Habitat use by lowland tapirs (*Tapirus terrestris* L.) in the Tabaro River valley, southern Venezuela

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Abstract: This study presents an analysis of habitat use by lowland tapirs (*Tapirus terrestris* L.) in the Tabaro River valley of southern Venezuela. Five different habitat types were recognized in the study area and their proportions determined. Treefall gaps within these habitats were also analyzed as a distinctive type. The presence of tapirs was determined by following fresh tracks, counting tracks found by walking along transects and creeks, and checking gaps and closed-canopy areas of equal size for browsing signs. The numbers of tracks and sightings recorded near to and away from the water were compared for two periods of the year to assess changes in habitat use due to the availability of fruits of one food-plant species. Assessment of habitat use by counting or following tracks in each habitat type was biased toward moist soils. Tapirs forage preferentially in gaps and use all areas of the forest, but a significantly larger number of signs was found in lower elevation areas. A preference for lower elevation areas is correlated with the abundance of the commonest food-plant species. Tapirs may change their foraging behavior and habitat use to ingest more fruits of plant species in season.

Résumé : Nous avons étudié l'utilisation de l'habitat par des tapirs *Tapirus terrestris* L. dans la vallée de la rivière Tabaro, dans le sud du Vénézuéla. Cinq types d'habitats ont été reconnus et leurs proportions relatives dans la zone d'étude ont été déterminées. Des vides laissés par des arbres tombés dans ces habitats ont également été intégrés dans les analyses. La présence des tapirs était détectée par observation des pistes fraîches, par dénombrement des pistes le long de transects et le long des ruisseaux et par recherche de signes de broutage dans les zones découvertes et dans des zones de forte couverture de mêmes dimensions. Nous avons comparé les nombres de pistes et de rencontres enregistrées près ou loin de l'eau, à deux moments de l'année, dans le but d'évaluer les déplacements reliés à la disponibilité des fruits d'une espèce consommée. Le dénombrement et l'observation des pistes dans chaque type d'habitat permettent d'établir que les tapirs préfèrent les sols humides; ils cherchent leur nourriture surtout dans les zones découvertes et utilisent toutes les zones de la forêt, mais un nombre significativement plus grand de signes de leur présence a été enregistré dans les zones basses. Cette préférence pour les zones basses a pu être reliée à l'abondance de l'espèce consommée la plus abondante. Les tapirs peuvent modifier leur comportement de quête de nourriture et leur utilisation de l'habitat pour consommer plus de fruits des espèces de saison.
[Traduit par la Rédaction]

Introduction

Information on how an animal uses the environment is crucial for developing appropriate conservation and management plans (Caughley and Sinclair 1994). Lowland tapirs (*Tapirus terrestris*) have a selective diet (Salas and Fuller 1996). Because Neotropical rain forests are not uniform habitats and some plant species occur in particular habitat types within these forests (Prance 1979; Foster and Brokaw 1982; Hartshorn and Hammel 1991; Kalliola et al. 1991; Salo et al. 1986), this selectivity could be strongly correlated with habitat use and foraging patterns. In this article, three different foraging behaviors related to habitat use by lowland tapirs are analyzed.

First, tapirs may forage preferentially around gaps (Fragoso 1991a). This hypothesis was tested and possible explanations

for this behavior are evaluated here. It has been proposed that absolute abundance and (or) diversity of plants and abundance of food-plant species may affect the browsing behavior of and habitat selection by okapis (*Okapia johnstoni*), an ungulate species in the Ituri forest of Zaire (Hart and Hart 1989). Like okapis, tapirs are large-bodied forest browsers, so the diversity and abundance of plants are evaluated here as variables possibly related to tapirs' foraging behavior.

Second, tapirs' use of gaps may differ among habitat types. Bodmer (1991) followed tracks of lowland tapirs in forest areas near Iquitos (northeastern Peru) and found that 15% of the tracks were in dry habitat, 45% in moist habitat, and 40% in wet habitat. Arguably, his methodology could have been biased toward moist and wet soils, and he failed to relate use to specific behaviors (Palomares and Delibes 1992). Naranjo (1995a) recorded tracks and sightings of Baird's tapirs in Corcovado National Park, Costa Rica, and found that they used lower elevation areas more frequently than expected. This study also aims to depict differences in habitat use for browsing among habitat types. Differences in the absolute number and (or) diversity of plants in gaps among different habitat types and the abundance of the commonest food-plant species are analyzed here as possible variables correlated with this behavior.

Third, tapirs may alter their foraging patterns and habitat use according to the availability of fruits. It is well known by local hunters that tapirs show fidelity to trails leading to commonly visited wallowing and feeding places such as fruit patches (Eisenberg 1989; Naranjo 1995*b*; personal observation). Indeed, lowland tapirs apparently change their foraging behavior to include more of the ripe fruits of the palm *Mauritia flexuosa* (Bodmer 1990). As is stressed by Bodmer (1990), the availability of *M. flexuosa* fruits on the forest floor affects tapirs' foraging patterns and perhaps habitat use. In Corcovado National Park, Baird's tapirs spent up to 15 min in ripe fruit patches and consumed approximately 75% of the available fruits in the patch (Naranjo 1995*b*). Fruit patches are ephemeral resources and tapirs' habitat preferences may vary according to the fruiting season of the plant species in their diet. A test was conducted to see if tapirs change their habitat use according to the availability of patches of one plant species, *Micropholis melinoneana* (Sapotaceae).

Even though a direct methodology (e.g., radio tracking) was not used in this research to determine the locations of the tapirs and type of behavior they were engaged in, information on the location of tracks and browsing signs was combined with information on how the animals alter their foraging behavior according to fruit and forage availability to derive an approximation of how tapirs use their surroundings.

Methodology

This research was conducted in the Tabaro River valley in southern Venezuela (6°21′17.9″N, 64°59′47.9″W; 120 m asl). A brief description of the study area is also provided in Salas and Fuller (1996), and a detailed description will be published elsewhere. Data on lowland tapirs' foraging behavior were gathered from October 1990 to June 1992, January to June 1993, and January to May 1994, mostly in the dry season. Thus, the habitat-use patterns reported here mainly reflect the tapirs' behavior in the dry season.

Five different habitat types were identified in the Tabaro River valley: creeks, inundated forests, terra firme forests, hillsides, and hilltops. Creek habitats include the shores of seasonal or permanent streams (sometimes extending several metres from the water) and any islands in the creeks. Certain plant species grow exclusively on river or creek shores (Kalliola et al. 1991; Salo et al. 1986). The inundated forests include any lowland forests that are seasonally under water. Terra firme habitats are forested areas that are a few metres higher than the inundated forests (see Salo et al. 1986). Hillsides are slopes of mountains and hills; several species of plants are apparently characteristic of this kind of habitat and of hilltops (Terborgh and Anderson 1994). Hilltops are the somewhat flat tops of the mountains and hills in the study area. Treefall gaps within each of these habitat types, as opposed to closed-canopy areas, were also recognized as distinctive habitats.

The abundance of each habitat type was determined as its proportional distance along the 22.5 km of transects and trails in the study area. The transects were placed every 500 m to form a grid covering 300 ha of the forest, and were oriented north–south and east–west. In addition, eight minor trails were set within this grid. These trails were 1 km long, parallel to each other, oriented north–south, and began in the basal transect of the grid (see Salas and Fuller 1996). A χ^2 test of homogeneity was performed to determine if a particular habitat was predominant. Treefall gaps can be more abundant and (or) larger in some kinds of habitat. To determine if treefall gaps were more numerous in particular habitat type, the number of gaps in each kind of habitat was compared with the expected number of gaps (estimated by multiplying the total number of gaps recorded by the proportion of each kind of habitat), using a χ^2 goodness-of-fit test. To determine if gaps were larger in any habitat type, the lengths of gaps along the transects in each habitat type were compared among habitat types with a one-way analysis of variance.

An effort was made to follow tracks to assess how tapirs use their habitats. Tracks were followed until they were lost; special care was taken to find and follow tracks in dry soils to reduce bias favoring track locations in moist soil areas. The distance covered following a track within each habitat type was recorded and compared with the expected value (calculated by multiplying the total distance covered by the relative abundance of each habitat type), using a χ^2 goodness-of-fit test. Another method of assessing tapirs' habitat use was to record tracks found by walking along the transects and trails and along creeks at the study site. Data recorded in this way were corrected for the proportion of area inspected (measured as the distance covered) within each habitat type and compared with expected values (estimated using the availability of each habitat type) with a χ^2 goodness-of-fit test. Every transect, trail, or creek was walked once a week or less. Even though similar methodologies were used in previous tapir studies (e.g., Fragoso 1991*b*; Bodmer 1991), they may strongly underestimate use in dry areas. To determine bias, the results obtained with these methodologies were compared with the abundance of other kinds of signs (i.e., browsing signs and sightings) recorded by walking along transects and creeks in each kind of habitat. Only plants distinctively browsed by tapirs (i.e., broken stems, branches with tooth marks, and (or) tapir tracks underneath) were recorded to minimize error due to counting browsing signs from other ungulates (e.g., brocket deer, *Mazama americana*, and peccaries, *Tayassu* sp.). The difference between the percentage of the distance covered following tracks and the proportion of other signs was so marked that no statistical test was performed to determine significance. A χ^2 goodness-of-fit test was done to compare the numbers of tracks observed by walking along transects and creeks with the expected numbers. The expected numbers were obtained by multiplying the total number of tracks found by the proportion of other signs in each habitat type. A significant deviation from the expected values would suggest bias in counting tracks.

The use of browsing signs as a measure of habitat selection may be less biased than counts of tracks, and these signs can be related to a specific behavior. In each habitat type 15 gaps were sampled for browsing signs, for a total of 75 gaps encompassing 6 ha of forest. These gaps were selected at random among all the gaps present within the 300-ha grid, including those not located along transects and trails. The mean area of the gaps inspected within each habitat type was determined and 15 areas of that mean size under closed canopy were selected at random and sampled in each habitat type. The numbers of browsing signs in gaps and closed-canopy areas were compared using a paired analysis of variance.

To determine if tapirs showed any preference for gaps in particular habitat types, browsing data from gaps only were analyzed. Pearson's correlation coefficient was used to determine if the number of browsing signs was correlated with the size of the gap. The results were significant for four habitat types ($r^2 > 0.44$, $P < 0.05$ in four cases). Therefore, an analysis of covariance was performed to test for preference among habitat types, using the natural logarithm of gap size as the covariate.

To determine the number of species and density of plants in each habitat type, five quadrats of 5 × 5 m were placed at random in gaps within each kind of habitat. The size of the quadrats was chosen so that they were no larger than the gap area but not too small to include enough plants. The same number of quadrats of the same size were also placed in closed-canopy areas, for a total of 50 quadrats. Plants potentially browsed by tapirs were identified and counted. Only plants at least 30 cm high and up to but no

Table 1. Proportion of each habitat type, number of treefall gaps, and total length of gaps along transects in each habitat type in the Tabaro River valley, southern Venezuela.

	C	IF	TF	HS	HT
Proportion of each habitat type (%)[a]	5	19	34.4	33.5	9.1
No. of gaps along transects in each habitat type[b]	10	39	70	78	12
Total length of gaps along transects in each habitat type (m)[c]	145	695	1025	1130	215

Note: C, creeks; IF, inundated forests; TF, terra firme forests; HS, hillsides; HT, hilltops.

[a]Cell values are significantly different (test of homogeneity, $\chi^2 = 37.86$, 4 df, $P < 0.01$).

[b]The number of gaps and the expected number of gaps in each habitat type are not significantly different ($\chi^2 = 1.18$, 4 df, $P > 0.1$, $\beta = 0.23$ for a medium effect size (sensu Cohen 1988)). The expected number of gaps was calculated by multiplying the total number of gaps (209) with the proportion of each habitat type.

[c]The length of gaps along transects in each habitat type is not significantly different (one-way analysis of variance, $F_{[4,204]} = 0.625$, $P > 0.1$, $\beta = 0.167$ for a medium effect size).

more than 5 cm in diameter at breast height (dbh) were considered. According to personal observations and reports from other authors, these are the size limits of plants on which tapirs can browse (Terwilliger 1978; Williams 1978).

The first set of analyses performed compared the numbers of plants and numbers of species between gaps and closed-canopy areas, using paired analyses of variance. The second set of analyses compared the numbers of plants and numbers of species in gaps among the five different habitat types, using one-way analyses of variance.

The plant species most frequently browsed by tapirs (*Amphirrox latifolia*, Violaceae; Salas and Fuller 1996) was considered for analysis to see if habitat choice was correlated with abundance of preferred food-plant species. Pearson's correlation coefficient was calculated between the abundance of *A. latifolia* browsing signs found in gaps and the abundance of *A. latifolia* in the 25-m² quadrats among habitat types. The degree of correlation between the abundance of *A. latifolia* browsing signs and the total abundance of browsing signs in gaps was also evaluated with Pearson's correlation coefficient.

Tapirs eat the fruits of at least 33 plant species (Salas and Fuller 1996). One of these species is *M. melinoneana*, a tree that grows mainly near the Tabaro River, and tapirs apparently show a strong preference for its fruits (personal observation). To evaluate if the distribution of patches of fruiting *M. melinoneana* in the forest is correlated with habitat selection by tapirs, the sightings and tracks within 500 m of and 500–2000 m from the river were counted and compared between the fruiting season of *M. melinoneana* (January to May) and the rest of the year, using a χ^2 goodness-of-fit test. Data were collected for 3 consecutive years, from January 1992 to May 1994. An effort was made to count each track only once, and search effort is assumed to have been equal for both areas. The expected number of signs for each area was calculated using the proportion of distance covered while searching for signs during each part of the year. A significant departure from the expected number of signs would show that the fruiting season of *M. melinoneana* is correlated with the presence of tapirs near the river. As mentioned earlier, information on the location of tracks may be biased if it is used to determine habitat preferences. However, such information is used here, because it is not taken as a measure of the

Table 2. Distance walked along transects and creeks, distance walked following tracks of tapirs, and numbers of tracks found along transects and creeks and other signs (browsing signs, sleeping places, and sightings) recorded in each habitat type in the Tabaro River valley, southern Venezuela.

	C	IF	TF	HS	HT
Distance walked along transects and creeks (km)	54.2	103.4	182.2	118.2	34.5
Distance walked following tracks (m)	4139	472	629	0	0
No. of tracks found along transects and creeks[a]	44	30	12	5	9
No. of other signs	11	13	13	12	5

Note: C, creeks; IF, inundated forests; TF, terra firme forests; HS, hillsides; HT, hilltops.

[a]Data are corrected for the proportion of distance walked along transects and creeks in each habitat type. The number of tracks found differs significantly from expected values calculated using the proportion of each habitat type ($\chi^2 = 424$, 4 df, $P < 0.01$), and the proportion of other signs in each habitat type ($\chi^2 = 56$, 4 df, $P < 0.01$).

spatial presence of the animals in the forest but as an indication of their presence in an area at different times.

Results

The commonest habitat types at the study area are terra firme forests (34.4%) and hillsides (33.5%). Inundated forests are well represented (19%) and creeks and hilltops are the least common habitat types (5 and 8.1%, respectively) (test of homogeneity, $\chi^2 = 37.86$, 4 df, $P < 0.01$; Table 1). Treefall gaps (a total of 209) are evenly represented in number (goodness-of-fit test, $\chi^2 = 2.465$, 4 df, $P > 0.1$, $\beta = 0.23$ for a medium effect size (sensu Cohen 1988)) and total gap area (analysis of variance, $F_{[4,204]} = 0.625$, $P > 0.1$, $\beta = 0.167$ for a medium effect size) in all habitat types (Table 1). In other words, no habitat type has more or larger gaps than the others.

The first method employed to estimate habitat use was to follow tracks. Almost 80% of the distance covered by following tracks was in creek habitats, the least represented habitat type (Table 2). This finding alone suggests a significant preference for creek habitats by tapirs. Records of the locations of browsing signs, sleeping places, and sightings collected by walking along transects and creeks indicate that tapirs use all habitat types in less unbalanced proportions (Table 2).

The second method used to assess habitat use by tapirs was to record the location of tracks found by walking along transects and creeks. Data were corrected for the proportion of distance walked in each habitat type (Table 2). Results show that 43.7% of tapir tracks were found in creek habitats. Significant differences were found when these results were compared with the abundance of each habitat type (goodness-of-fit test, $\chi^2 > 424$, 4 df, $P < 0.05$; Table 2). However, these results also differ from the proportion of other signs found in each habitat type (Table 2), indicating that this

Table 3. Average numbers of plants >30 cm high and <5 cm dbh recorded in five 25-m² quadrat samples in treefall gaps and closed-canopy areas within each habitat type in the Tabaro River valley, southern Venezuela.

	Treefall gaps		Closed canopy	
	Mean	SD	Mean	SD
Creeks	42	11.6	41.6	17.43
Inundated forests	40.4	10.69	42.8	13.07
Terra firme forests	64.4	52.08	45.2	11.52
Hillsides	60.8	19.92	57.2	12.6
Hilltops	55.4	11.78	48.4	7.16

Note: The difference in mean values within treefall gaps among habitat types is not significant (one-way analysis of variance, $F_{[4,20]} = 0.85$, $P > 0.5$, multiple $R = 0.38$, $\beta > 0.8$). The difference in mean values between treefall gaps and closed-canopy areas within each habitat type is not significant (paired analysis of variance, $F_{[1,40]} = 0.896$, $P > 0.35$, multiple $R = 0.413$, $\beta > 0.8$).

Table 4. Average numbers of plant species >30 cm high and <5 cm dbh recorded in five 25-m² quadrat samples in treefall gaps and closed-canopy areas within each habitat type in the Tabaro River valley, southern Venezuela.

|	Treefall gaps		Closed canopy	
	Mean	SD	Mean	SD
Creeks	18.8	5.26	22.2	6.76
Inundated forests	19	3.67	19.2	9.65
Terra firme forests	22.6	7.8	23.8	6.22
Hillsides	30	5.15	28.6	2.7
Hilltops	24.6	2.3	22.2	4.32

Note: The difference in mean values within treefall gaps among habitat types is significant (one-way analysis of variance, $F_{[4,20]} = 3.99$, $P < 0.05$, multiple $R = 0.67$). Tukey's simultaneous inference test shows that hillside habitats differ significantly from creeks and inundated forests in average number of species. The difference in mean values between treefall gaps and closed-canopy areas within each habitat type is not significant (paired analysis of variance, $F_{[1,40]} = 0.015$, $P > 0.35$, multiple $R = 0.413$, $\beta > 0.8$).

methodology is also biased (goodness-of-fit test, $\chi^2 > 56$, 4 df, $P > 0.05$).

Tapir browsing signs were more commonly found in treefall gaps (Fig. 1). Indeed, there is a significant difference in the numbers of browsing signs between closed-canopy areas and gaps (paired analysis of variance, $F_{[1,140]} = 84.423$, $P < 0.01$). A comparison of data from gaps among the five different habitat types shows that there is a significant difference between the numbers of browsing signs on hilltops and in the other habitat types, suggesting that tapirs prefer to forage in lower parts of the forest (i.e., creek habitats, inundated forests, and terra firme forests) (analysis of covariance, $F_{[4,68]} = 2.545$, $P < 0.05$, and post-hoc Tukey's test; the logarithm of gap area was used as the covariate) (Fig. 1).

Three different variables are used here to predict tapirs' habitat preferences. First, they may prefer areas with higher densities of plants of all kinds (both food and nonfood species). This hypothesis was tested by comparing the numbers of

Fig. 1. Average numbers of tapir browsing signs in treefall gaps (open bars) and closed-canopy areas (solid bars) within each habitat type in the Tabaro River valley, southern Venezuela. Habitat types are as follows: C, creeks; IF, inundated forests; TF, terra firme forests; HS, hillsides; HT, hilltops. Vertical lines represent standard deviations. The differences between gaps and closed-canopy areas are significant (two-way analysis of variance, $F_{[1,40]} = 84.423$, $P < 0.01$). A significantly larger number of browsing signs was found in gaps in creeks, inundated forests, and terra firme forests (analysis of covariance, $F_{[4,68]} = 2.545$, $P < 0.05$, and post-hoc Tukey's test; the logarithm of gap area was used as the covariate).
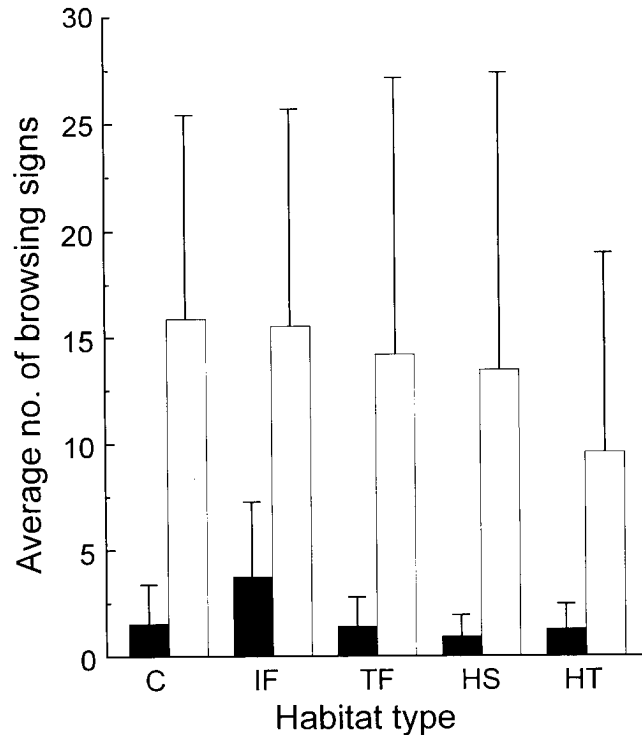
plants in quadrat samples between gaps and closed-canopy areas and comparing the numbers of plants in quadrat samples in gap areas among habitat types. In either case the result was not significant (paired and one-way analysis of variance, respectively, $F < 0.896$, $P > 0.35$, with 1,40 and 4,20 df, respectively; $\beta > 0.8$ in both cases) (Table 3). However, caution should be exercised when evaluating these results because the tests had very little power and there is a high risk of making a Type II error (Cohen 1988). A second pair of tests was performed using the number of species of plants found in quadrats in each habitat type. In this case, a significant difference was found among habitat types when only gap areas were considered (one-way analysis of variance, $F_{[4,20]} = 3.99$, $P < 0.05$; Table 4), but not between treefall gaps and closed-canopy areas (paired analysis of variance, $F_{[1,40]} = 0.015$, $P > 0.5$; $\beta > 0.8$, a low-power test; Table 4). Tukey's test of simultaneous inference showed that hillside habitats have a larger number of species than inundated forests and creek habitats. Hilltops and terra firme forests do not differ significantly in number of species from any other habitat type. These results do not resemble tapirs' habitat use; apparently there is no relationship between habitat

Table 5. Correlation between the abundance of *Amphirrox latifolia* plants and the number of tapir browsing signs in gaps among habitat types in the Tabaro River valley, southern Venezuela.

	Abundance of plants	No. of plants browsed in gaps	Total no. of plants browsed in gaps
Creeks	14	162	240
Inundated forests	25	148	230
Terra firme forests	3	89	213
Hillsides	1	86	199
Hilltops	0	24	129

Note: Data on the abundance of *A. latifolia* were collected from five 25-m^2 quadrat samples placed at random in treefall gaps and closed-canopy areas in each habitat type. Data on the number of plants browsed were collected by inspecting 15 gaps at random in each habitat type. The correlation between the abundance of *A. latifolia* plants and the number of *A. latifolia* plants browsed in gaps among habitat types is significant ($r^2 = 0.819$, $n = 5$, $P < 0.05$). The correlation between the number of *A. latifolia* plants browsed and the total number of plants browsed in gaps among habitat types is significant ($r^2 = 0.946$, $n = 5$, $P < 0.05$).

use and plant species diversity. Finally, a significant positive correlation was found between the abundance of *A. latifolia* browsing signs in gaps and the abundance of *A. latifolia* in quadrat samples ($r^2 = 0.819$, $n = 5$, $P < 0.05$; Table 5). Thus, tapirs browse more of this species of plant in the areas where it is more abundant. In addition, a significant correlation was found between the total abundance of browsing signs and the abundance of *A. latifolia* browsing signs ($r^2 = 0.946$, $n = 5$, $P < 0.05$; Table 5). In other words, tapirs appear to browse more in areas with higher densities of *A. latifolia*.

A significant difference (goodness-of-fit test, $\chi^2 = 29.4$, 3 df, $P < 0.001$) was found between the numbers of tracks and sightings of tapirs within 500 m of and away from the main river (500–2000 m) when the two periods of the year were compared (Table 6). Thus, there is a positive correlation between the availability of fruit patches in a particular area and the presence of tapirs. This suggests that tapirs may select habitat types seasonally, according to the abundance of fruits of particular species.

Discussion

A first attempt was made to determine habitat use by tapirs with the use of methodologies similar to those reported in the literature (Bodmer 1990; Fragoso 1991*b*). These methodologies could be biased; evidence may be more easily found in moist soils (see Naranjo 1995*a*). Indeed, the results obtained here, either by following tracks or by recording their location along transects and creeks, underestimated the use of some areas of the forest. The abundance of other signs collected also by walking along transects and creeks indicate more frequent use of dry soil habitats than is reported by recording or following tracks (Table 2).

The results presented here also show that tapirs forage preferentially in gaps, which are distinctive patches of secondary forest species (Brokaw and Scheiner 1989). Accordingly, Fragoso (1991*b*) and Naranjo (1995*a*) report Baird's tapirs using secondary forest at a higher frequency than

expected. Why do tapirs forage preferentially around gaps? It is possible that the density of palatable plants is higher in gaps, helping to explain why tapirs seem to prefer these areas of the forest. Nevertheless, no difference was found in the density of plants between gaps and closed-canopy areas. It is also possible that the diversity of plants in gaps is higher, potentially offering the animals a more mixed diet. Again, no significant difference was found in the diversity of plants between gaps and closed-canopy areas. Most likely, neither the abundance nor the diversity of plants influences the browsing behavior of tapirs.

Tapirs may browse preferentially in gaps to maximize their intake of food or energy. For instance, the risk of predation may force an animal to spend the least time necessary to acquire food (Stephens and Krebs 1986). But apparently there are no predators of adult tapirs (not including humans) in Neotropical forests. The only report in the literature of an adult tapir being eaten by a jaguar is in Quigley (1987), and he could not confirm that the jaguar killed the tapir. Other studies of jaguars do not report tapir kills (Emmons 1987; Rabinowitz and Nottingham 1986; Crawshaw and Quigley 1991). Schaller and Vasconcelos (1987) and Schaller and Crawshaw (1980) mention tapirs as prey but fail to report any kills. It is also possible that food limitations may force an animal to obtain the maximum possible amount of energy within a finite period of time (Stephens and Krebs 1986). Tapirs browse on plants everywhere in the forest (Fig. 1), and the abundance of food plants in the understory is greater than the amount of food that tapirs eat. Also, there is no reason to believe that tapirs are constrained in foraging time. Thus, they may not be foraging in gaps to increase foraging time efficiency.

Another possible explanation of habitat selection for browsing by tapirs is the increased palatability of plants in gaps (Cates and Orians 1975; Marquis 1992; Shure and Wilson 1993; Hart and Hart 1989). It is likely that the combination of increased palatability and higher density of plant material in gaps has an effect on tapir foraging behavior. Palatable material may be hard to find in the understory, and gaps may provide a dense patch of edible forage. According to this hypothesis, tapirs would be predicted to be less selective (i.e., browse on a larger variety of plant species) when foraging in gaps. This was indeed the case in the Tabaro River valley (Salas and Fuller 1996).

In addition to the fact that tapirs forage preferentially in gaps, some selectivity for particular habitats apparently exists. Since gap size and availability are factors that determine habitat use by tapirs when browsing, and gaps are evenly distributed in all habitat types in the study area (Table 1), no selectivity for any particular habitat type should exist. Interestingly, tapirs seem to avoid gaps in higher elevation areas (Fig. 1). Hence, one or more additional variables may play a role in habitat use for browsing by tapirs. These results concur with reports on Baird's tapirs (e.g., Naranjo 1995*a*). Naranjo (1995*a*) found Baird's tapirs more frequently than expected in low-elevation secondary forests in Corcovado National Park, Costa Rica.

It is possible that differences among habitat types in the absolute abundance of plants in gaps may be affecting habitat use by tapirs. But no differences among habitat types were found in the number of plants in gaps. A second possibility

Table 6. Numbers and expected numbers of tracks and sightings of tapirs recorded within 500 m of and 500–2000 m away from the main river during two periods of the year in the Tabaro River valley, southern Venezuela; data were collected during 3 consecutive years (1992–1994).

	No. of records		Expected no. of records[a]	
	<500 m	500–2000 m	<500 m	500–2000 m
January–March	52	33	28	34
April–December	25	52	42	58

Note: The difference between the number of records and expected values is significant ($\chi^2 = 29.3$, 3 df, $P < 0.05$).

[a]Expected values were calculated by multiplying the total number of records ($n = 162$) with the proportion of distance walked in each area during each period of the year.

is that plant species diversity may be higher in some habitat types in the forest. In Madre de Dios, Peru, differences in soil composition within the same forest create significant differences in plant species diversity (Gentry 1988; Dumont et al. 1990). In the Tabaro River valley, significant differences were found in plant species composition among habitat types. However, there is no apparent relationship between habitat use by tapirs and these differences in plant diversity. The only variable found here to be correlated with habitat use by tapirs among gaps in the five habitat types was abundance of food-plant species. Unfortunately, with the methods used here it is impossible to say if this reflects a cause or is an effect of habitat use by the animals.

Because tapirs have a selective diet, and break down and kill saplings of many selected tree species, Salas and Fuller (1996) speculate that tapirs may affect the composition of the tree community in the forest. It was found in this research that tapirs forage preferentially in low-elevation areas, therefore it is possible that they have a greater effect on the recruitment of tree species of such areas.

Tapirs eat a significant quantity of fruits (see Bodmer 1991; Salas and Fuller 1996), therefore they could be seeking patches of ripe fruits on the forest ground. Those patches will be located in areas of the forest where a particular tree species is more abundant. This is clearly a habitat-selection behavior that differs from the browsing activities described above. Bodmer (1990) documented and analyzed how tapirs use patches of fruits. The clumped distribution of the fruits requires the animal to change its foraging behavior to maximize the number of fruits ingested. Accordingly, these changes in behavior may cause tapirs to spend more time in habitats where the fruiting species is more common.

This hypothesis was indirectly tested by comparing the numbers of tracks found in the areas where a particular species of tree grows with those in other areas of the forest when *M. melinoneana* is fruiting and when it is not. The results suggest that tapirs spend more time near the main river when this species is fruiting. This change in habitat use and foraging patterns by tapirs is well known by the local Indians, who build stands under *M. melinoneana* trees where tapirs can be easily killed when they come to eat the fruits.

The methods used here could not determine whether *M. melinoneana* fruit patches cause tapirs to spend more time near the river. For instance, it could be the presence of patches of other species near the river whose fruits ripen at the same time as *M. melinoneana* that causes tapirs to spend

more time there. Additionally, the possibility that the use of fruit patches is affecting habitat selection for browsing, or vice versa, was not considered in our analyses. Since tapirs can walk long distances during the night (Eisenberg 1989; Williams 1978; personal observation), use of browsing habitats and fruit patches may be considered independent events.

Acknowledgments

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