	7.4	2.9
<i>Byrsonima laevigata</i> (Poir.) DC. (Malpig.)	Mt	7.4	0.8
<i>Sacoglottis cydonioides</i> Cuatrec (Humir.) ^b	Tt	3.7	10.6
<i>Elephantomene eburnea</i> Barneby & Krukoff (Menisp.) ^b	L	3.7	0.2
<i>Ficus</i> sp. (Mora.)	Et/Tt	3.7	0.3
<i>Parinari excelsa</i> Sabine (Chryso.) ^b	Tt	3.7	7.5
<i>Piper</i> sp. (Piper.)	S	3.7	0.1
<i>Chrysophyllum</i> sp. (Sapot.)	Tt	3.7	0.1
<i>Quiina</i> sp. (Quiin.)	Mt	3.7	0.1
cf. <i>Cheilochignum</i> (Hippocr.)	L	3.7	0.1
cf. <i>Psychotria</i> (Rub.)	S	3.7	0.1
cf. <i>Stryphnodendron polystachyum</i> (Mim.)	Tt	3.7	0.1
<i>Brosimum parinarioides</i> (Miq.) Kleinh. (Mora.)	Tt	3.7	<0.1
<i>Helicostylis tomentosa</i> (Poepp & Endl.) Rusby (Mora.)	Tt	3.7	<0.1
<i>Psychotria</i> cf. <i>kappleri</i> (Rub.)	S	3.7	<0.1
<i>Fusaea longifolia</i> (Aubl.) Safford (Anno.)	St	3.7	<0.1
<i>Parahancornia fasciculata</i> (Poir.) Benoist ex Pichon (Apo.)	Tt	3.7	<0.1
<i>Geissospermum laevis</i> (Vell.) Miers (Apo.)	Mt	3.7	<0.1
<i>Rauvolfia paraensis</i> Ducke (Apo.) ^b	Mt	3.7	<0.1
<i>Ambelania acida</i> Aubl. (Apo.)	St	3.7	<0.1
<i>Chrysophyllum</i> cf. <i>venezuelanense</i> (Sapot.)	St	3.7	<0.1
<i>C. eximium</i> (Pierre) Pennington (Sapot.)	Mt	3.7	<0.1
<i>Manilkara</i> cf. <i>bidentata</i> (A.DC.) Chevalier (Sapot.)	Tt	3.7	<0.1
<i>Cayaponia</i> sp. (Cucur.)	L	3.7	<0.1
<i>Vochysia</i> sp. (Vochy.)	Tt	3.7	<0.1
<i>Jacaratia spinosa</i> (Aubl.) A.DC. (Caric.)	Mt	3.7	<0.1
<i>Jessenia bataua</i> (Martius) Burret (Arec.) ^b	Mt	3.7	<0.1
<i>Cordia</i> sp. (Bora.)	Mt	3.7	<0.1

^a Biological types: Tt = tall tree, Mt = medium tree, St = small tree, Et = epiphytic tree, S = shrub, L = liana.

^b > 0.5-cm large, very hard seed.

mented habitat use and the diet of tapir in a similar forest of Venezuela, and recorded that some abundant dicot species were browsed most frequently in closed canopy forest, with a preference for gaps. This contrasts with Bodmer's data from floodplain forest of Peru where Araceae and Poaceae dominated in the tapir's diet.

Habitat factors affect fruit consumption by tapir. In both French Guiana and Amazonian Peru (Bodmer 1990), frugivory of lowland tapir was greater than frugivory of Baird's tapir in Central American forests (Terwilliger 1978; C. Foerster, pers. comm.). In French Guiana, tapir's fruit diet had a greater diversity than in Peru, where a supra-abundant palm species was heavily exploited. Salas (1996) suggested that tapir may select habitat types seasonally, according to the abundance of particular fruit species (Fragoso 1997). As in Baird's tapir of Costa Rica (C. Foerster, pers. comm.), the fruit consumption of Guianan tapir followed the fruit availability. In Peru, Bodmer (1990) did not find dietary seasonal variation due to the exploitation of extended flooded areas when fruit were scarce.

In this study, the proportion of stomach samples containing intact seeds was approximately twice the proportion recorded by Bodmer (1990) in Peru. This difference apparently is related to the comparatively small size of the seed species ingested by tapir in French Guiana. Our data confirm that the

largest seeds (e.g., *M. flexuosa*) mostly are spat out rather than swallowed and that despite tapir's powerful masticatory capacity, many other seed species (including unprotected ones) are ingested without being crushed by the molars. Therefore, the tapir may be an important potential seed disperser, whereas other Neotropical ungulates are known to act as seed predators (Kiltie 1981, Bodmer 1989, Henry 1994). The tapir, however, cannot be viewed as a dispersal agent of all intact seeds that are found in its stomach. Janzen (1981, 1982) showed that the role of Baird's tapir as predator or disperser depends on the species of plant ingested. This author observed that a cecal digester like the tapir kills all or a large proportion of the seeds species it swallows (e.g., *Enterolobium cyclocarpum*, *Cassia grandis*) when these are sacrificed and germinate during gut passage. Nevertheless, germination experiments conducted by D. Sabatier (unpublished data) with seed species defecated by a captive lowland tapir showed that unprotected seeds (e.g., *Geissospermum laevis* and *P. guianensis*) survive passage in the gut, with germination rates similar to that of seeds extracted from fresh fruits. Rodrigues *et al.* (1993) found viable unprotected seeds of two species in droppings of lowland tapir in southeastern Brazil. Tapir defecate in water or in dry seasonal streams and ponds (Eisenberg 1989, Bodmer 1991), a habitat that may be unfavorable to species unable to withstand immersion; however, exceptions to this behavior have been observed in French Guiana (D. Sabatier & F. Feer, pers. obs.) and other areas (Fragoso 1997, Naranjo 1995). In French Guiana, the tapir has a possible role as disperser of species (e.g., *G. laevis* and *P. guianensis*) that are not known to be eaten by other dispersers (Guillotín *et al.* 1994, Julliot 1996). Well protected dormant seeds of species such as *S. mombin* may take advantage of tapir consumption and dispersal. *Spondias* spp. are consumed and potentially dispersed by tapir in Costa Rica (Janzen 1985), Peru (Bodmer 1991), and Venezuela (Salas & Fuller 1996). Janzen (1985) has argued that *S. mombin* evolved under selective pressure from frugivorous megafauna that affected seed fate in a manner similar to that of the tapir. Today, *S. mombin* is dispersed by other vertebrates (Janzen 1985, Guillotín *et al.* 1994). The effectiveness of seed dispersal (e.g., Schupp 1993) by tapirs requires quantitative and qualitative data.

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- BODMER, R. E. 1989. Frugivory in Amazon ungulates. Ph.D. dissertation, University of Cambridge, Cambridge, England.
- . 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). *J. Zool. (Lond.)* 22: 121-128.
- . 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23: 255-261.
- BOGGAN, J., V. FUNK, C. KELLOFF, M. HOFF, G. CREMERS, AND C. FEUILLET. 1997. Checklist of the plants of the Guianas (Guyana, Surinam, French Guiana), 2nd edition. Smithsonian Institution Press, Washington DC. 226 pp.
- DEMMENT, M. W., AND P. J. VAN SOEST. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *Am. Nat.* 125: 641-672.
- EISENBERG, J. H. 1989. Mammals of the Neotropics. Vol. 1. The northern Neotropics. University of Chicago Press, Chicago, Illinois.
- EMMONS, L. H., AND F. FEER. 1997. Neotropical rain forest mammals: a field guide, 2nd edition. University of Chicago Press, Chicago, Illinois. 307 pp.
- FRAGOSO, J. M. V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *J. Ecol.* 85: 519-529.
- GUILLOTÍN, M., G. DUBOST, AND D. SABATIER. 1994. Food choice and food competition among the three major primate species of French Guiana. *J. Zool. (Lond.)* 233: 551-579.
- HENRY, O. 1994. Saisons de reproduction chez trois Rongeurs et un Artiodactyle en Guyane française, en fonction des facteurs du milieu et de l'alimentation. *Mammalia* 58: 183-200.
- JANZEN, D. H. 1981. Digestive seed predation by a Costa Rican Baird's tapir. *Brenesia* 19/20: 99-128.
- . 1982. Seeds in tapir dung in Santa Rosa National Park, Costa Rica. *Brenesia* 19/20: 129-135.
- . 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. *J. Trop. Ecol.* 1: 131-155.
- JULLIOT, C. 1996. Fruit choice by red howler monkeys (*Alouatta seniculus*) in a tropical rain forest. *Am. J. Primatol.* 40: 261-282.
- KILTIE, R. A. 1981. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 13: 141-145.
- NARANJO, E. J. 1995. Hábitos de alimentación del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. *Vida Silv. Neotrop.* 4: 32-37.

- PACK, K. S., O. HENRY, AND D. SABATIER. 1999. The insectivorous–frugivorous diet of the golden-handed tamarin, *Saguinus midas midas*, in French Guiana. *Fol. Primatol.* 70: 1–7.
- RODRIGUEZ, M., F. OLMOS, AND M. GALETTI. 1993. Seed dispersal by tapir in southeastern Brazil. *Mammalia* 57: 460–461.
- SABATIER, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Rev. Ecol. (Terre et Vie)* 40: 289–320.
- , AND M.-F. PREVOST. 1990. Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane française. *Bois et Forêts des Tropiques* 219: 31–56.
- SALAS, L. A. 1996. Habitat use by lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela. *Can. J. Zool.* 74: 1452–1458.
- , 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. *Vegetatio* 107/108: 15–29.
- TERWILLIGER, V. J. 1978. Natural history of Bairds tapir on Barro Colorado Island, Panama Canal Zone. *Biotropica* 10: 211–220.
- WILLIAMS, K. D. 1984. The Central American tapir (*Tapirus bairdii* Gill) in northwestern Costa Rica. Ph.D. dissertation, Michigan State University, East Lansing, Michigan.

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