BIOTROPICA 34(3): 468-474 2002

Habitat Use and Diet of Baird's Tapirs (*Tapirus bairdii*) in a Montane Cloud Forest of the Cordillera de Talamanca, Costa Rica¹

ABSTRACT

Results from 24 transects showed that tapirs were less abundant in areas with higher human presence. They also preferred less steep areas, especially as browsing sites. An analysis of feces showed that fibers were the largest component (40–55%) followed by leaves (10–30%) and twigs (15%). Bamboo (*Chusquea* spp.) was found in all samples and probably accounts for the high proportion of fibers. Twenty-seven plant species were identified to be eaten by tapirs.

RESUMEN

Estudios en 24 transectos señalan que las dantas son menos abundantes en sectores con mayor presencia humana. Las dantas resultaron ser más abundantes en pendientes bajas utilizadas como áreas de alimentación. Análisis adicionales de heces mostraron un contenido de 40–55% de fibras, 10–30% de hojas y 15% de ramitas. Todas las muestras contenían restos de bambú (*Chusquea* spp.) que probablemente corresponden al alto contenido de fibras. Finalmente se identificaron 27 especies de plantas que las dantas consumen.

Key words: alimentation; Costa Rica; danta; forestry; habitat use; mammal; montane cloud forest; tapir; Tapirus bairdii.

BAIRD'S TAPIR (TAPIRUS BAIRDII GILL) IS THE LARGEST TERRESTRIAL Neotropical mammal. Its range stretches from Veracruz in southeastern Mexico to the western cordillera of the Andes of Ecuador (Eisenberg 1989). It has been categorized as vulnerable according to the IUCN Red List of Threatened Animals (IUCN 1982) and populations in many areas are threatened by both the fragmentation of forests and hunting. In Costa Rica, the largest remaining populations of tapirs are in Corcovado/Osa, Guanacaste/ Santa Rosa, Arenal, the Cordillera Volcánica Central, the Llanuras de Tortuguero, and in the Cordillera de Talamanca/La Amistad (Matola *et al.* 1997). Most of these areas are partially protected by national parks. Baird's tapirs are protected by Costa Rican law (Matola *et al.* 1997).

Habitat use and foraging of Baird's tapir have been studied on Barro Colorado Island, Panama (Terwilliger 1978), in Belize (Fragoso 1987), in the Santa Rosa National Park, Costa Rica (Williams 1984), and in the Corcovado National Park, Costa Rica (Naranjo 1995a, b; Foerster 1998). All these studies were located in lowland rain forest or deciduous forests. In Costa Rica, the least fragmented forest types are pluvial lower montane forests and pluvial montane forests. The former occur at elevations from 1400 to 2300 m and make up a total of 21 percent of the remaining forests that have 80 percent or higher canopy closure. The latter occur at elevations from 2300 to 3200 m and make up 8 percent of all the remaining forests in Costa Rica (Sánchez-Azofeifa 1996). Very little is known about tapirs at this elevation. Therefore, the main goal of this study was to gather information on habitat use and diet of tapirs in a montane forest.

The study area was located in the northwestern part of the Cordillera de Talamanca near the village of Villa Mills, Costa Rica (Fig. 1). Elevation ranges from 2600 to 3200 m, and the forests are classified as "Tropical Montane Cloud Forests" (Kappelle 1996) dominated by two species of oak (*Quercus costaricenses* and *Q. copeyensis*). The structure of these forests is homogeneous at a large scale but very heterogeneous at a small scale; the heterogeneity is due to small and medium-size gaps caused by fallen branches or trees, and to variation in slope, soil, or dominating species like bamboos of the genus *Chusquea* (Blaser 1987).

The forests of the Talamanca mountain range are not only the largest continuous forested area in Costa Rica but also play an important role as biological corridors for tapirs and other large mammals. This is because they connect tropical rain forests of the lowlands with montane forests, as well as connecting the Atlantic and Pacific sides of the country. The climate in the study area is characterized

¹ Received 15 March 2000; revision accepted 3 November 2001.

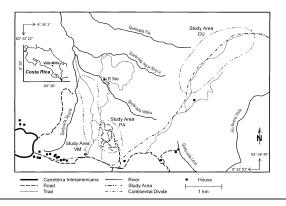


FIGURE 1. Location of the three study areas: Villa Mills (VM), Parcelas (PA), and Cerro Cuericí (CU).

by a dry season from January to April and a wet season from May to December. Mean annual rainfall at 3000 m is 2642 mm and the mean annual air temperature is 10.9°C, with a maximum of 22°C and a minimum below 0°C (Blaser 1987).

For this study, three sub areas were chosen (Fig. 1): (1) *Villa Mills* (VM)—This is the area closest to the village of Villa Mills. Elevation ranges from 2500 to 2800 m and the vegetation is all primary forest. The area is part of the Rio Macho Forest Reserve, established in 1964 (Kappelle 1996). Local people use the trails in this area a few times a week. (2) *Parcelas* (PA)—This area is used in an ongoing project on sustainable forestry carried out by the Centro Agronomico Tropical de Investigacion y Enseñanza (CATIE) in collaboration with the Ministerio de Ambiente y Energía (MINAE). Elevation ranges from 2650 to 2750 m. It consists of 11 different research plots in which 20–30 percent of the basal area of all trees was harvested in 1991 (Beek & Sáenz 1996). To extract the timber, an access road 5 m wide was built in 1990. Smaller logging tracks lead from this road to the different plots. During this study, there were no logging activities. The roads are not accessible to the public by car, but are frequently used by local people and visitors on foot. A more detailed description of the project can be found in Beek and Sáenz (1996). (3) *Cerro Cuerici* (CU)—This area lies on a mountain ridge of the continental divide and elevation ranges from 2800 to 3200 m. Much of this area is within Chirripó National Park, which was founded in 1975 (Kappelle 1996). This primary forest contains large old stands of bamboo (*Chusquea* spp.) and is rarely passed by pedestrians on the trail leading to Cuericí.

Tracks were used to determine the presence of tapirs. Twenty-four transects were laid, eight in each of the three study areas. In VM and CU, transects were laid perpendicular to the trail (alternating to the left and to the right) and had a length of 200 m, with 200 m separating them. The starting point of the first transect was selected randomly within 400 m of the trail. In PA, existing transects in eight of the plots of the CATIE/MINAE project were used. These were 120–220 m long and the distance between two transects was in some cases less than 200 m. Transects were visited 21 times between March and July 1999. They were usually checked in the morning between 0500 and 1100 h, and at least four days passed before the same transect was visited again.

The sampling unit was a 20 m length of transect, which is referred to here as a segment. The presence of tracks and the following habitat variables were recorded for each segment: height of the herb layer in cm (HERBH); percent cover of the herb layer (HERBC); height of the shrub layer in m (SHRUBH); percent cover of the shrub layer (SHRUBC); height of the tree layer in m (TREEH); percent cover of the tree layer (TREEC); passability (PASS); visibility in m (VIS); slope in degree (SLOPE); altitude in m (ALT); distance to the next water body in m (WATER); and distance to the closest human settlement in km (HUMSET). Following Kappelle (1996: 49), the herb layer was defined as all plants between 0.2 and 1.5 m tall and the shrub layer included all plants between 1.5 and 6 m tall. Height was measured as the average height of the plants in one layer. Passability was measured on a scale of 0 to 3, where 0 means that one can walk in a straight line without breaking any plants while 3 means that it is almost impossible to pass.

Area					Tracks		
	Transects			Days with			
	Ν	Total length (m)	Number of segments	Days with tracks ^a	tracks corr. ^{a,b}	Number of tracks ^c	
VM	8	1600	80	7	5.6	8	
PA	8	1280	65	4	4.0	7	
CU	8	1600	80	13	10.4	21	
Total	24	4480	225	24	19.0	36	

TABLE 1. Number of transects and tracks found in the three different areas.

^a Several tracks in the same area on the same day were only counted once.

^b Corrected for different total length of transects.

^c Several tracks on one transect on the same day were only counted once.

Kruskal–Wallis one-way ANOVA was used to test each single variable for differences between locations with and without tracks, and locations in which the animal browsed as opposed to just walking through. Discriminant analysis (DA) was used to determine the variables that best distinguish those locations. The DA assumes a multivariate normal distribution of the data, which rarely applies to ecological data (including that presented here); however, despite this limitation, the results of the DA give important information concerning the relationships between the variables (Williams 1984). Four variables were eliminated from the analysis; these included WATER, because there were missing values due to the impossibility of finding all small and temporal water bodies, and TREEH, HUMSET, and ALT, because they mainly separated VM and PA from CU and varied much less within the areas.

Feces are a good indicator of the composition of tapir diet. In his study on lowland tapirs (Tapirus terrestris), Bodmer (1991, pers. comm.) found that the composition of feces corresponded well with the composition of samples taken from stomach contents. Results from Foerster (1998) obtained by direct observations of Baird's tapirs in Corcovado also corresponded well with results obtained through fecal analysis by Naranjo (1995b) in the same area. Feces were collected on transects and in other regions of the study area. Samples were dried in the sun and stored in plastic bags for further analysis. The frequency technique (described in Naranjo 1995b) was used to determine the proportions of leaves, twigs, fibers, seeds, and fine material in the feces. All particles smaller than 1 mm² were considered fine material. For the analysis, a subsample of the feces was broken up and spread out on a 16.5×16.5 cm² square. One hundred points were systematically sampled using a comb with ten needles, spaced 1.5 cm, on ten columns, which were also separated by 1.5 cm. Any material present at the tip of a needle was identified and recorded. Three replicates were made for each pile of feces. MANOVA was used to find differences in the composition between different areas. Larger fragments of leaves and twigs found in the feces were identified to obtain information on the species eaten by tapirs. Furthermore, plants observed in the field that had been browsed by tapirs were identified; however, only browsed plants that were close to fresh tracks were taken into account.

Tracks were found on 7 days in VM, on 4 days in PA, and on 13 days in CU (Table 1). To determine the variables that influenced the presence or absence of tapirs in the different segments, the data from all areas were pooled. Of the total 226 segments on all transects, tracks were found on 35. The number of segments with tracks was almost equal in all three areas. Discriminant analysis showed a significant difference between segments with tracks and those without tracks (Wilks' lambda = 0.896, P < 0.005). Both DA and the Kruskal–Wallis one-way ANOVA indicated that SLOPE and HERBC were the most important variables (Table 2). Segments with tracks had a less steep slope and a lower herb cover.

Due to the small-scale heterogeneity of the environment, the possibility was high that a tapir might pass through an area it would not actively select. Therefore, the same analyses were used to test if there was a significant difference between segments in which tapirs just walked through (N = 18) and segments in which they browsed on plants (N = 17). Only SLOPE was significantly different (Kruskal–Wallis $\chi^2 = 5.946$, P < 0.005) with $8 \pm 7^\circ$ in segments in which they browsed and $18 \pm 12^\circ$ in segments through which they walked. The height and cover of the herb layer did not seem to influence the choice of a browsing site.

for description of variables.					-
Variable	Without tracks $\bar{x} \pm SD$	With tracks $\bar{x} \pm SD$	TCS	K–W χ^2	K–W P
HERBH	58 ± 24	53 ± 20	0.213	1.350	>0.05
HERBC	34 ± 22	24 ± 17	0.559	7.261	< 0.01
SHRUBH	3.1 ± 1.0	3.7 ± 1.7	-0.558	2.639	>0.05
SHRUBC	48 ± 26	52 ± 28	-0.171	0.691	>0.05
TREEC	81 ± 18	80 ± 26	0.052	0.263	>0.05
PASS	2.1 ± 0.8	2.0 ± 0.9	0.172	0.665	>0.05
VIS	7 ± 8	6 ± 6	0.059	0.030	>0.05
SLOPE	18 ± 12	13 ± 11	0.471	5.469	< 0.05

TABLE 2. Difference in the variables among segments in which tracks were found and segments in which no tracks were found. Discriminant analysis: TCS = total canonical structure; Wilks' lambda = 0.896, P < 0.005. See text

Feces were found at five different locations, of which three were on transects. Although tapirs have been reported to preferentially defecate in water (Terwilliger 1978, Naranjo 1995b; cf. Acosta et al. 1996), four of the five defecation sites discovered in this study were located on land (two of them less than 50 m from a small river). The fifth was in a small temporal river. A possible explanation could be that the rivers in the study area are fast running and have relatively steep banks, making them unsuitable as defecation sites. Four dung piles were found on two sites, one on site 3 and two on site 1. Each pile consisted of 20 to 40 balls. Different piles on the same site were usually about the same age, which indicated that the animal used the site for a couple of days but not over a longer time period. If the same site had been used over several months, older feces would have been noticed at the same place, as decomposition takes about three to four months.

Fibers made up the highest proportion of the 13 piles analyzed for composition (3 from VM and the rest in CU), while twigs and leaves were found in about equal and relatively low proportions. MANOVA and a univariate F-test showed that the proportion of leaves and fibers was significantly different between the two areas while twigs and fine particles were about equal (Table 3).

Twenty plant species eaten by tapirs were identified on browsing sites. An additional seven plant species were identified from leaves and twig parts found in feces (Table 4). Remains of Chusquea spp. were found in all fecal samples. The high proportion of fibers was probably due to these species. Other species frequently encountered were Q. costaricenses and several ferns that could not be identified. In the field, Anthurium spp., Chusquea spp., Buddleja spp., Columnea sp., and various ferns were often browsed. Usually, the tips of younger plants (<1 m) were eaten. Most of the time, some leaves remained on the plant. Often only one or two species were eaten in the same place, even though other plants eaten on other occasions were available. In many places, only a small number of plants were eaten before the animal moved on.

While Acosta et al. (1996) found that mountain tapirs (Tapirus pinchaque) in Colombia have a well developed network of trails and sleeping and resting places, in this study, trails were found almost exclusively in places with dense vegetation and were scarce in more open areas. Foraging and sleeping places were only used a few times. Tracks were rarely found twice at the same place. Areas with gentle slope were preferred for browsing but virtually all available slopes were used to some degree. Tracks, usually going straight up or down, were found on slopes up to 45°. Forage appeared to be more or less equally available in all parts of the transects; thus, the availability of forage did not appear to influence

TABLE 3.	Composition of the fecal samples and differences between the two areas. MAINOVA: Wilks lambda $P < 0.001$.				Wilks lambda = 0.356
	% All	% VM	% CU	F	Р
Twigs	14.4	14.3	14.4	0.001	>0.05
Leaves	15.3	26.0	11.7	50.099	< 0.001
Fibers	50.0	42.6	52.5	4.184	< 0.05
Fine	20.3	17.1	21.4	0.896	>0.05

Composition of the feed samples and differences between the two areas MANOVA: Wilks lambda = 0.356TADLE 2

Name	Family	Common name	Source
<i>Ilex pallida</i> Standl.	Aquifoliaceae	azulillo	f
Anthurium spp.	Araceae	anturio	b
Dendropanax sp.	Araliaceae	cacho de venado	b
Geonoma hoffmanniana H. Wendl. ex			
Spruce	Arecaceae	súrtuba	f
Jessea multivenia (Benth. ex Oerst.)			
H. Rob. & J. Cuatrec.	Asteraceae	quiebracha	Ь
Undetermined sp.	Bromeliaceae	piñuelas	f
Burmeistera sp.	Campanulaceae	*	Ь
Cecropia polyphlebia J. D. Smith	Cecropiaceae	guarumo	Ь
Hedyosmum bonplandianum Kunth	Chloranthaceae	aguila	Ь
Cornus disciflora Mociño & Sessé	Cornaceae	lloró	Ь
Weinmannia trianaea Wedd.	Cunoniaceae	arrayán	Ь
<i>Macleania</i> sp.	Ericaceae	colmillo	f
Vaccinium consanguineum Klotzsch	Ericaceae		f
Escallonia myrtilloides (Ruiz & Pav.)			
Sleum.	Escalloniaceae	carnitora	Ь
Quercus copeyensis C. H. Müll.	Fagaceae	roble	f
Q. costaricensis Liebm.	Fagaceae	encino	f
<i>Columnea</i> sp.	Gesneriaceae	santurio	Ь
Buddleja spp.	Loganiaceae	salvia	Ь
Miconia sp.	Melastomataceae	lengua de vaca	b
Miconia sp.	Melastomataceae	uña de gata	b
<i>Myrsine</i> sp.	Myrsinaceae	madurillo	Ь
<i>Fuchsia microphylla</i> Kunth	Onagraceae	madroncillo	Ь
Peperomia sp.	Piperaceae	hoja para escribir	Ь
<i>Chusquea</i> spp.	Poaceae	cañuela	b, f
Polypodium sp.	Polypodiaceae		b, f
Rhamnus oreodendron L. O. Williams	Rhamnaceae	duraznillo	Ь
Zanthoxylum sp.	Rutaceae	lagartillo	b
4 Unidentified species of ferns.			b, f

TABLE 4. Plants found to be eaten by tapirs at (b) browsing sites and from (f) fecal analysis.

the presence of tapirs in the study area. Indeed, areas with less herb cover even seemed to be preferred. Naranjo (1995a) had also found a significant influence of slope on the habitat use of tapirs in Corcovado while the vegetation seemed to be of less importance.

Elevation within a range of 2500 to 3200 m did not seem to influence the use of an area. More tracks were found in the higher area (CU) but this was probably due to other factors, particularly disturbance. The fact that tapirs use areas above the tree line was seen on an excursion to Chirripó in July 1999, when fresh tracks and feces were found in the area of "Lago Chirripó" at an elevation of 3650 m in the paramo vegetation.

As in other areas (Terwilliger 1978, Williams 1984, Naranjo 1995b, Foerster 1998), tapirs in the study area exhibited a varied diet. Some plants, however, seemed to be preferred over others. The proportion of 12 to 26 percent leaves in the diet is low compared to 67 percent found for tapirs in Corcovado (Foerster 1998) and 30 percent for lowland tapirs (Bodmer 1991). On the other hand, the proportion of fibers in the diet was much higher in this study. *Chusquea* spp. seems to be of special importance. Species of this genus were found in all fecal samples and the high fiber content of the feces indicates a high proportion of these species in the diet of tapirs. This is supported by the difference in the composition of feces from VM and CU. Feces from CU, where *Chusquea* spp. are more abundant, contained more fibers and fewer leaves than feces found in VM. *Quercus costaricenses, Anthurium* spp., *Buddleja* spp., and *Columnea* sp. were often selectively browsed. These species are common in all parts of the forest. Although fruits were found to be an important part of the tapir diet in the lowlands (Terwilliger 1978, Williams 1984, Bodmer 1991, Naranjo 1995b, Foerster 1998), they seem to be of little importance in this study area. This can be explained by the low availability and small size of the fruits in montane cloud forests at this elevation. Therefore, tapirs in this study area do not seem to have an important role as seed dispersers as suggested by Olmos (1997) for the lowlands. Acorns may make some contribution

to the diet of tapirs during the fruiting period of the oak trees, which occurs every four years or less (Camacho & Orozco 1998). Williams (1984) found them to be eaten in large numbers by tapirs in the Santa Rosa National Park.

Greater proximity to the village can explain the lower number of tracks in VM and PA compared to CU. Due to intensive hunting in the past (C. Solano, pers. comm.) and disturbance by humans and dogs, these areas probably are still avoided. Nevertheless, tracks and a sleeping place were found as close as 300 m from the next house. The difference between VM and PA could also be related to a higher presence of humans in PA. Tracks found on forest roads on different occasions indicate that tapirs did not avoid them; however, forest roads and trails allow easier access to the forest and local people use them to collect firewood and non-timber forest products like wild berries, mosses, and plants. This causes a constant disturbance that could make tapirs avoid these areas. Some control of these activities with restrictions on time and/or area being used would be important in a larger forest management project.

Except for the human disturbance, the impact of the forestry project in PA seems to be low. In all places in PA where tracks were found, there were many browsing signs, which indicates that the habitat is suitable for tapirs despite the timber extraction. Sites with a gentle slope are preferred for forestry but are also the ones most used by tapirs for foraging. This should be taken into consideration when planning forestry projects. While dense stands of *Chusquea* inhibit the growth of tree saplings (Widmer 1998), they are very important for tapirs as foraging and sleeping places. Therefore, some stands of *Chusquea* should be left to grow old within a managed area.

Forest activities are temporally concentrated in this region; felling cycles are estimated to be about 28 years for the forest in the study area (L. Quirós, pers. comm.). This causes a disturbance for tapirs only during a relatively short time period. Providing that there are sufficiently large, undisturbed areas in which tapirs can retreat during this time, they will probably start using the area again shortly after the disturbance.

I thank CATIE for support given to this work and MINAE for permission to work within the Chirripó National Park. A special thanks goes to Grace Sáenz, Ligia Quirós, Geoffrey Venegas, and Marlen Camacho. I also thank Oscar Araya Mena and Alvaro Abarca Abarca for assistance in the field; Johnny Perez Nuñez from CATIE for help with statistics; José González from INBio and Marvin Mena Granados for their help with identification of plant material; Eduardo Carrillo from CATIE and Mike MacCoy from the Universidad Nacional in Heredia for suggestions on the methods; Dr. P. J. Edwards and Dr. Frank Klötzli from the Swiss Federal Institude of Technology, Robin Schramm, Jennifer Marion Adeney, and Lucio Pedroni for valuable suggestions on the manuscript; Yvonne Widmer-Edwards for help in preparing the project in Switzerland; my family for their support during the entire study; and the Collado family for their hospitality every time I went to Heredia.

- Acosta, H., J. Cavelier, and S. Londoño. 1996. Aportes al conocimiento de la biologia de la danta de montaña *Tapirus pinchaque*, en los Andes Centrales de Colombia. Biotropica 28: 258–266.
- BEEK, AUS DER R., AND G. SAENZ. 1996. Impacto de las intervenciones silviculturales en los robledales de altura: estudio de caso en la Cordillera de Talamanca, Costa Rica. Rev. For. Centroamericana 17: 30–37.
- BLASER, J. 1987. Standörtliche und waldkundliche Analyse eines Eichenwolkenwaldes (*Quercus* spp.) der Montanstufe in Costa Rica. Göttinger Beiträge zur Land- und Forstwirtschaft in den Tropen und Subtropen.
- BODMER, R. E. 1991. Influence of digestive morphology on resource partitioning in Amazonian ungulates. Oecologia 85: 361–365.
- CAMACHO, M., AND L. OROZCO. 1998. Patrones fenológicos de doce especies arbóreas del bosques montano de la Cordillera de Talamanca, Costa Rica. Rev. Biol. Trop. 46: 533–542.
- EISENBERG, J. F. 1989. Mammals of the Neotropics, volume 1: The northern Neotropics—Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, Illinois.
- FOERSTER, C. R. 1998. Ecología de la danta Centroamericana *Tapirus bairdii* en un bosque húmedo tropical de Costa Rica. M.S. thesis. Universidad Nacional, Heredia, Costa Rica.
- FRAGOSO, J. M. 1987. The habitat preferences and social structure of tapirs. M.Sci. thesis. University of Toronto, Ontario, Canada.
- IUCN. 1982. The IUCN mammal red data book, part 1. International Union for Conservation of Nature and Natural Resources, Gland, Switzerland.
- KAPPELLE, M. 1996. Los bosques de roble (Quercus) de la Cordillera de Talamanca, Costa Rica: biodiversidad, ecología, conservación y desarrollo. Universidad de Amsterdam y Instituto Nacional de Biodiversidad (INBio). Amsterdam, The Netherlands and Santo Domingo de Heredia, Heredia, Costa Rica.
- MATOLA, S., A. D. CUARÓN, AND H. RUBIO-TORGLER. 1997. Status and action plan of the Baird's tapir (Tapirus bairdii).

In D. M. Brooks, R. E. Bodmer, and S. Matola (Compilers). Tapirs—Status survey and conservation action plan, IUCN/SSC tapir specialist group, pp. 29–45. IUCN, Gland, Switzerland.

NARANJO, P. E. 1995a. Abundancia y uso de habitat del tapir (*Tapirus bairdii*) en un bosque tropical humedo de Costa Rica. Vida Silvestre Neotrop. 4: 20–30.

—. 1995b. Habitos de alimentación del tapir (*Tapirus bairdii*) en un bosque tropical húmedo de Costa Rica. Vida Silvestre Neotrop. 4: 32–37.

OLMOS, F. 1997. Tapirs as seed dispersers and predators. *In* D. M. Brooks, R. E. Bodmer, and S. Matola (Compilers). Tapirs—Status survey and conservation action plan, IUCN/SSC tapir specialist group, pp. 3–9. IUCN, Gland, Switzerland.

SANCHEZ-AZOFEIFA, G. A. 1996. Assessing land use/cover change in Costa Rica. Ph.D. dissertation. University of New Hampshire, City, New Hampshire.

TERWILLIGER, V. J. 1978. Natural history of Baird's tapir on Barro Colorado Island, Panama Canal Zone. Biotropica 10: 211–220.

WILLIAMS, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology 64: 1283–1291.

WILLIAMS, K. D. 1984. The Central American tapir (*Tapirus bairdii* Gill) in northwestern Costa Rica. Ph.D. dissertation. Michigan State University, East Lansing, Michigan.

Mathias W. Tobler²

Proyecto Silvicultura de Bosques Naturales CATIE, Turrialba Costa Rica

² Current address: Eselweidweg 30, 8833 Samstagern, Switzerland; e-mail: matobler@gmx.net

¹ Received 10 September 1999; revision accepted 23 September 2001.