# Diet of the lowland tapir (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela

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**Abstract**: In this study we document the diet, determine diet selection, and evaluate the seed-dispersal role of lowland tapirs (*Tapirus terrestris* L.) in the Tabaro River valley of southern Venezuela. The diet was assessed by checking treefall gaps and closed-canopy areas of equal size for browsing signs, examining droppings for seeds and fruit remains, and casually asking experienced Ye'kwana Indian hunters. Plants browsed by tapirs were identified and counted. The abundance of each plant species at the study site was determined using 25-m$^2$ quadrats and compared with its abundance in the diet to determine selectivity. Because tapirs defecate in water, their role as seed dispersers was examined by analyzing the distribution of diet species using a data base of the locations of trees at the study site. Information from the 25-m$^2$ quadrats was used for lianas and shrubs. Results show that tapirs selectively browse on 88 out of at least 256 plant species, consistently avoiding more species in closed-canopy areas. Some species occur significantly more frequently in the diet than their relative abundance in the forest. Tapirs eat fruits of 33 species; 2 of these are mainly found near the water and 9 away from the water.

**Résumé** : Nous avons étudié le régime alimentaire et le choix des aliments chez le tapir *Tapirus terrestris* L. dans la vallée de la Tabaro, dans le sud du Vénézuéla, et évalué le rôle de cet animal dans la dispersion des graines. Le régime alimentaire a été déterminé par recherche de traces de broutage dans des zones découvertes et dans des zones à forte couverture de surfaces égales, et par interrogation de chasseurs indiens Ye'kwana expérimentés. Les plantes broutées par les tapirs ont été identifiées et comptées. L'abondance de chaque espèce de plante dans la région étudiée a été déterminée par inventaire de quadrats de 25 m$^2$ et comparée à son abondance dans le régime des tapirs afin d'évaluer la sélectivité. Comme les tapirs défèquent dans l'eau, leur rôle dans la dispersion des graines a été examiné par analyse de la répartition des espèces de plantes consommées à partir d'une base de données sur l'emplacement des arbres au site étudié. L'information tirée de l'inventaire des quadrats a été utilisée dans le cas des lianes et des buissons. Les résultats ont démontré que les tapirs sélectionnent 88 des quelque 256 plantes différentes présentes et qu'ils évitent toujours un plus grand nombre d'espèces dans les zones à forte couverture. L'abondance de certaines espèces dans le régime est parfois significativement plus grande que leur abondance relative dans la forêt. Les tapirs mangent les fruits de 33 espèces, dont 2 poussent surtout près de l'eau et 9 autres, loin de l'eau.
[Traduit par la Rédaction]

## Introduction

Browsing by Neotropical ungulates may have an effect on plant communities (see Dirzo and Miranda 1991; Terborgh 1992; Terborgh and Wright 1994), therefore knowledge of their diet selection is crucial to understanding the mechanisms by which these plant communities are affected. In this paper we speculate about the role of lowland tapirs (*Tapirus terrestris*) in Neotropical forests by looking at their diet selection and seed-dispersal pattern. The diet of the lowland tapir is presented and evaluated in light of the availability of each plant species in the forest, to depict any selectivity. In addition, we assess the relevance of tapirs as seed dispersers by analyzing the spatial distribution of species whose fruits they eat.

Plant-species assemblages in tropical forests follow a typical log-normal curve, with a few common species and a "tail" of rare species (May 1975; Gentry 1988; Hammel 1990; Foster and Hubbell 1990; Foster 1990; Prance 1990). Consequently, if tapirs are not selective browsers, the occurrence of plant species in their diet may follow the same pattern. To evaluate this hypothesis, the frequency of occurrence of a plant species in the diet and its frequency in the habitat were determined and compared.

Diet selectivity has been reported for a variety of tropical browsers (e.g., okapis (*Okapia johnstoni*), Hart and Hart 1989; giraffes (*Giraffa camelopardalis*), Pellew 1984; white-tailed deer (*Odocoileus virginianus*), Vangilder et al. 1982). There are also reports on the diet of three of the four living species of tapirs. Terwilliger (1978) reported Baird's tapirs eating plant species proportionally to their abundance in the area. However, Baird's tapirs completely avoided some plant species and occasionally ignored others, which the author recognized as evidence of diet optimization. In Costa Rica, Williams (1984) found at least 54 plant species in the diet of Baird's tapirs in Santa Rosa National Park, whereas Naranjo (1995) found 94 diet species in Corcovado National Park. Janzen (1982) offered 381 species of wild plants to a captive tapir, which rejected 55% and unambiguously accepted only 29% of them. Medway (1974) reported Malayan tapirs

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(*T. indicus*) to be very selective. Williams (1978) reported Malayan tapirs browsing on 115 different species of plants and being selective for 27 of these species. Castellanos (1994) reported 62 plant species browsed by Andean tapirs (*T. pinchaque*), 7 of which were highly selected. To our knowledge, ours is the first detailed list of plants eaten by lowland tapirs, and the first analysis of their selectivity.

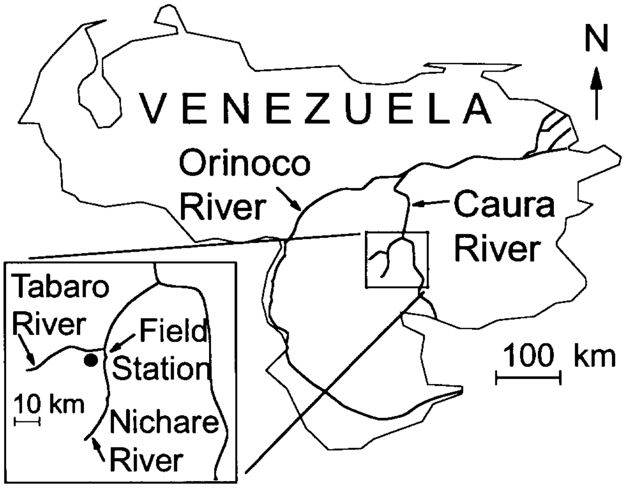
Tapirs ingest fruits of several species of plants (Bodmer 1990, 1991; Castellanos 1994; Eisenberg 1989; Janzen 1981), thereby removing their seeds from the parent trees and becoming potential seed dispersers. In addition, Janzen (1981) demonstrated that only 12% of the seeds of the Guanacaste tree survive passage through a captive Baird's tapir's gut. This finding suggested that tapirs are potential seed dispersers and they have been considered to be such ever since (Bodmer 1990, 1991; Varela 1992; Rodrigues et al. 1993; Eisenberg 1989; Redford and Eisenberg 1989). However, the effectiveness of dispersal (e.g., Schupp 1993) by tapirs has never been evaluated and thus is worth questioning.

Reports of seed germination in tapir dung (e.g., Varela 1992; Rodrigues et al. 1993) are claimed to be evidence of the seed-dispersal role of tapirs. But the effectiveness of a disperser relies on "the quantity of seeds dispersed and the quality of dispersal provided each seed" (Schupp 1993, p. 15). The quality of dispersal depends in part on the location where the seeds are deposited by the vector animal. The Amazonian forest is not homogeneous, and tropical plant species' distribution patterns may be limited by many environmental and biotic factors (Dumont et al. 1990; Kubitzki and Ziburski 1994; Denslow 1980; Salo et al. 1986; Schupp 1993; Schupp et al. 1989). Accordingly, the relevance of tapirs' dispersal role depends on the probability of dropping the seeds in the appropriate kind of habitat (De Steven and Putz 1984; Schupp 1993; Janzen 1983). But tapirs defecate in water or in dry seasonal streams and ponds (Eisenberg 1989; Fragoso 1991*a*; Bodmer 1991; C. Forester, personal communication; personal observation, but see exceptions to this behavior in Fragoso 1994 and Naranjo 1995). Thus, any plant species potentially dispersed by tapirs must grow near the water. The role of tapirs as seed dispersers is evaluated here by analyzing the distribution of plant species whose fruits are consumed by tapirs.

## Methodology

This research was conducted in a tropical rain forest located in the Tabaro River valley of southern Venezuela (6°21′17.9″N, 64°59′47.9″W; 120 m asl) (Fig. 1). The study site is very similar to a "seasonal swamp forest in upland valleys" (sensu Kahn and Mejía 1990) regarding palm species composition and general geomorphological characteristics, and best fits a "floodplain forest" (sensu Prance 1979) regarding rainfall and flooding patterns. No specific climatic records for the Tabaro River valley are available. However, records from two stations <50 km away show an annual average rainfall of 3115 mm and an average temperature of 26.5°C. There is a seasonal pattern of rainfalls, the heaviest rains occurring between June and September, whereas a dry season begins in November and extends through May.

**Fig. 1.** Location of the study area in Venezuela.



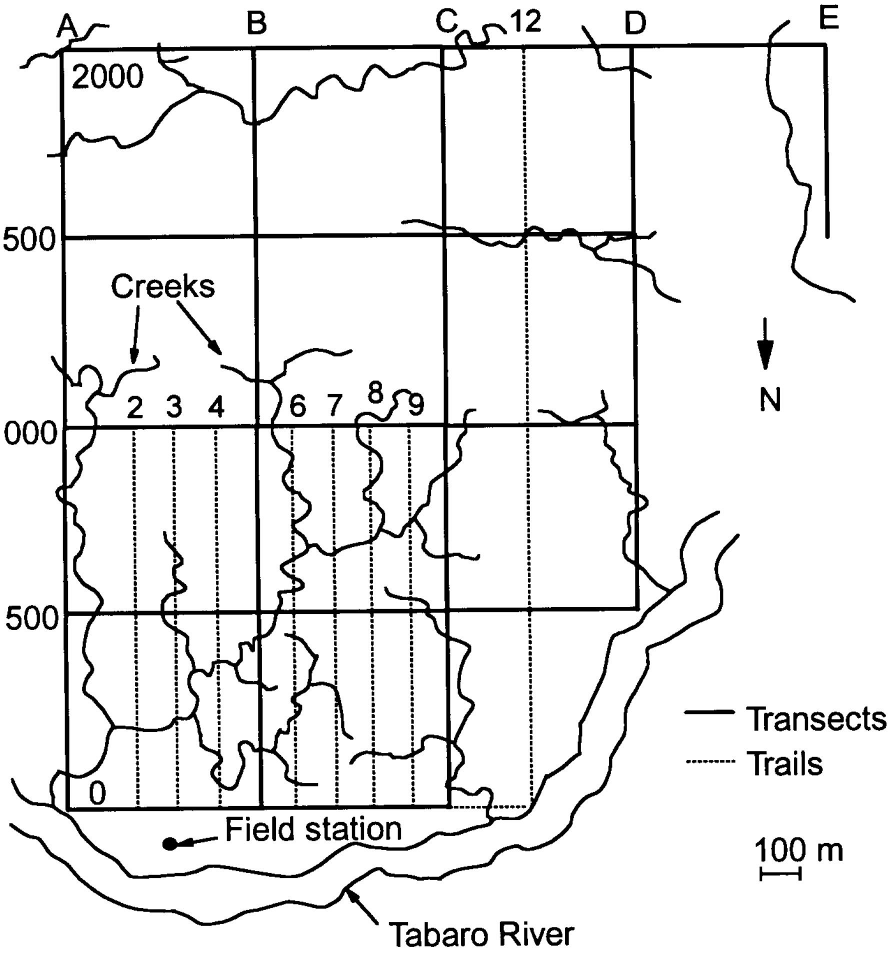
There are no human settlements in the Tabaro River valley. The nearest Indian community, that of the Ye'kwana Indians, is more than 40 km down the Nichare River, approximately 4 h by boat (the Tabaro River is a tributary of the Nichare River) (Fig. 1). There are no roads or airstrips close by and the nearest village is 2 days downriver. Thus, the area is very pristine and remote. Some Indians, as well as recent settlers, make sporadic incursions to the Nichare River to hunt. For this reason, in 1987 an agreement was made between representatives of the Ye'kwana Indian Community and EcoNatura, a local nongovernmental organization, to stop hunting in or near the Tabaro River valley. Before this agreement, however, hunters rarely killed animals in or near the Tabaro River.

In 1990 a field station was constructed approximately 2 km up from the mouth of the Tabaro River, and a system of transects was made (Fig. 2) to collect information about the community of trees of the forest. The transects were placed systematically ever 500 m to form a grid that covers 300 ha (transects 0–2000 and A–E; Fig. 2) and are oriented north–south and east–west. Another eight minor trails were set for a smaller scale sample of vegetation within this grid. These trails are 1 km long, parallel to each other, oriented north–south, and begin in the basal transect (trails 2–4, 6–9, and 12; trail 12 is 2 km long; Fig. 2). In total, 22.5 km of transects were constructed.

The study area was classified into five different habitat types, each with a distinctive floristic composition and (or) geomorphology: creek habitats, inundated forest, terra firme forest, hillside, and hilltop. Creek habitats include creek and river shores in forested areas (sometimes extending several metres from the water) and any islands in the creeks. Several plant species are unique to this kind of habitat (see Salo et al. 1986) and tapirs browse on them (personal observation). The inundated forest habitats are lowland forests that flood during the rainly season. Terra firme habitats are forested areas that are a few metres higher than the inundated forests, and thus remain above the water during the floods. Hillside habitats are slopes of mountains and hills. Hilltops are the somewhat flat tops of the mountains and hills at the study area. The 22.5 km of transects cut across all habitat types; 5% is creek habitat, 19% is inundated forest habitat, 34.4% is terra firme habitat, 33.5% is hillside habitat, and 8.1% is hilltop habitat (Salas 1996). These values are taken here as representative of the abundance of each habitat type at the study site. Forest openings (gaps) are also important and distinctive habitat types in Neotropical forests (Denslow 1980), and tapirs prefer to forage in them (Salas 1996; Fragoso 1991*b*). These openings represent an average of 14% of the forest (estimated from their abundance along the transects) and are proportionally distributed in each of the five different habitat types (Salas 1996). A gap in creek habitat is defined here as an opening in the canopy around creeks that allows more light to reach the ground.

Information on lowland tapir foraging behavior was collected from October 1990 to June 1992, January to June 1993, and January to May 1994. Gathering data is very difficult during wet periods,

**Fig. 2.** Location of transects, trails, and creeks in the study area.



so most of the information reported here is from the dry periods of the year.

The lowland tapir diet was determined by collecting evidence of browsing during walks along the transects and creeks and walks in random directions outside the trails. Tapirs pull down and break stems and branches of some of the plants they browse upon, leaving tooth marks in the bark. Evidence of this behaviour and the presence of tracks at such sites were used to identify tapir browsing signs; only those browsing signs unequivocally made by tapirs were recorded. Approximately 1120 km was walked in search of signs. Each time, a different trail (or set of trails) was chosen for inspection, and trails were not inspected again at least within the next 4 days. In addition, 15 gaps were examined in each habitat type. The average area of these gaps was determined and 15 closed-canopy areas of this average size were examined in each habitat type. In total, 75 gaps and 75 closed-canopy areas were inspected, covering 57 958 $m^2$ of forest. Species whose fruits were eaten by tapirs were identified by examining fruit remains and seeds in 206 droppings found in creeks. When a dropping was found, it was thoroughly inspected and any seeds or fruit parts found were collected for later identification. All identifications were made by comparing the samples with museum collections and with seeds of fruits collected in situ. Finally, experienced Ye'kwana hunters were casually asked if ripe fruits found on the ground, or other plants around browsing signs, were plant species eaten by tapirs. A list of food-plant species was made, including the part of the plant eaten (e.g., fruit, leaf, stem, or whole sapling). Botanical samples were collected from each species on the list and deposited in local herbaria and the Missouri Botanical Garden for identification.

To assess the availability of plants, 10 quadrats were placed in each habitat type, 5 in closed-canopy and 5 in treefall gap areas, for a total of 50 quadrats. Each quadrat measured 5 × 5 m, adding up to 1250 $m^2$ of forest understory sampled. All plants available to tapirs found in the quadrats were counted and botanical samples were collected for identification in herbaria. Any plant taller than 30 cm and up to but no more than 5 cm in stem diameter was considered to be available to tapirs; these sizes are suitable for tapirs to browse (see Terwilliger 1978; Williams 1978; personal observation). Since tapirs pull down vines and lianas, any vine with a stem accessible to tapirs was considered available. A list of all plant species present in each habitat type was made, pooling all plant species browsed and all plant species recorded in the quadrat samples in a particular habitat type.

The percentage of species available to but avoided by tapirs in each habitat type was determined. This percentage was calculated by dividing the total number of plant species available to tapirs in each habitat type by the total number of species known to be browsed by tapirs in each habitat type. Tapirs browse preferentially in gaps; more browsing signs were found in gaps (Salas 1996). It is therefore possible that tapirs find more of their preferred browse in gaps, or alternatively, that they are less selective when browsing in gaps. Data were evaluated to document any difference in selectivity between gaps and closed-canopy areas. A *t* test (using the arcsine transformation of values) was used to compare the average percentage of plant species avoided in gaps with the average percentage of plants avoided in closed-canopy areas.

For each species, the number of plants browsed in all habitat types was also recorded and compared with their availability to

**Table 1.** Number of species found and number of species avoided by lowland tapirs in treefall gaps and closed-canopy areas in each habitat type in the Tabaro River valley, southern Venezuela.

| | Closed canopy | | Treefall gaps | | Total | |
|---|---|---|---|---|---|---|
| | No. of species found | No. of species avoided | No. of species found | No. of species avoided | No. of species found | No. of species avoided |
| Creeks | 67 | 55 (82) | 42 | 75 (56) | 84 | 43 (51) |
| Inundated forests | 63 | 52 (83) | 42 | 70 (60) | 85 | 49 (58) |
| Terra firme forests | 78 | 74 (95) | 54 | 74 (73) | 106 | 59 (56) |
| Hillsides | 74 | 68 (92) | 63 | 95 (66) | 105 | 59 (56) |
| Hilltops | 64 | 58 (90) | 60 | 90 (67) | 93 | 58 (62) |
| Total | 198 | 97 (49) | 193 | 88 (46) | 237 | 88 (37) |

**Note:** Numbers in parentheses represent the percentage of species avoided in each habitat type. The difference in average percentages of plants avoided between closed-canopy areas and treefall gaps is significant ($t$ test = 5.76, 8 df, $P < 0.001$; arcsine transformation of the values).

assess selectivity in the diet of tapirs. A regression line was fitted between the abundance of plant species in the quadrats and the number of times they were recorded as browsed. The analysis of variance of the regression provides a test for the significance of the regression and, thus, for the relationship between the two variables (Draper and Smith 1981). A significant regression implies a significant relationship between the abundance of plant species in the habitat and in the diet of tapirs. The three most common species in the diet of tapirs (*Amphirrox latifolia*, *Mabea* cf. *piriri*, and *Heteropsis flexuosa*) are the only species that are abundant in both the diet and the habitat. These species were removed from the data set and the regression was calculated again.

To evaluate the potential role of tapirs as seed dispersers, we determined the spatial distribution of species whose fruits are consumed by tapirs. For this purpose, the five habitat types in the study area were divided into habitats near to and away from the water. Creeks and inundated forests were considered to be habitats near the water, and terra firme forests, hillsides, and hilltops were considered to be habitats away from the water. It should be noted that in the Tabaro River valley all the dropping collected were found in water bodies (either seasonal or permanent).

A pre-existing data base of the distribution of trees in the study area was available for our analyses (Salas and Goldstein 1992).[2] This data base was created by measuring, mapping, and tagging all the trees >20 cm dbh located within 15 m of each side of the 2 km long transects 0, C, and B and the first 1500 m of transect A. Botanical samples of each tree species were collected and identified at the Missouri Botanical Garden. The habitat types along the transects were recorded and used to determine where every individual tree was found. This sample covered 18.7 ha of forest, 75% of which was in habitats near the water and 25% was in habitats away from the water. Information from the 25-$m^2$ quadrats was used to assess the distribution of lianas and vines. This sample covered 500 $m^2$ (40%) of forest near the water and 750 $m^2$ (60%) away from the water. Additionally, all palms >5 cm dbh were identified, measured, mapped, and tagged along transect B in order to assess the distribution of palm species. This sample covered 6 ha of forest, 18% of it in habitats near the water and 82% in habitats away from the water.

The distribution pattern of each plant species potentially dispersed by tapirs between habitats near to and away from the water was determined with binomial tests. Our null hypothesis was that all plant species whose fruits are eaten by tapirs are randomly distributed in the forest. The proportion of habitat sampled away from the water in each of our sampling procedures was used as the expected proportion of plants of each species found away from the water. For example, under the null hypothesis, if our sample contains *n* trees of a species, approximately 75% of those trees should be found away from the water. A positive significant deviation from this expected proportion beyond the 95% confidence limits (i.e., an observed proportion significantly larger than 75%) identifies a tree species found mainly in habitats away from the water; such a species is considered to be not dispersed by tapirs. On the other hand, if significantly more than 25% of the trees are found near the water, the species is considered to be most frequently found near the water and is potentially dispersed by tapirs.

The presence of two plants of the same species close together may be the outcome of two seeds dispersed by the same tapir at the same time (i.e., the same dispersal event). Therefore, to avoid pseudoreplication (Hurlbert 1984), only plants recorded >100 m from each other were considered in the analysis. The distance of 100 m is approximately twice the average length of a habitat type along the transects and is considered here to be sufficiently far away that it can be assumed that there is no relationship between two plants of the same species. This condition reduces the number of plants of each species that could be used for this analysis, diminishing the chances of finding a significant difference. Binomial tests were performed only on species with more than five individuals.

## Results

In the Tabaro River valley, we recorded and identified 1227 tapir browsing signs. Lowland tapirs browsed on at least 88 different species of plants and ate the fruit of at least 33 species of trees, palms, and lianas. Pooling all the plant species found in the understory and gap areas gave a total of 237 different species. Tapirs avoided at least 149 of these species, exhibiting strong selectivity in their diet. The proportion avoided in each habitat varied from 56 to 95% (Table 1). The three most frequently found species in the forest were avoided by tapirs (a species of Araceae, *Bauhinia guianensis*, and an unidentified species). On the other hand, species such as *Cecropia sciadophylla* and *Aparisthmium cordatum* are uncommon in the forest but common in the diet of tapirs. The three species most frequently browsed by tapirs (*Amphirrox latifolia*, *Mabea* cf. *piriri*, and *Heteropsis flexuosa*) were relatively common in the habitat. Tapirs also are more selective ($t$ test, $t = 5.76$, 8 df, $P < 0.001$; arcsine

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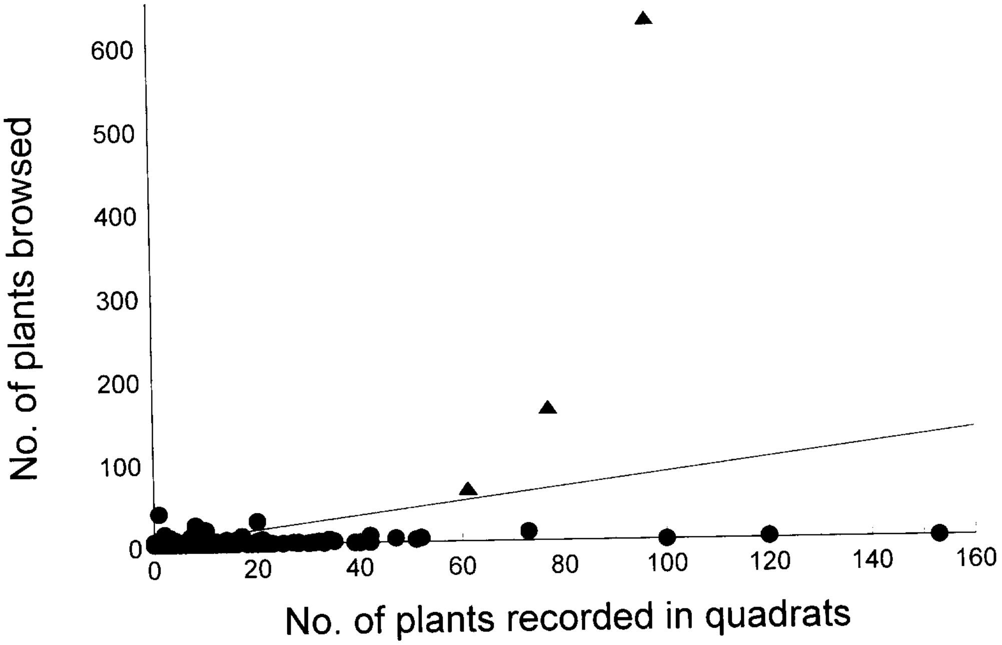
[2] L.A. Salas and I.R. Goldstein. 1992. Base de datos de la cuadrícula de vegetación Dedemai. Unpublished manuscript, The Wildlife Conservation Society, International Programs, 185th Street and Southern Boulevard, New York, NY 10460, U.S.A.

**Fig. 3.** Regression analysis of the number of tapir browsing signs recorded for each plant species versus the abundance of each species in the quadrats. Each point represents a plant species; triangles represent the three commonest species in the diet. The regression is significant ($F_{[1,205]} = 31.3$, $P < 0.05$). However, if the three commonest species are removed, the regression is not significant ($F_{[1.202]}$ $P > 0.1$; ($\beta = 0.08$ for a small difference sensu Cohen 1988).



transformation of the values) when browsing on plants in closed-canopy areas. A consistently larger percentage of plant species was avoided in closed-canopy areas. A detailed list of the number of plants recorded for each species in the quadrats in closed-canopy and gap areas, and the number of plants browsed by tapirs is provided in an Appendix.[3]

The regression of the number of tapir browsing signs recorded for each species versus the abundance of each species in the habitat was significant ($F_{[1,205]} = 31.3$, $P < 0.05$) (Fig. 3). This result indicates that tapirs do not have a selective diet (i.e., the abundance of plant species in the diet of tapirs depends on their abundance in the habitat). However, if the three commonest species in the diet of tapirs are removed from the data set, the regression is not significant ($F_{[1,202]} = 1.248$, $P > 0.1$; $\beta = 0.08$ for a small effect size sensu Cohen 1988). This analysis includes data from 205 species and indicates that tapirs have a selective diet.

The analysis of distribution patterns of plant species potentially dispersed by tapirs shows that only one shrub species and one tree species could be potentially dispersed by tapirs (i.e., are more frequently found near the water). On the other hand, at least nine species of trees are not dispersed by tapirs (they are mostly found away from the water). We were unable to test preference for 15 species of trees, palms, and lianas because sample sizes were too small (Table 2). Three species of trees, two palms, and two lianas did not show any significant deviation from the expected frequency. These results may be due to low statistical power or may indicate that some of these species are habitat generalists. Because of the small sample sizes for all these species (7–28 plants were recorded), the power of the test is 12% at best, and thus the probability of finding a significant difference is very small (Cohen 1988).

It can be argued that because our data were mostly gathered during the dry season, many plant species potentially dispersed by tapirs were not recorded. We asked a Ye'kwana hunter to keep stomach samples of tapirs killed by community members in the Caura and Nichare rivers (Fig. 1). Twenty-eight stomach samples were collected; of these, 18 were collected in the wet season and none contained remains of fruits. In Corcovado National Park, Costa Rica, Naranjo (1995) found that Baird's tapirs eat fruits more frequently in the dry season.

## Discussion

Lowland tapirs do not eat plants of every single species in the forest. Needless to say, there is a high diversity of understory species and saplings, and tapirs eat only a fraction of available species (Table 1). An initial analysis of the abundance of species in the habitat and their abundance in the diet of tapirs suggested a positive relationship (Fig. 3). However, this result is not supported if the analysis is performed when the 3 commonest species in the diet of tapirs are not included (and 204 other species are included). Thus, we conclude that there is no relationship between the abundance of plant species in the habitat and their abundance in the diet of tapirs. In addition, tapirs seem to avoid more plant species (i.e., be more selective) in closed-canopy areas than in gaps.

Gap-specialist species (also called secondary-forest or pioneer species) invest little in building chemical or mechani-

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[3] Copies of the Appendix may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0S2, Canada.

**Table 2.** Numbers of plants recorded and numbers away from the water for all species whose fruits are eaten by lowland tapirs in the Tabaro River valley, southern Venezuela.

| | Life form | No. recorded[a] | No. away from the water |
|---|---|---|---|
| *Anacardium giganteum* | Tree | 20 | 18[b] |
| *Anomospermum reticulatum* | Liana | 8 | 5 |
| *Burseraceae* sp. | Tree | 15 | 14[b] |
| *Chrysobalanaceae* sp. | Tree | 9 | 6 |
| *Couma macrocarpa* | Tree | 18 | 16[b] |
| *Dacryodes peruvianum* | Tree | 33 | 29[b] |
| *Dipteryx odorata* | Tree | 1 | 1 |
| *Dipteryx punctata* | Tree | 2 | 0 |
| *Ficus* sp. | Tree | 1 | 0 |
| *Ficus* sp. | Tree | 3 | 3 |
| *Garcinia macrophylla* | Tree | 0 | 0 |
| *Gustavia coriacea* | Shrub | 24 | 8[c] |
| *Helicostylis tomentosa* | Tree | 17 | 16[b] |
| *Inga oerstediana* | Tree | 11 | 9 |
| *Jessenia bataua* | Palm | 18 | 15 |
| *Macropholis eggensis* | Tree | 26 | 23[b] |
| *Menispermaceae* sp. | Tree | 0 | 0 |
| *Micropholis melinoneana* | Tree | 10 | 5[d] |
| *Oenocarpus bacaba* | Palm | 28 | 22 |
| *Parinari excelsa* | Tree | 0 | 0 |
| *Pourouma bicolor* | Tree | 30 | 26[b] |
| *Pourouma guianensis* | Tree | 14 | 13[b] |
| *Protium crenatum* | Tree | 7 | 6 |
| *Pseudolmedia laevis* | Tree | 21 | 19[b] |
| *Sapotaceae* sp. | Tree | 3 | 3 |
| *Spondias mombin* | Tree | 1 | 0 |
| *Tabernaemontana sananho* | Shrub | 1 | 0 |
| Unidentified species | Liana | 14 | 10 |
| | Tree | 0 | 0 |
| | Tree | 1 | 0 |
| | Shrub | 0 | 0 |
| | Shrub | 0 | 0 |
| | Shrub | 0 | 0 |

[a] Not all records are included, to avoid pseudoreplication.

[b] Significant deviation from expected frequency; found mainly away from the water (binomial test, expected frequency = 75% of trees found away from the water, $P < 0.05$).

[c] Significant deviation from expected frequency; found mainly near the water (binomial test, expected frequency = 40% of plants found near the water, $P < 0.05$).

[d] Significant deviation from expected frequency; found mainly near the water (binomial test, expected frequency = 25% of trees found near the water, $P < 0.05$).

cal deterrents that retard growth. Instead they allocate energy as high concentrations of proteins and nutrients in buds and leaves and grow fast while the gap is open. Conversely, shade-tolerant (or primary forest) plant species allocate energy to building up a battery of chemical and mechanical deterrents to discourage herbivores and thus have a very slow growth rate (Whitmore 1989; De Steven 1988; Canham 1989; Shure and Wilson 1993; Cates and Orians 1975; Molofsky and Fisher 1993). This difference in growth strategies of plants may influence the diet of tapirs (i.e., they may prefer secondary forest species with less toxins), and account for the observed difference in browsing selectivity between closed-canopy and gap areas. Furthermore, significantly more browsing signs were found in gaps than in closed-canopy areas of the same size (Salas 1996).

According to our results, very few species can be potentially dispersed by tapirs in the Tabaro River valley. Tapirs are potential dispersers of at least two species of plants but do not disperse at least nine. And yet several other aspects of the quality of the dispersal (such as the survival of seeds passing through the digestive system of tapirs) and the quantity of the dispersal (such as how many seeds are removed by tapirs relative to other potential dispersers) remain to be evaluated for the two plant species potentially dispersed (see Schupp 1993). For instance, *Micropholis melinoneana* and *Gustavia coriacea* seeds lack a hard shell that would protect them from the hostile environment in the gut of tapirs. Indeed, we never found any seeds of these species alive in tapir dung, and we do not believe that tapirs disperse them. In general, our results suggest that the the dispersal role of tapirs may not be as relevant as previously claimed in the literature. More detailed studies are still needed to evaluate the quantity and quality of dispersal by tapirs before they can be considered important seed dispersers.

Tapirs' browsing behavior and diet selection may have relevant ecological consequences. Treefall gaps are considered regeneration spots in tropical forests (Brokaw and Scheiner 1989; Hubbell and Foster 1990; Hartshorn 1990). In young and mature forests, species composition is a function of the size and abundance of pioneer species in gaps (Connell 1989). Some tropical tree species are gap specialists, and because forest openings are a limited resource for these plant species (Brokaw and Scheiner 1989), they germinate and grow fast when a gap is created and before the canopy closes again (De Steven 1988). Consequently, if browsing has detrimental effects on the plants (Dirzo and Miranda 1991; Austin and Urness 1992), the selective browsing of tapirs may directly affect the recruitment of food-plant species in the forest and indirectly favor the species excluded from the diet.

Tapirs may also affect forest composition by dispersing seeds or by preying on them. Rodrigues et al. (1993) stressed the possible role of tapirs as seed dispersers after finding viable seeds of *Euterpe edulis* and *Virola oleifera* in two droppings of lowland tapir in southeastern Brazil. Both these species are commonly found near the water, but the seeds are small (i.e., <2 cm in diameter) and may be more effectively dispersed by birds and monkeys. In the Tahuayo River, Peru, Bodmer (1991) found intact seeds in 18 stomach, cecal, and fecal samples of lowland tapirs. Of 56 seed samples, 26 were damaged (Bodmer 1991). Fragoso (1994) reported the use of "latrines" or particular sites in nonflooded areas of the Amazon forest in northern Brazil where tapirs defecate and make piles of dung. Viable seeds of the palm *Maximiliana maripa* may be found in these dung piles, indicating a possible dispersal role of tapirs (Fragoso 1994). Janzen (1981) found that 78% of guanacaste (*Enterolobium cyclocarpum*) seeds and all carao (*Cassia grandis*) seeds were killed after being ingested by Baird's tapirs.

In combination, tapirs' characteristic browsing behavior of pulling down and breaking the branches and stems of saplings of several tree species, their dietary selectivity, and their potential seed dispersal and predation roles make them important agents affecting the recruitment of Neotropical tree species. By killing the seeds and saplings of many species, tapirs reduce their probability of reaching maturity, enhancing the chance of survival of the species avoided or dispersed. The effects of selective browsing, seed dispersal, and (or) seed predation by tapirs are difficult to evaluate and predict. The effects of browsing on the plant and animal communities have been documented for several species of herbivores in different environments. African elephants (*Loxodonta africana*) can create major landscape changes (Barnes 1983; Laws 1970). White-tailed (*Odocoileus virginianus*) deer can affect hemlock (*Tsuga* sp.) regeneration, resulting in the dominance of sugar maples in some areas of the Porcupine Mountains in Michigan, U.S.A. (Frelich and Lorimer 1985; similar examples are given in Austin and Urness 1992; Irons et al. 1991; Wolff 1978).

In the northwestern U.S.A., the longer term dynamics of forests appear to be more influenced by larger scale phenomena such as fires. Thus, the importance of herbivory in the composition, structure, and dynamics of forests depends on the scales of other disturbances (Woodward et al. 1994). Major blowdowns occur in areas of the tropics exposed to storms, but apparently no large-scale disturbances occur in the Amazon Basin, therefore Neotropical ungulates, especially tapirs, may play a fundamental role in the dynamics of these forests.

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