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THE CENTRAL AMERICAN TAPIR (TAPIRUS BAIRDII GILL)
IN NORTHWESTERN COSTA RICA

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THE CENTRAL AMERICAN TAPIR (*TAPIRUS BAIRDII* GILL) IN NORTHWESTERN COSTA RICA

By

Keith David Williams

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ABSTRACT

THE CENTRAL AMERICAN TAPIR (TAPIRUS BAIRDII GILL)
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By

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Tapirs were studied in Santa Rosa National Park (SRNP) between February 1981-83. A population of 17-26 animals was estimated to exist there.

In SRNP 54 plant species were positively identified as tapir forage. An additional 68 species were browsed by tapirs, deer, peccaries or horses. When the availability of leafy forage diminished in the dry-season due to the abundance of deciduous plants, tapirs consumed large quantities of fallen fruits.

A tame zoo tapir was presented with pair-wise choices of 61 plant species, 40 known to be tapir browse. Relative selectivity could be determined only broadly and there were seasonal differences with some species tested. Percentage acceptability was found to be an imprecise method for determining preferences.

Seeds and fruit parts of 33 species were identified in tapir dung. The seeds of five of these species were small, occurred only once or twice, and were probably ingested with browse as were 20 other unidentified seed species.

The germination potential for six seed species which passed through the tapir gut alive were tested. Four demonstrated improved potential, one exhibited no change, and one showed a possible decrease of potential.

Three tapirs were captured and radio-collared. A female was lassoed and two free-ranging males were captured with projectile syringes containing 2 mg of etorphine hydrochloride with acepromazine. The males were radio-tracked for 12-hour daytime and night-time periods between March and December 1982. The female was located only 19 times between May 1981 and December 1982.

Activity ranges of the two male tapirs were estimated using a non-parametric computer method for determining utilization distributions. The night-time range of 1.80 km^2 for one male tapir was 12 times that of his daytime range; that for the other male, 1.61 km^2 was 6 times his daytime range. Estimated activity ranges were utilized to examine habitat use and preferences.

Tapirus bairdii was found to prefer a structurally multi-layered forest. Ideally this contains mature evergreen trees, woody shrubs and saplings in the understory, and patches of dense cover for daytime retreat, all located near permanent water.

Recommendations for tapir conservation in SRNP, and Costa Rica generally, were made.

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INTRODUCTION

Present-day tapirs, one-third of the triad of living Perissodactyls (tapirs, equids, rhinos) have changed little in form since the Miocene. Once widespread, they are now restricted to the tropical zones of Southeast Asia (*Tapirus indicus*) and Central and South America (*T. bairdii*, *T. terrestris*, *T. pinchaque*).

The neotropical species are believed to have arrived during different periods of faunal interchange between the continents of North and South America and not as a result of post-arrival differentiation of one or more parent stocks (Hershkovitz, 1969:13).

Quaternary movement was almost entirely by way of the Isthmian land bridge, but in later epochs land-based mammals could have utilized either this passage or travelled via the Antilles (Hershkovitz, 1969). *Tapirus terrestris* may have reached the eastern side of the Andean Cordilleras via this route. Hershkovitz (1969:26) believes that prototypes of *terrestris* and *pinchaque* "almost certainly reached South America by the oversea route, but at widely separated periods when climates and continental topographies were significantly different." *Tapirus bairdii* is considered (Hershkovitz, 1969) to be a late arrival in Middle America arriving in the late Tertiary to Recent periods.

Tapirus bairdii is a large (250 kg bodyweight) herbivore which historically occupied habitats including dry forest, monsoon forest and paramo from southern Veracruz and eastern Oaxaca Provinces in southern Mexico (Leopold, 1959) through the several Central American countries to the west coasts of Colombia and Ecuador. In Colombia they were reported to be sympatric with _T. terrestris_ in the northwest (Hershkovitz, 1954). Though Hershkovitz (1969:26) states that "inter-specific competition is not a factor in limiting tapir dispersal" no studies have been made to verify this. The species has been extirpated from El Salvador and possibly Mexico (IUCN, 1982) but is still fairly common in Belize (J. Fragoso, unpubl. ms.) and presumably also in adjacent, undeveloped areas of Guatemala. IUCN (1982) effectively summarizes the situation in other Latin American countries.

Historically, the area now called Costa Rica was almost entirely forested and it can be securely stated that _T. bairdii_ occurred over most of the country. The drier northwest region and the paramos, however, probably always supported less-dense populations. Vaughan (1983:17) lists a pre-conquest dense-forest coverage (80-100% cover) suitable for _T. bairdii_ as 48,845 km^2. By 1940 one-third of that forest cover had been removed, and by 1977 only one-third remained (15,901 km^2) (Vaughan, 1983). In 1977 an additional 7,882 km^2 of forest of 45-80% cover existed (Vaughan, 1983).

Costa Rica has a well-established national park system. Additional forested lands are maintained by the Forestry Service, the Agricultural Development Institution (indian reservations), the Organization for Tropical Studies, and the Tropical Science Center. These account for 23% of the national territory (Vaughan, 1983).

Tapirs and many other wildlife species are totally protected by law in Costa Rica. Except in the national parks, however, the enforcement of this law is extremely limited due to a virtual total lack of wildlife law officers. Other civil authorities, such as the police or rural guard, are either unaware of or choose to ignore wildlife law enforcement.

This study was initiated to establish base-line data on the species and to improve the meagre understanding of its natural history so that management recommendations could be made on a scientific basis.

STUDY AREA

Established in 1971, Santa Rosa National Park (SRNP) was the first national park in Costa Rica. Its 10,800 ha, situated in the northwest province of Guanacaste (Figure 1), are bounded by the Inter-American Highway to the east, the Gulf of Guayabo to the west, and cattle ranches to the north and south.

Topographically, it can be divided into 3 parts: the upper plateau, lower valleys, and intermediate hillsides. Canyons are steep in the upper reaches of the 3 largest westward-flowing rivers (Nisperal, Calera, and Poza Salada). Virtually all of the park has been disturbed (A notable exception is the upper reaches of the Rio Poza Salada.) and much of the plateau area is man-induced savanna with disjunct forest patches. Santa Rosa has a 200-year history as a cattle ranch. It has been cut-over for marketable timber, has had patches cleared for subsistence agriculture by squatters, and the tidal mangrove swamps have been modified for the production of salt (the Trino Davila salina). Bonoff and Janzen (1980) and Janzen (1980) give habitat descriptions applicable to the entire park.

The rainfall is concentrated in one wet-season between late April-May and late November. A dry period ("veranillo") of about 3 weeks occurs usually in July. 1982 was an unusually dry year. In SRNP, the dry-season is characterized by strong NE trade-winds, the loss of leaves in deciduous forests, and the drying-up of rivers

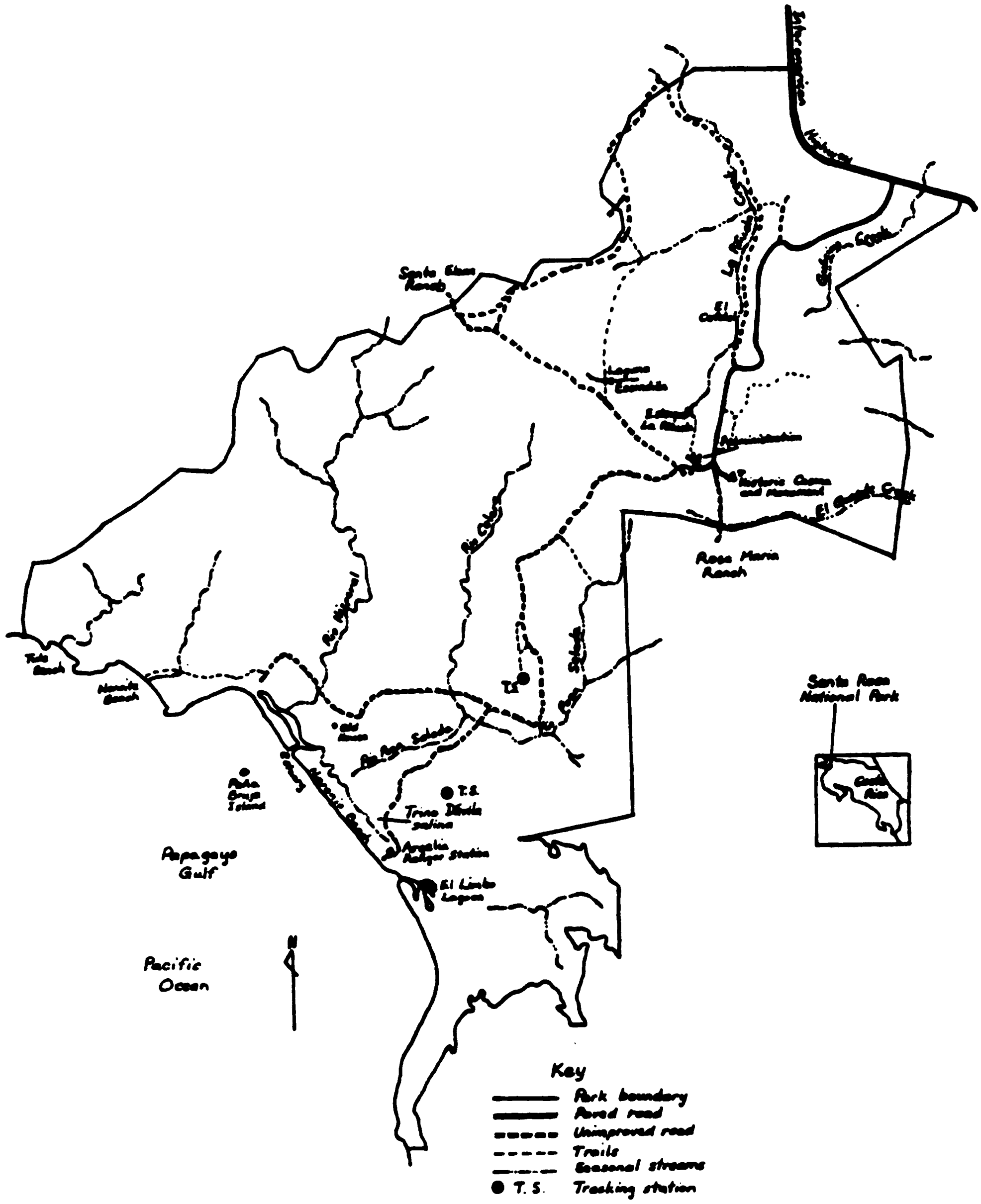


Figure 1. Santa Rosa National Park, Guanacaste Province, Costa Rica.

and streams. The very low dry-season water availability contrasts with that available in the wet-season when rivers fill and some local flooding occurs.

Park guards regularly patrol the area and the poaching of park animals is considered to be negligible. During the peak of the dry-season, horses used for patrols are permitted to range freely on the plateau and are required to use the few waterholes available.

National Parks Service policy is to return SRNP to a semblance of its pre-ranch appearance. Traditionally, national parks are considered to be extensive areas of distinct, naturally-occurring, vegetative cover and its associated animal life. Many national parks contain other natural phenomena. Where such areas are not available for national park designation, it is commendable when smaller areas of such vegetative cover are grouped and protected by national park legislation. Management to permit these smaller areas to expand and coalesce then serves national park goals.

This situation occurs in SRNP where habitat management is limited to burns of the savanna grasses and the planting of 1 ha plots of the fast-growing tree *Bursera simaruba* and *Ficus* spp. Burns, ideally used to suppress herbaceous vegetation (especially the tall pasture grass *Hyparrhenia rufa*) and encourage the re-establishment of woody vegetation, frequently become wildfires and destroy regrowth of woody species at the forest edges.

Light use is made by visitors of the few marked trails and the beaches. Visitor use is heavier in the dry season. Most of the park is undisturbed by human activities throughout the year.

The investigator resided in the park for the duration of the study which was continuous from February 1981 to February 1983. While all areas of the park were visited, the study was concentrated in the lower reaches of the Naranjo beach watershed and on the upper plateau to the north of the administration area (Figure 1).

METHODS

A. Forage consumption

As in Malaysia (Williams, 1978; Williams and Petrides, 1980), direct observation of browsing tapirs was rarely possible and indirect methods of determining what, when and how tapirs browsed had to be used. Three methods were adopted:

(1) Direct observations of browsed plants

Transect lines were walked through all habitat types in order to locate browsed plants. Lines were spaced at 50 m intervals, or as close to this as possible, using roads, rivers and trails as beginning and ending points. Browsed plants were recorded as to total height, height browsed, number of leafy tips eaten, whether the plant evidently had been broken, and if it had regenerated after browsing. A sample of each browsed species was collected, pressed and dried for later identification. As tapirs often break woody vegetation to reach foliage, special attention was given to damaged plants. Any that had been browsed by tapirs, as evidenced by teethmarks or other mode of browsing (Figure 2) were noted. It was not always possible to distinguish between tapir and deer (Odocoileus virginianus) browse with certainty unless it was damage-associated. Browse below 75 cm height also could have been taken by peccaries (Tayassu tajacu and T. pecari).

(2) Forage choice tests

To ascertain relative preferences for 61 plant species (40 of which were known tapir browses), an experiment was conducted between

Figure 2. Examples of tapir-browsed saplings, Santa Rosa National Park, Costa Rica, 1982.

September 4 and November 14, 1982. Plants were collected from forests and forest edges in the upper plateau of SRNP and placed in large plastic bags which were sealed. Woody samples always included at least one growing tip and an abundance of leaves or leaflets. Herbaceous samples were taken as whole plants, or with at least three intact leaves. Vines and climbing ferns were collected as lengths with attached leaves or pinnae.

Plants were gathered in the early afternoon and were transported to the higher elevation and cooler climate of San Jose. The following morning, and for the following two consecutive mornings, the plants were offered to a male tapir in the San Jose Zoo (Parque Zoologico Simon Bolivar) prior to its regular feeding time. The tapir had been wild-caught but had been in captivity for more than 9 years. Zoo records did not include data concerning its approximate age or place of origin. The normal food of this tapir, a small individual, consisted of crudely-chopped vegetables, bananas and rice polishings (husks). Fallen leaves from an overhanging guava (*Psidium guajava*) were readily consumed, as were occasional fruits from the same tree.

Plant samples were offered two species at a time to enable pairwise comparisons to be made. The tapir readily accepted proffered plants and stood at the feeding site in excess of 50 minutes each day. At each trial it was assured that the tapir first had been given ample opportunity to smell both proffered species. After foliage was chosen from one of the two samples, that sample was removed and recorded as the preferred species. The second species was then tested as to acceptability. Rejection of a sample was indicated by the tapir turning his head to one side, by his pushing his nose around the sample in search of something else, or by the sample being briefly chewed and spat out. On very few occasions both samples in the species-pairs offered were rejected. Time limitations and the very large number of possible combinations precluded the testing of all combinations.

(3) Macroscopic fecal analysis

Regular efforts were made in SRNP to find fresh tapir dung. Tapir droppings were encountered most often in pools along watercourses during the dry-season and also in gullies and other pools during the wet-season. A total of 124 dung samples were collected and washed over three graduated wire-mesh screens to collect seeds and identifiable plant fragments. Seeds were classified as alive if they were firm to the touch and showed no evidence of possible penetration by digestive fluids. Fruit availability to tapirs was recorded from observations of plants made throughout the year.

B. Ingested seeds and germination

Following washing, live seeds collected from tapir dung were placed on moist paper in plastic petri dishes. At the same time seeds taken from mature forest fruits were similarly treated. The petri dishes were examined each two days initially, and at varying intervals later, and the number of germinated seeds recorded. Germination was signaled by the emergence of the epicotyl.

C. Tapir capture and radio-collaring

Four methods of capturing tapirs were attempted but only lassoing and immobilization by darting were successful.

(1) Lassoing

Lassoes used for catching horses and cattle were thrown by experienced local personnel to capture a stationary tapir resting in a pond during daylight hours.

(2) Darting

Blinds were set up near pools in dried-up river-beds that tapirs were known to frequent. Nocturnal vigils were kept from about 4:00 p.m. until 6:00 a.m. Daytime searches for tapirs were also undertaken. The drug "Immobilon" (etorphine hydrochloride 2.45 mg ml^{-1} with acepromazine) was used in conjunction with a long-range "Cap-chur" gun and projectile syringes. "Revivon" (diprenorphine), a specific antagonist of etorphine, was used to counter "Immobilon's" effect. Tapirs were darted in the rump.

Once captured, tapirs were fitted with radio-collars. Collars had 10 cm whip antennas and were supplied by Telonics, Inc., of Arizona. Transmitter frequencies were in the 150 MHz band.

(3) Trapping

Six traps of sawn timber, each with two woven-wire drop-gates, were set in the forests on tapir trails of recent use. Five were placed near water-holes. Initially, three traps 1.5 m wide x 4 m long with sides 1.5 m high were constructed. Later, the trap size was changed to 2.5 m wide x 3 m long and the parts made so that the devices could be completely disassembled for movement to another site. Each trap gate was designed to be sprung on a tapir's contact with a nylon trip-line set 30-40 cm high near the center of each trap. Guide fences (1 m high) were built to each gate post, or so as to lead an animal to the trap gate from either side (Williams, 1978 and 1979b) depending on the locality. Traps were camouflaged with vegetation taken from the forest and baited with bananas, maize, and local fruit. The bait was placed in a wire basket in the top center of the trap.

(4) Snaring

Rope snares were set on tapir trails and near water-holes when and where they could be monitored easily. Aldrich snare-release mechanisms (Anderson, 1971: 511) were constructed from 0.25 inch steel construction rod. Bananas were placed near snares as bait.

D. Radio-tracking

Two permanent radio-tracking sites were established atop steep hills overlooking the lowlands of the Naranjo basin. At each site two end-mounted 5-element yagi antennas, supplied by Telonics, Inc., were erected. Signals received by the identical antennas passed through a modifier designed to produce a deep, narrow null when the antennas were pointed at the transmitter and to peak maximally the signals on either side of the null. In practice the null was often a broad 10^{o}-15^{o} and the mid-point was taken as the correct direction to the transmitter. A degree-disk and pointer was attached to the antenna mast-support to facilitate readings.

From these tracking stations, bearings to radio-collared tapirs were taken each 15 minutes, when possible, over two consecutive nights (6:00 p.m. - 7:00 a.m.) or two consecutive days (7:00 a.m. - 6:00 p.m.) each week. Additional locations of the instrumented males and all locations of the female were obtained by either finding their bedding sites or by triangulation from known ground locations using a 5-element yagi antenna and a smaller H-antenna.

Data for the two males, obtained by telemetry, were analyzed by computer using the "utilization distribution" (UD) method of Anderson (1982) for the estimation of home range size. The method uses a Fourier transformation to smooth the bivariate probability density function (UD) and home range is estimated by drawing equal height contours (MAP - Minimum Area vs. Probability) around the UD. Readings for daytime (6:00 a.m. - 6:00 p.m.) and night-time (6:00 p.m. - 6:00 a.m.) were analyzed separately. Only the areas which accounted for 95% of an animal's activity (MAP (0.95)) were used to estimate home range so that outlying locations would not upwardly bias the estimate. Average daytime and night-time hourly movements by the male tapirs were calculated. The percentages of success of efforts made each hour to locate the male tapirs also were determined.

Locations of the instrumented female could be obtained only during daylight and were considered too few to analyze using Anderson's (1982) UD method.

E. Habitat description and use

In order to determine which vegetation-cover types were most used by the two radio-collared, male tapirs, the interspersion of the types occurring in the lower Naranjo basin was diagrammed from an aerial photograph. Delineated types were then checked with ground-truth surveys during the dry-season as leaf-loss permitted a better identification of deciduous areas. Observations of species dominating the canopy and present in the understory were made, along with plotless basal-area estimates using a "Panama" angle-gauge. Ten basal-area readings were taken at 25-pace intervals and averaged.

Anderson's (1982) UD, equal-height contours at MAP (0.95) and MAP (0.50) were employed to determine the extent of use by the radio-collared males of delineated vegetative-cover types. Generated contour diagrams and the habitat map were reduced to a common scale and the contour diagrams overlayed on the habitat map.

RESULTS

A. Habitat description

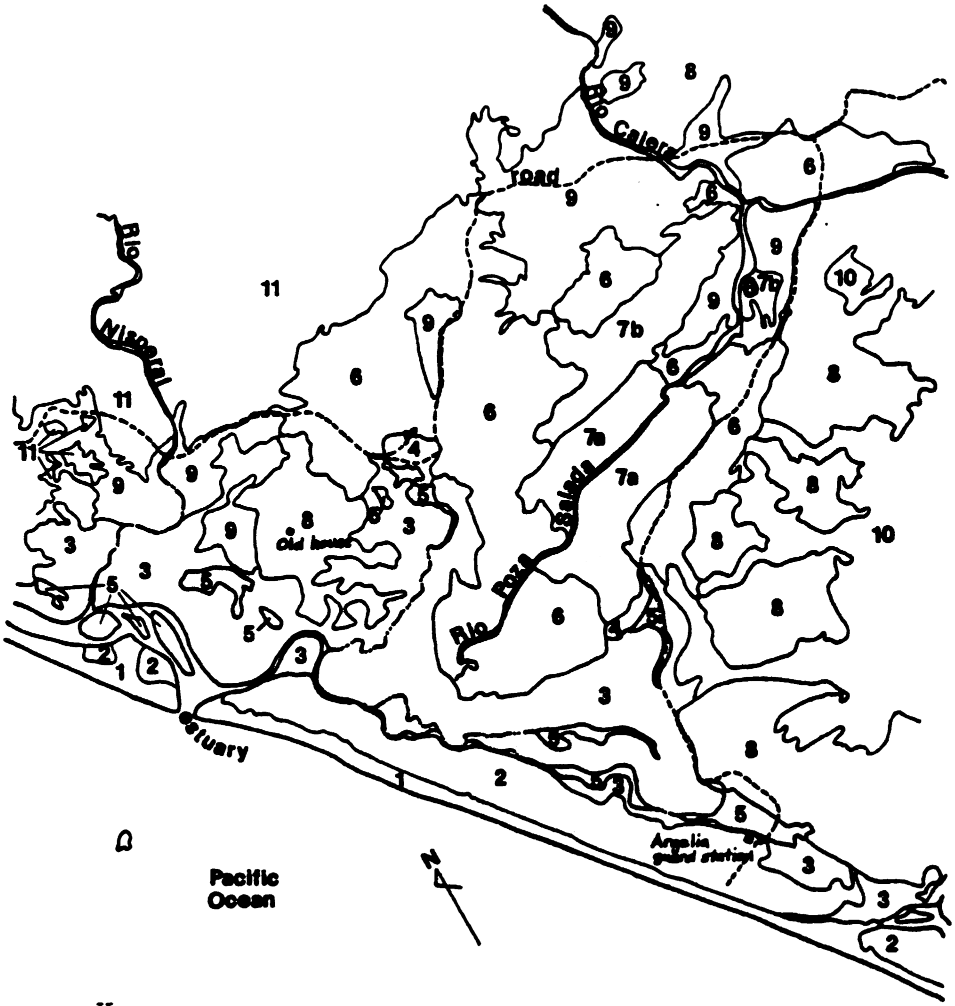
Data on the movements of radio-collared tapirs were concentrated in the park lowlands where the interspersion of vegetation types is complex (Figures 3 and 3a). Described below are the major types which are delineated.

Upper beach (2)

Situated between the ocean and tidal mangrove swamps, the upper reaches of the beach sands were vegetated mostly with woody plants between sapling and small tree size and with a basal area of 14.3 m^2 ha^{-1}. Dominant trees were *Simarouba glauca*, *Gliricidia sepium* and *Bursera simaruba*. Occasional mesquite (*Prosopis juliflora*) were present. The canopy was 1-5 m in height, with an occasional emergent to 10 m and a canopy closure of 20%. The understory was open. Understory species included *Acacia* spp., *Bursera simaruba* and *Haematoxylon brasiletto*. Ground cover was very sparse except where large clumps of *Bromelia pinguin* occurred. The area near the Argelia guard station was regenerating after complete clearing.

Mangrove swamps (3)

These consisted of *Rhizophora mangle* (red) and *Avicennia germinans* (black), with an interspersion of *Conocarpus erectus* and *Laguncularia racemosa* (white mangrove). *Rhizophora mangle* formed a tangled barrier



Key

1 Beach
2 Upper beach
3 Mangrove swamps
4 <u>Prosopis-Caesalpinia</u> seasonal swamps
5 Tidal mud-flats
6 Lowland riparian forest
7a Regenerating lowland riparian forest
7b Regenerating lowland riparian forest
8 Lowland deciduous forests
9 Lowland mixed forests
10 Hillside mixed forests
11 Dry scrubland

Figure 3. Vegetative-cover types in the Naranjo basin, Santa Rosa National Park, Costa Rica, 1981-82.

Figure 3a. View westwards overlooking the park lowlands and the Pacific Ocean, Santa Rosa National Park, Costa Rica, December, 1982. The dry bed of the Rio Poza Salada is at the center-left.

of buttress roots at the center of the drainage of the Trino Davila salina. Stems were small-pole to pole size forming a canopy which varied from ground level (at the edge of the mud-flats) to 10 m. No other plant species were present. Shade was plentiful in this tidal zone.

Prosopis-Caesalpinia seasonal swamps (4)

These were virtually mono-specific stands of *Prosopis juliflora* to 7 m height with occasional emergent *Caesalpinia coriaria* to 10 m. Branch tangles formed the understory. There was no ground cover and land-crab holes were plentiful. These areas were swampy only in the wet-season. The transition zone between these swamps and the surrounding forest types contained numerous, large *Conocarpus erectus* trees.

Lowland riparian forests (6)

Covering a large percentage of the lowlands area, these forests have been disturbed through many years of selective logging, subsistence agriculture and fires. The canopy, whose tallest trees reach to 25 m, included *Pithecellobium saman*, *Manilkara zapota*, *Ficus* spp., *Brosimum alicastrum*, *Mastichodendron capriri* and *Enterolobium cyclocarpum*. The basal area was 23 m^2 ha^{-1}. The large, canopy trees produced a cool forest. Canopy cover ranged up to 70%. The understory was highly variable, due to differences in canopy closure, ranging from few to many saplings, and from a clear forest floor to one covered by regrowth and vine patches. Roadsides and forest light-gaps near the Rio Poza Salada were covered with the large herb *Peteviera alliciae*.

Regenerating lowland riparian forests (7a, 7b)

These areas have experienced a significantly different recent history. Around 1963, as evidenced by aerial photos, they were completely cleared of vegetation for agriculture. Photos taken in 1976 show regrowth over 7a areas and partial regeneration over 7b areas. The basal area for 7a forest was 17.7 m^2 h^{-1} and for 7b forest 12.4 m^2 ha^{-1}. Small to medium trees dominated by Guazuma ulmifolia, Cecropia peltata, Enterolobium cyclocarpum and Pithecellobium saman covered 7a forest. Understory species included Acacia spp., Psychotria spp., Piper spp., Zizyphus guatamalensis, Trichilia hirta and Malvaviscus arboreus. Ground cover consisted of woody seedlings, Selaginella spp. and Lygodium venustum, a climbing fern which also enters the understory. Guazuma ulmifolia, Bursera simaruba and Ficus spp. dominated 7b forest.

Lowland deciduous forests (8)

These forests were covered with many small saplings to medium-sized trees (Calycophyllum candidissimum) to 13 m with a basal area of 17.3 m^2 ha^{-1}. The understory was easy to walk through. There were occasional specimens of the large columnar cactus, Lemaireocereus aragonii and the prostrate cylindrical cactus, Nyctocereus hirschtianus. Ground cover consisted primarily of seedling woody species. The deciduous forests were very hot during the dry-season. Near the old house above the estuary, there were large patches of Opuntia elatior.

Hillside mixed forests (10)

Following the high ridge and drainages to the east of the Naranjo Valley was a forest of mixed evergreen and deciduous trees.

Size classes ranged from saplings to large trees up to 25 m in height. There was approximately a 50% canopy closure with shade available year-round. The dense understory contained many shrubs and vine tangles (Pachyptera hymenea). There were a few herbs scattered among woody seedlings of Lonchocarpus orotinus on the forest floor.

Lowland mixed forests (9)

This was a very open forest with isolated clumps of evergreen species and canopy trees to 20 m (Manilkara zapota). Other dominants included Bursera simaruba, Calycophyllum candidissimum and Ficus spp. Basal area was 19.8 m^2 ha^{-1}. Understory shrubs and saplings (Acacia spp., Lonchocarpus spp., Jacquinia pungens, Aphelandra deppeana, Cochlospermum vitifolium, Bursera simaruba) were plentiful. Ground cover consisted of sparse woody seedlings.

B. Forage use

Tapirs in SRNP took leaves, stems, flowers and fruits from the forest understory and edge. Plant forms consumed were herbs, vines, a fern, shrubs and saplings. In addition, the male tapir in the San Jose Zoo accepted an epiphytic aroid. Fifty-four identifiable plant species are known to have been browsed by tapirs in SRNP (Table 1). Another 68 species were taken there by tapirs, deer, peccaries or range horses (Table 2).

Plant growth in SRNP is seasonal. Many species are deciduous and throughout much of the dry-season do not provide forage for tapirs. The decline in foliage production during the dry-season, however, appeared to be offset by an increase in fruit availability to tapirs during the years of this study (Figure 4).

Table 1. Plants browsed by tapirs in Santa Rosa National Park, Costa Rica, 1981-83.

Family	Species	Mature Form	Maximum diameter at point of break (cm) (sample size)	Maximum original height of a broken sample (m)	Parts eaten
Acanthaceae	*Aphelandra deppeana*	shrub	2.0 (18)	2.95	Branchlets and leaves
Anacardiaceae	*Spondias mombin*	tree	1.3 (4)	4.1	Branchlets and top leaves
Bignoniaceae	*Godmania aesculifolia*	tree	1.5 (1)	1.95	Branchlets and leaves
	Tabebuia ochracea	tree	1.5 (1)	1.6	Branchlets and leaves
Boraginaceae	*Cordia alliodora*	tree	1.0 (6)	1.5	Branchlets and leaves
	Cordia guanacastensis	shrub	1.5 (4)	2.05	Branches, leaves, fruits
	Cordia panamensis	tree	1.2 (1)	1.75	Branchlet tips and leaves
	Cordia sp.	shrub	1.1 (1)	2.2	Branchlet tips
	Tournefortia hirsutissima	tree	- (1)	-	Tops of young shoots
Burseraceae	*Bursera simaruba*	tree	3.6 (19)	2.55	Branches and leaves
Caesalpinaceae	*Bauhinia ungulata*	tree	0.9 (1)	1.6	Branchlets and leaves
	Cassia papillosa	shrub	Unable to break at 1.7 cm (1)		Branch ends and leaves
	Cassia sp.	treelet	1.2 (1)	2.44	Branches and leaves
	Swartzia cubensis	tree	1.1 (1)	-	Branch ends and leaves
Cochlospermaceae	*Cochlospermum vitifolium*	tree	4.5 (23)	3.15	Branches and leaves
Conpositae	*Onoseris onoseroides*	herb	1.4 (17)	1.9	Stem top, leaves and flowers
	Verbesina gigantea	herb	1.8 (4)	1.2	Stem top, leaves and flowers
Ebenaceae	*Diospyros nicaraguensis*	tree	1.2 (1)	1.75	Branchlets and leaves
Elaeocarpaceae	*Muntingia calabura*	tree	2.0 (12)	2.3	Branches and leaves
Fabaceae	*Aeschynomene elegans*	tree	- (2)	-	Branchlets and leaves
	Desmodium sp.	treelet	0.7 (3)	-	Branches and leaves
	Diphysa robinioides	tree	1.3 (1)	2.0	Branchlets and leaves
	Machaerium biovulatum	tree	2.2 (9)	2.0	Branches and leaves
	Machaerium kegelii	large vine	1.5 (1)	2.92	Larger, older leaves
Fern	*Lygodium venustum*	scandent fern	-	-	Stems and pinnae
Hippocrateaceae	*Hemiangium excelsum*	tree	1.5 (1)	2.05	Stems, branches and leaves
	Unidentified sp.				
Malpighiaceae	*Malpighia glabra*	shrubby tree	1.5 (4)	-	Branch ends and leaves
	Unidentified sp.				
Malvaceae	*Malvaviscus arboreus*	shrub	0.7 (5)	2.1	Branches, leaves

Table 1 (cont'd.).

Family	Species	Mature Form	Maximum diameter at point of break (cm) (sample size)	Maximum original height of a broken samples (m)	Parts eaten
Moraceae	Brosimum alicastrum	tree	1.5 (2)	1.4	Branchlets and leaves
Piperaceae	Piper marginatum	shrub	- (2)	-	Branches and leaves
	Piper tuberculatum	shrub	- (3)	-	Branches and leaves
Polygonaceae	Coccoloba venosa	treelet	1.5 (1)	2.8	Branch ends and leaves
	Coccoloba sp.	tree	2.0 (1)	2.4	Branch ends and leaves
	Triplaris malaenodendron	tree	- (1)	2.0	Branchlets and leaves
Rhamnaceae	Zizyphus guatemalensis	tree	-	-	-
Rubiaceae	Genipa americana	tree	1.0 (6)	-	Top of plant and leaves
	Guettarda macrosperma	tree	1.4 (1)	2.3	Branch ends and leaves
	Hamelia patens	tree	3.0 (6)	3.0	Branch ends and leaves
	Psychotria microdon	shrub	-	-	-
	Psychotria nervosa	shrub	0.8 (1)	1.5	Branches and leaves
	Psychotria trichotoma	shrub	-	-	-
Sapindaceae	Allophyllus occidentalis	treelet	1.0 (2)	-	Branch ends and leaves
	Thouinidium decandrum	tree	1.3 (3)	2.2	Branch ends and leaves
Solanaceae	Physalis (ignota or pubescens)	shrub	-	-	-
Sterculiaceae	Byttneria aculeata	scandent shrub	1.1 (16)	-	Stems and leaves
Meliaceae	Trichilia hirta	tree	0.6 (3)	1.8	Branch ends and leaves
	Trichilia sp.	tree	1.2 (1)	1.95	Branchlets and leaves
Mimosaceae	Acacia sp.	tree	-	-	Branchlets and leaves
	Calliandra emarginata	shrub	1.0 (1)	1.75	Branches and leaves
	Inga vera	tree	1.2 (3)	1.95	Branch ends and leaves
	Lysiloma desmostachya	tree	0.7 (3)	2.01	Branches and leaves
	Mimosa guanacastensis	shrub	0.7 (1)	1.5	Branchlets and leaves
	Mimosa pigra	spreading shrub	- (6)	-	Branch ends, tips of older leaves
	Piptadenia flava	shrub	0.5 (1)	1.5	Branch ends and leaves

Table 2. Plant species consumed by either tapirs, deer, peccaries or range horses in Santa Rosa National Park, Costa Rica, 1981-1982. (These could not be positively identified as tapir browse.)

Family	Species	Mature form
Acanthaceae	*Justicia* sp.	herb
	Ruellia sp.	-
Amaranthaceae	*Iresine* sp.	-
Anacardiaceae	*Astronium graveolens*	tree
Bignoniaceae	*Arrabidaea patellifera*	liana
	Tabebuia impetiginosa	tree
	Tabebuia rosea	tree
	Other unidentified spp.	-
Boraginaceae	*Cordia* sp.	-
	Tournefortia sp.	-
	Unidentified sp.	-
Caesalpinaceae	*Cassia biflora*	tree
	Cassia hayesiana	shrub
	Cassia sp.	-
Capparidaceae	*Capparis frondosa*	shrub
Celastraceae	*Maytenis* cf. *jamaicensis*	shrub
Commelinaceae	*Commelina erecta*	herb
Compositae	*Eupatorium* sp.	herb
	Hyptis sp.	herb
	Isocarpha atriplicifolia	herb
	Melampodium divaricatum	herb
	Melanthera aspera	herb
	Mikania micrantha	vine
	Wedelia calycina	herb
	Other unidentified spp.	-
Convolvulaceae	*Ipomoea trifida*	herbaceous vine
	Ipomoea sp.	h. vine
	Merremia umbellata	h. vine
Dilleniaceae	*Tetracera volubilis*	woody vine
	Unidentified sp.	-

Table 2 (cont'd.).

Family	Species	Mature form
Elaeocarpaceae	Sloanea terniflora	tree
Euphorbiaceae	Acalypha sp.	herb
Fabaceae	Centrosema sagittatum	herbaceous vine
	Dalea carthagenensis	shrub
	Dioclea megacarpa	woody vine
	Lonchocarpus costaricensis	tree
	Lonchocarpus orotinus	tree
	Machaerium arboreum	shrubby vine
	Piscidia carthagenensis	tree
	Platymiscium pleiostachyum	tree
Labiatae	Hyptis verticillata	herb
Liliaceae	Smilax spinosa	vine
Malvaceae	Guazuma ulmifolia	tree
	Unidentified spp.	
Meliaceae	Trichilia trifolia	tree
	Trichilia sp.	-
Mimosaceae	Albizzia caribeae	tree
	Desmanthus virgatus	shrub
	Lysiloma auritum	tree
	Pithecellobium saman	tree
Moraceae	Trophis racemosa	tree
Myrsinaceae	Ardisia revoluta	shrub
Piperaceae	Piper amalago	shrub
	Piper jacquemontianum	shrub
	Piper pseudo-fuligineum	shrub
Polygalaceae	Securidaca sylvestris	woody vine
Polygonaceae	Coccoloba (Janzen 10915)	tree
Rhamnaceae	Gouania polygama	herbaceous vine
Rubiaceae	Alibertia edulis	shrub
	Calycophyllum candidissimum	tree
	Chiococca alba	shrubby vine
	Exostema caribeaum	shrub
	Exostema mexicanum	shrubby tree
	Psychotria sp.	shrub
	Randia echinocarpa	tree

Table 2 (cont'd.).

Family	Species	Mature form
Sapindaceae	*Paullinia cururu*	woody vine
	Serjania caracasana	herbaceous vine
	Serjania schiedeana	herbaceous vine
	Unidenfied spp.	vines
Sterculiaceae	*Melochia* sp.	-
	Unidentified spp.	-
Theophrastaceae	*Jacquinia pungens*	shrub
Tiliaceae	*Luehea candida*	tree
	Luehea sp.	tree
	Unidentified sp.	-
Urticaceae	Unidentified spp.	-
Zygophyllaceae	*Guaicum sanctum*	tree

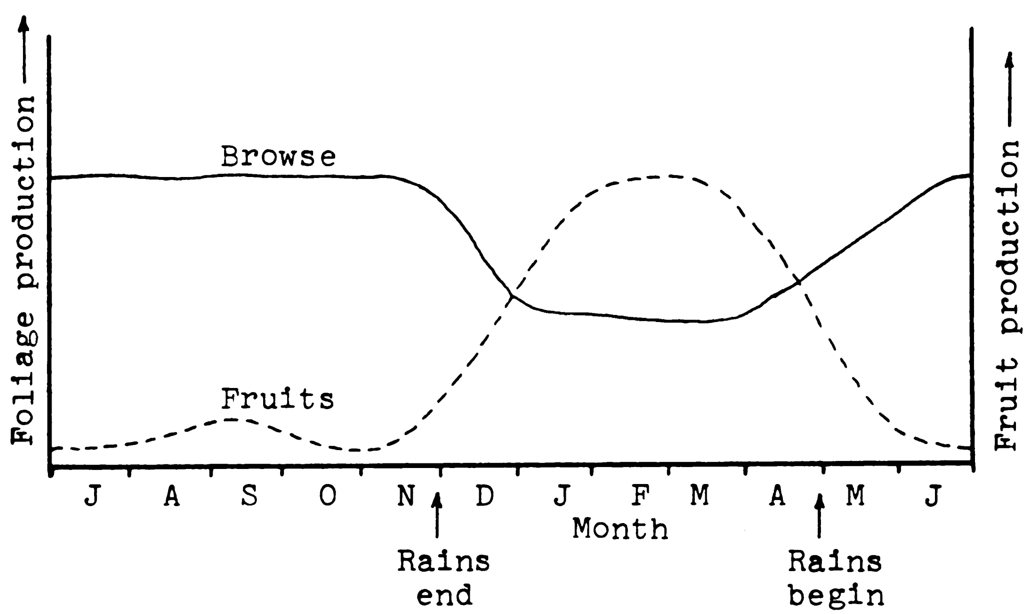


Figure 4. General outline of alternating year-round production of browse and fruits consumed by tapirs in Santa Rosa National Park, Costa Rica, 1981-82.

Thorns on plants apparently did not deter tapirs in SRNP. They readily ate Mimosa pigra, M. guanacastensis and Byttneria aculeata all of which possess sharp, recurved thorns, and Machaerium biovulatum which as a sapling has strong, short, blunt thorns along the trunk.

The distribution of the heights at which 135 plants were broken by tapirs ranged between 0.55 m and 1.42 m (Figure 5). Only 7 (5.2%) of the plants were broken above a height of 1.20 m. Tapirs in SRNP rarely reached above this height to break down browse, though they are reported to be able to do so by standing on their hind legs (Terwilliger, 1978). One Bursera simaruba sapling, 3.6 cm DBH, could not be broken at a height of 1 m and, as evidenced by teeth scrapings, the tapir had worked its way up the sapling to grasp it at a height of 2 m. It snapped at a height of 1.75 m and 5 of the 6 branch ends and their leaves were eaten. The sixth branch was broken off but left lying on the ground.

On two occasions saplings (5 m and 3.2 m height) were uprooted and foliage consumed. It appeared that these had been pushed over when the tapir attempted to snap the sapling.

For each species, the largest diameter at the point of break varied considerably (Table 1). These diameters are dependent on the number of observations and the fragility of the stem or trunk. That fragility is determined by the species and the wood density.

Deer were frequently observed, during daylight hours, to consume large amounts of forest-edge, herbaceous forage as well as woody material. They did not break browsed plants but plucked individual

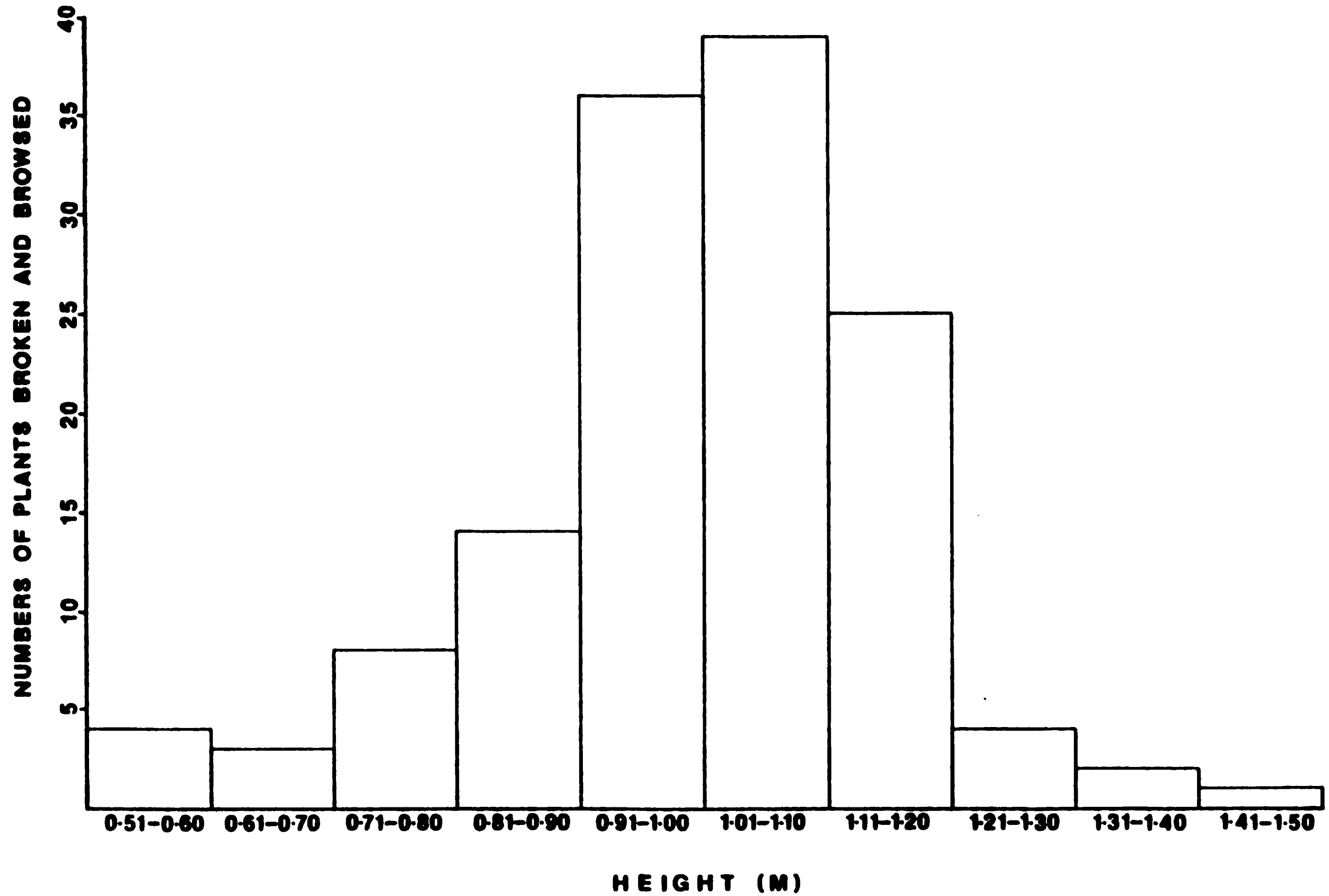


Figure 5. Heights at which 135 plants were broken by tapirs in Santa Rosa National Park, Costa Rica, 1981-82.

leaves and growing tips from them. Plant damage by rutting bucks was easily identified as such.

Microscopic analysis of tapir and deer fecal samples is incomplete.

C. Forage choice trials

The tapir's choices in the pair-wise trials were often contradictory. They enabled only a broad categorization of relative selectivity as illustrated by the 19 preference divisions that could be determined among species (Table 3). These broad divisions, however, did demonstrate that, in these trials, percentage acceptability was not an accurate criterion by which to rank selectivity (Table 3).

Plant texture apparently did not affect choice. Herbaceous, succulent species (Commelina erecta, Philodendron scandens), the small leaves and hard stems of Hemiangium excelsum, Crescentia alata and Quercus oleoides, the smooth leaves and soft stems of Trophis racemosa, Brosimum alicastrum and Piper amalago, and the spiny leaflets of the palm Acrocomia vinifera were all readily eaten. Mimosa pigra, a shrub of roadsides and riverbanks, possesses sharp, centimeter-long, recurved thorns. The thorns appeared to cause little concern to the zoo tapir.

Both green and dried Cecropia peltata leaves were avidly eaten when offered to the zoo tapir. Dried C. exima leaves were taken from the forest floor by Tapirus bairdii in Panama (Terwilliger, 1978) and it is possible that dried Cecropia leaves may be a significant dietary item for free-ranging tapirs in SRNP. Green leaves are less likely

Table 3. Order of relative selectivity of plant species fed a San Jose Zoo adult male tapir. Letters indicate the species in a division in which no difference in relative selectivity was demonstrated.

	Species	Plant Family	Percent Acceptability	Number of Trials
a	*Acrocomia vinifera*	Palmae	100	3
a	*Allophyllus occidentalis*	Sapindaceae	89.2	37
a	*Apeiba tibourbou*	Tiliaceae	100	28
a	*Aphelandra deppeana*	Acanthaceae	83.3	54
a	*Brosimum alicastrum*	Moraceae	100	28
a	*Bursera simaruba*	Burseraceae	100	76
a	*Calliandra emarginata*	Mimosaceae	100	21
a	*Cassia biflora*	Caesalpinaceae	100	8
a	*C. hayesiana*	Caesalpinaceae	100	25
a	*Cecropia peltata*	Moraceae	100	38
a	*Cochlospermum vitifolium*	Cochlospermaceae	100	58
a	*Commelina erecta*	Commelinaceae	100	38
a	*Crescentia alata*	Bignoniaceae	75	20
a	*Guazuma ulmifolia*	Sterculiaceae	100	46
a	*Hemiangium excelsum*	Hippocrateaceae	100	54
a	*Inga vera*	Mimosaceae	92	25
a	*Luehea speciosa*	Tiliaceae	100	13
a	*Machaerium biovulatum*	Fabaceae	100	65
a	*Malvaviscus arboreus*	Malvaceae	98.2	57
a	*Mimosa pigra*	Mimosaceae	100	30
a	*Muntingia calabura*	Elaeocarpaceae	100	59
a	*Philodendron scandens*	Araceae	100	7
a	*Piper amalago*	Piperaceae	100	29
a	*P. jaquemontianum*	Piperaceae	96.2	26
a	*P. marginatum*	Piperaceae	100	20
a	*P. pseudo-fuligineum*	Piperaceae	92.3	26
a	*Psychotria nervosa*	Rubiaceae	98.5	68
a	*Quercus oleoides*	Fagaceae	100	42
a	*Spondias mombin*	Anacardiaceae	100	62
a	*Swartzia cubensis*	Caesalpinaceae	95.2	21
a	*Thouinidium decandrum*	Sapindaceae	82.8	29
a	*Trophis racemosa*	Moraceae	100	47
	Byttneria aculeata	Sterculiaceae	100	12
	Bursera tomentosa	Burseraceae	80	25
	Tetracera volubilis	Dilleniaceae	63.6	11
b	*Gouania polygama*	Rhamnaceae	66.7	27
b	*Hyptis verticillata*	Labiatae	50	20
c	*Genipa americana*	Rubiaceae	73.7	38
c	*Trichilia hirta*	Meliaceae	60	15
d	*Alibertia edulis*	Rubiaceae	59.7	62
d	*Cordia alliodora*	Boraginaceae	60.6	33
d	*Hamelia patens*	Rubiaceae	57.9	38
d	*Stachytarpheta jamaicensis*	Verbenaceae	62.5	16
e	*Centrosema sagittatum*	Fabaceae	70	20
e	*Serjania schiedeana*	Sapindaceae	66.7	12
	Tabebuia ochracea	Bignoniaceae	53.6	28

Table 3 (cont'd.).

Species	Plant Family	Percent Acceptability	Number of Trials
Onoseris onoseroides	Compositae	41.7	24
Lonchocarpus costaricensis	Fabaceae	42.9	14
Cordia panamensis	Boraginaceae	33.3	9
Lygodium venustum	Fern	38.1	21
Verbesina gigantea	Compositae	29.2	24
Acacia collinsii	Mimosaceae	33.3	3
Pithecellobium saman	Mimosaceae	18.2	11
Cordia guanacastensis	Boraginaceae	23.1	13
[f] *Desmodium* sp.	Fabaceae	16.7	6
[f] *Tabebuia rosea*	Bignoniaceae	7.7	13
[g] *Bauhinia ungulata*	Caesalpinaceae	0	15
[g] *Ipomoea trifida*	Convolvulaceae	0	1
[g] *Jacquinia pungens*	Theophrastaceae	0	3
[g] *Ocotea veraguensis*	Lauraceae	0	3
[g] *Sesbania emerus*	Fabaceae	0	6

to be taken because C. peltata is usually host to aggressive Azteca ants. Occasional small specimens (to 1.5 m, but usually less than 1 m height), however, do not support ants.

Preferred species (those superscripted with an "a" in Table 3) included 8 species that were not found browsed in SRNP: Trophis, Cecropia, Apeiba, Philodendron, Quercus, Cassia biflora, Acrocomia and Crescentia. Philodendron is an epiphyte sometimes found near the base of a tree and a browsed individual could easily be overlooked. Janzen (1981d), however, fed this Philodendron to a tame tapir which regurgitated the material. Acrocomia is a commonly-occurring palm of the dry savanna areas. Removal of leaflets easily could have gone unnoticed, as could twigs and leaves of the savanna tree Crescentia, and the forest tree Quercus. Other species would have been broken by tapirs and their browsing would have been located readily by transect search.

Of the five species completely rejected by the zoo tapir, Bauhinia ungulata was found to be utilized by tapirs or deer in SRNP, Jacquinia pungens was browsed by deer there, Sesbania emerus occasionally was eaten by range horses and Ipomea trifida was consumed by peccaries (Tayassu tajacu). Janzen (1981a) found live seeds of Bauhinia ungulata in tapir dung.

Fourteen leguminous species were tested. One herb (Sesbania) and one sapling (Bauhinia) were rejected. Only six species (Calliandra, Cassia biflora, Cassia hayesiana, Machaerium, Mimosa, Swartzia) were in the preferred group (superscript "a", Table 2). On two occasions Pithecellobium was chewed briefly and spat out. This occurred once each with Lonchocarpus, Inga and Sesbania.

Eight non-legumes also were chewed and spat out once or twice during the trials. These were three from the Rubiaceae (Alibertia (2), Genipa (2), Hamelia), two composites (Onoseris (2), Verbesina), a fern (Lygodium), Bursera tomentosa and Piper jaquemontianum.

It is generally thought that the alkaloid-containing Rubiaceae are unpalatable to herbivores. Yet Psychotria nervosa was rejected only once in 67 trials and the other three tested Rubiaceae were accepted 73.7%, 59.7% and 57.9% of the time. Williams (1978) and Williams and Petrides (1980) found that Rubiaceae species were a major component of the diet of Tapirus indicus in Malaysia.

On many occasions the same proffered plant samples were both accepted and rejected on the same day, or acceptance/rejection differed on consecutive days. This ambivalence could have been due to an affect of the simultaneously proffered species or to a trait of choice of the ambiguously-treated sample.

There were also differences in species acceptance at different periods of the trial. Aphelandra and Allophyllus were not eaten when first offered at the beginning of September. They were readily eaten thereafter. Gouania was accepted throughout October but rejected in mid-November. Verbesina was rejected in September and October but was accepted in mid-November. Acceptance of Verbesina corresponded with flowering of the species. Of the two times that Pithecellobium was accepted it was chosen over the highly accepted (100%) Spondias and Muntingia. These two acceptances occured at the beginning and end of a day's trial. Desmodium was accepted only the first time offered.

Many of the less-preferred samples were rejected most often towards the end of a day's feeding trial or rejected more often on the second or third day. This suggests that satiation was involved. These species, then, when offered many times at the same feeding, would have had their acceptability percentage biased downwards. Similarly, highly-preferred species which were offered few times (e.g. Philodendron, Cassia biflora, Acrocomia) could have been biased upwards.

D. Seeds in dung

Seeds and fruit parts of 33 species were identified in tapir dung. Additional seeds of 20 species were located but could not be identified. These unidentified seeds and eight of the identified seeds were small, occurred once or twice only, and were thought to have been ingested incidentally with vegetative plant parts. Damaged seeds and seeds that germinated in the gut were killed by digestive fluids.

There was a general correlation between fruit drop and consumption (Figure 6). Once on the ground fruits deteriorated in quality as a food source for tapirs due to larval attack and microbial decomposition. Fruits with soft, moist pulp (Manilkara zapota, Spondias mombin, S. purpurea, Zizyphus guatemalensis, Mastichodendron capriri, Guettarda macrosperma) decomposed rapidly.

Manilkara zapota ("nispero", "chicle"), a large, evergreen tree, occurs in the park lowlands. The spherical fruit 2-4 cm in diameter contains up to 8 radially-disposed seeds 1-2 cm in length. The seed coat is brittle. The fruit pulp was poorly digested, as indicated by the numerous, large, fruit pieces which were found in dung.

Spondias mombin ("jobo") is a deciduous tree producing many yellow-orange, ovoid fruits 3-4 cm in length. Each contains a large,

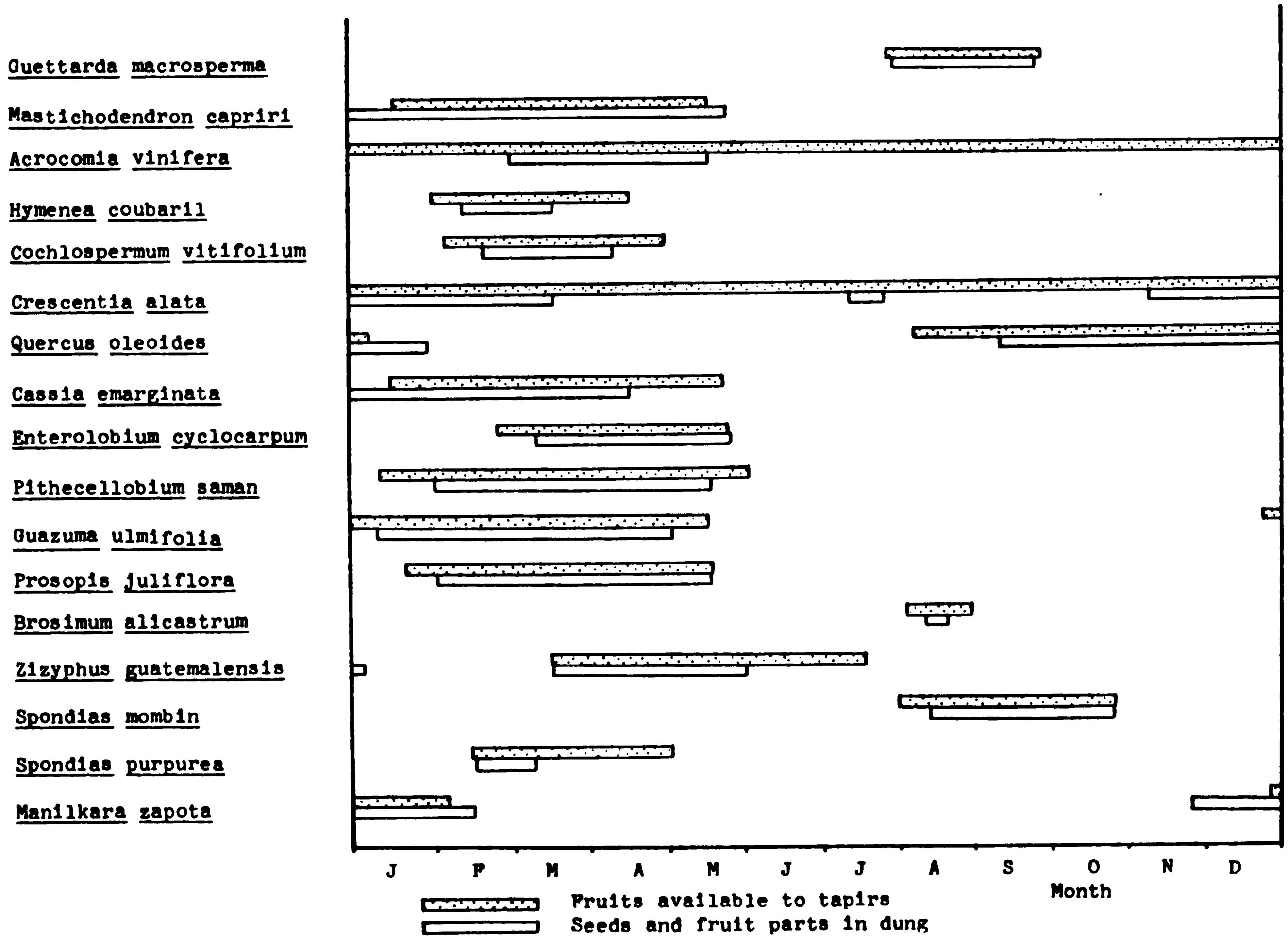


Figure 6. Relationship between fruit availability to tapirs and the occurrence of seeds or fruit parts in tapir dung in Santa Rosa National Park, Costa Rica, 1981-82.

fiber-covered, multi-seeded, hard nut 2-3 cm in length. Tapirs swallow the fruits and the contained nut after brief chewing. Three dung piles (one pile is one defecation) contained 251, 182, and 204 whole Spondias nuts, respectively. Only two shattered pieces of a Spondias nut were located and these were in one dung pile. The related S. purpurea ("jocote") produces a similar, though smaller fruit, red-yellow in color. It is a smaller tree and less common than S. mombin in SRNP. Janzen and Liesner (1980) state that it "may be native but so widely planted (that it is) hard to tell." Only two dung piles containing one and two S. purpurea nuts, respectively, were found.

The large evergreen tree, Zizyphus guatemalensis ("naranjillo"), produces hundreds of spherical, yellow fruits, 1.5-2.3 cm in diameter. Each fruit contains an ovoid, four-seeded nut up to 1.4 cm in length. Janzen and Liesner (1980) stated that the fruits fall from the tree completely in early July in SRNP. I found fruits falling from the first week of April until mid-July in SRNP. One nut was in a dung pile in mid-March. An aberrant individual may have fruited in late December-early January, as half of a Zizyphus nut was found in a dung pile on January 4, 1983. It is unlikely that the fragment was retained in the gut for the 5.5 months which elapsed from the last fruiting of the species.

Mastichodendron capriri ("tempisque") is a deciduous tree producing green, ovoid fruits, 2.5 cm x 3.0 cm, with a large, fragile seed. Only parts of seeds and fruits were found in tapir droppings.

Guettarda macrosperma ("madroño negro") in a small tree which produces purple-red, spherical fruits, 1-2.5 cm in diameter. They contain a hard, spherical seed ingested by tapirs with the fruit pulp.

Large numbers of seeds were found in old dung piles encountered in the field. One pile contained 207 Guettarda seeds.

Brosimum alicastrum ("ojoche") is a large evergreen tree bearing small (1.5-3.0 cm diameter), spherical fruits, green-brown in color. Both the fruit and seed are soft. Small pieces of seeds and fruits only, appeared in the dung piles examined.

The leguminous, beige, indehiscent pods of Prosopis juliflora ("mesquite"), 10-25 cm in length, contain a sweet pulp around hard, segmented seeds. Few seeds were ruptured and digested by tapirs; the majority passed through the gut intact. Small sections of intact pod also occasionally were found in dung piles. Prosopis occurs only in seasonal swamps in the park lowlands.

Guazuma ulmifolia ("guacimo") is a common, deciduous, small tree bearing large quantities of a dry, ovoid fruit 2-3 cm long, with a rough, uneven surface. The surface of the fruit is sweet and odiforous. The whole fruit is eaten by tapirs. The many small, gray seeds, 1.5-2.0 mm in diameter, are arranged in columns around a very hard core 0.7-1.0 cm in length. Many hundreds of seeds were found in tapir dung, the vast majority of which were live. The hard, fruit cores in 21 piles numbered up to 103 per pile.

The dark-brown, indehiscent pods of the large tree Pithecellobium saman ("cenízaro") are 10-15 cm in length and contain a number of very hard seeds, 1-1.5 cm long, between which is a viscous, sweet-tasting substance. The fruits are consumed whole. Approximately 33% of the P. saman seeds found in tapir dung had passed through the gut alive.

Enterolobium cyclocarpum ("guanacaste") is a large tree which can produce in excess of 5000 (Janzen, 1984b) distorted-disk fruits 8-10 cm in diameter. The fruit crop, however, was very poor in SRNP in 1982. The seeds, about 2 cm long, are very hard and require considerable force to crack (Janzen and Higgins, 1979). Live seeds, seed fragments, and fruit parts occurred in 13 dung piles. One pile contained parts from two fruits. No pile contained more than three live seeds and a total of only eight live seeds were encountered.

The dark-brown, indehiscent pods of the small tree Cassia emarginata are 20-30 cm long and 8-10 mm wide. They contain many small, brown, flattened seeds about 5 mm long, many of which passed through the gut intact; 109 live and 16 dead seeds were found in one of the 20 piles were contained seed parts or whole seeds.

Acorns from the Guanacaste oak, Quercus oleoides ("encino"), were consumed in large numbers by tapirs on the upper plateau of SRNP. The astringent fruits, about 2.5 cm in length, were well masticated. Shell fragments appeared to make up to 50% of the bulk of some dung piles examined.

The tall, semi-evergreen Hymanaea courbaril ("guapinol") produces hard, indehiscent, red-brown pods up to 15 cm long and 5 cm wide. The large, flattened seeds, about 3 cm in diameter, are surrounded by a dry, powdery pulp which tastes similar to dessicated coconut. Pod fragments were found in four dung piles; another pile contained two partially-digested seeds.

The common savanna palm, Acrocomia vinifera ("coyol"), up to 10 m in height, produces spherical fruits approximately 4 cm in diameter all-year round. Edible, fibrous pulp forms a thin layer 3-4 mm thick over a large nut. Pieces of the thin and brittle pericarp were found in eight dung piles. Three whole, fiber-covered nuts were located in one of these piles.

Bromelia pinguin ("piñuela") and *B. karatas* ("piñuela") are large, ground bromeliads with sharp, curved spikes along the leaf margins. *Bromelia pinguin* produces an elongate raceme of fruits; *B. karatas* fruits are sessile in the base of the plant. The fruits of both species are ovoid and 3-4 cm in diameter but *B. karatas* fruits are almost twice as long as those of *B. pinguin*. The fruits have a tough, fibrous pericarp surrounding a sweet pulp. Both species have similar, small brown seeds approximately 4 mm in length. Tapirs consume the whole fruit perhaps after brief chewing; fruit parts in dung were torn but still contained many live seeds.

Live seeds of *Ficus insipida* and of other *Ficus* spp. ("higuerón") were recovered from tapir dung. There are at least seven species of *Ficus* in SRNP (Janzen and Liesner, 1980). Of these, *F. insipida* produces the largest figs, 3-5 cm in diameter. Other figs range in size from 1-3 cm in diameter. The *Ficus* spp. produce fruits erratically throughout the year and all species are available to tapirs.

Five live *Bursera simaruba* ("indio desnudo") seeds, and other seed parts, were found in four dung piles. The spherical fruits, 1-1.5 cm in diameter and filled with three triangular seeds, are borne in panicles. They were blown frequently from trees while still attached to associated small branches and leaves. Fruits possibly were ingested by tapirs incidentally with foliage.

The normal dispersal mode of Cochlospermum vitifolium ("poroporo") seeds is by wind. The small, soft, curled seeds, approximately 5 mm in length, are attached to a fluffy material and packed into a dehiscent, spherical fruit about 6 cm in diameter. Most fruits mature and open on the tree in the latter half of the dry-season when trees are without leaves. Some fruits fall when immature, however, and mature, unopened fruits also were found occasionally. Some sapling C. vitifolium also produced fruits. Eleven dung piles contained seeds and fruit parts. While most seeds were dead, ten survived passage through the gut.

Crescentia alata ("jícaro," "calabash") fruits fall from the tree in an unripe (green) condition and ripen on the ground during the following 2-4 weeks. The ripe fruit is large, spherical (5-12 cm in diameter) and indehiscent, with a hard shell containing many soft seeds (one fruit 7.5 cm in diameter at the least axis contained 235 seeds). The dark-brown, ripe fruits have a molasses-like odor and the seeds are contained in a sweet, brown pulp. Crescentia fruits are available to tapirs year-round, though only trees located in moist sites produce fruits in the late dry-season. The fruits lose their odor as they slowly dry up. After 4-6 months they become gray-brown in color and are noticeably lighter in weight.

Although C. alata seeds are soft, many pass through the gut intact. Range horses are reported to consume only the pulp (Janzen, 1982); tapirs chew and swallow the entire fruit. Pieces of the hard shell up to 2.4 cm^2 were found in dung piles. One pile, collected June 10, 1981, contained the shell fragments of at least one complete fruit, 313 live seeds, 82 dead seeds, and 21 undeveloped (aborted) seeds. Live seeds were found in all dung piles which contained _C. alata_.

Numerous other small, live seeds were found in the dung piles examined. It was only possible to identify _Randia echinocarpa_, _Genipa americana_, _Ardisia revoluta_ (2 times), _Cordia guanacastensis_, _Psychotria nervosa_, _P. microdon_, _P. trichotoma_ and a dead composite seed. A fruit part of _Physalis_ sp. was also located.

E. Germination experiments

Five of the six species whose seeds were tested exhibited gut-passage effects. After 91 days neither the 50 _Zizyphus guatemalensis_ seeds taken from dung nor the 25 seeds taken from ripe fruits had germinated.

Two markedly different responses were obtained from _Pithecellobium saman_ seeds. Those taken from dung responded exponentially while those extracted from fruits responded linearly (Figure 7). Seeds that had passed through the tapir gut germinated at a faster rate for the initial 20 days. Over the 63 days of observations, 48% (n=25) of the seeds taken from dung germinated while only 34% (n=50) of seeds taken from ripe fruit did so.

Cassia emarginata seeds from dung and ripe pods showed an unexpected contrast (Figure 8). Seeds that had not passed through the tapir gut appeared to have germinated far more rapidly in the initial two days. Thereafter the rates of germination of both treatments were the same (P <.01). After 77 days 31.25% (n=48) of the seeds from pods and only 17.43% (n=109) of the seeds from dung had germinated.

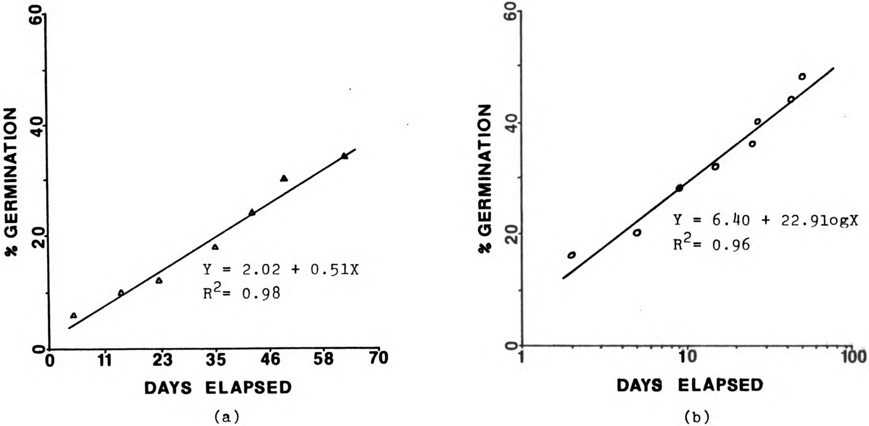


Figure 7. Percentage germination of Pithecellobium saman seeds taken from (a) fresh fruits, and (b) freshly-collected tapir dung, in Santa Rosa National Park, Costa Rica, 1982.

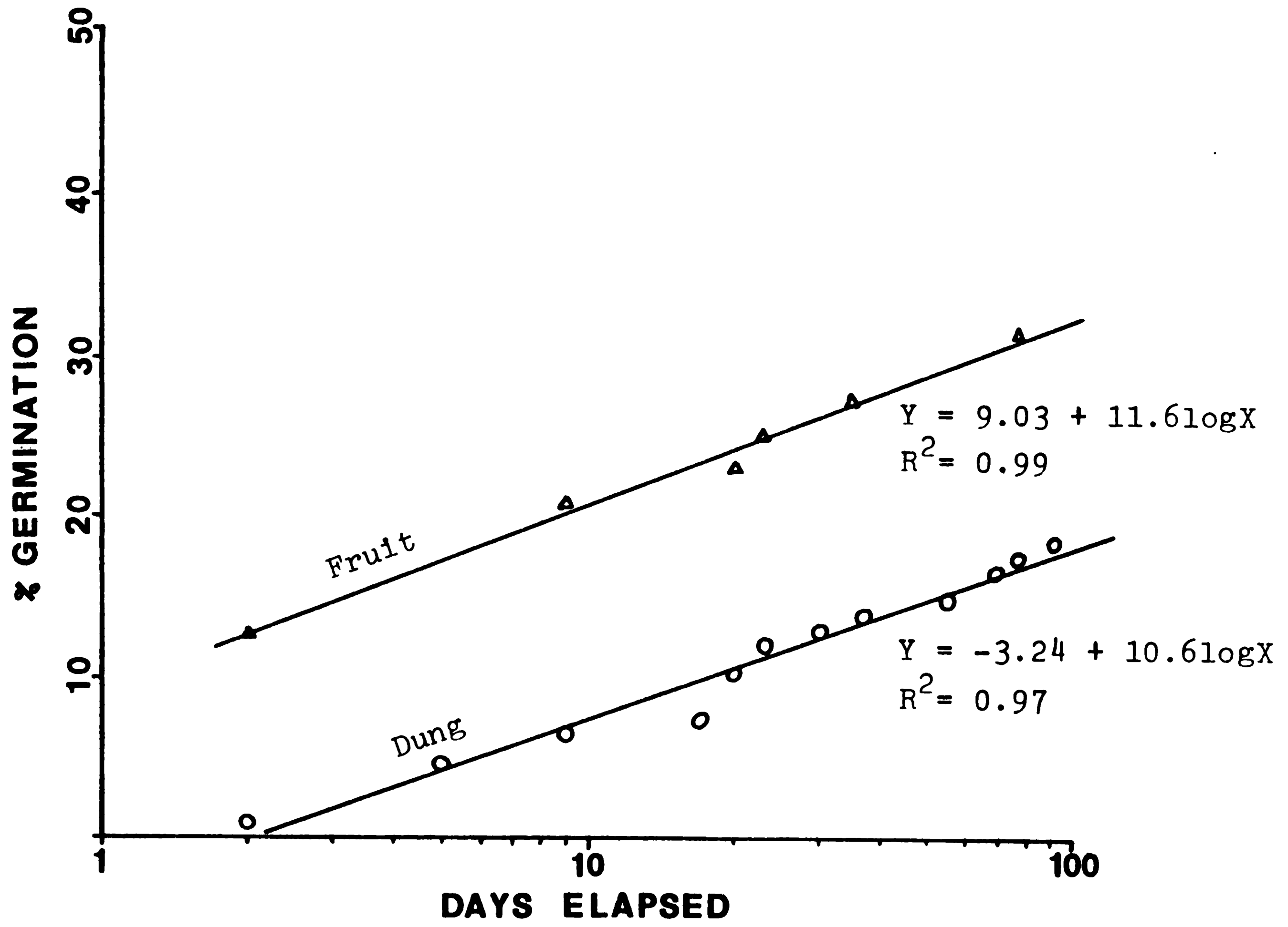


Figure 8. Percentage germination of _Cassia emarginata_ seeds taken from fresh fruits and freshly-collected tapir dung in Santa Rosa National Park, Costa Rica, 1982.

The result suggests that 12% of the seeds taken from dung and thought to be alive possibly were dead. If that 12% was dead there was no effect from gut passage on seeds that survived.

Seeds taken from ripe fruits of *Guazuma ulmifolia* germinated poorly (Figure 9); those taken from dung, however, showed an enhanced germination ability. Ninety-five percent of *Guazuma* seeds from dung that germinated did so in the initial 10 days. Twenty percent of dung seeds had germinated within 40 days while only 2% of seeds from fresh fruits had germinated. *Guazuma* seeds taken from fruits and placed in a moist medium developed a clear, jelly-like covering approximately 1 mm thick. This did not occur with seeds taken from dung where the coating apparently had been digested off the seeds. It seems that gut passage may be required for the removal of the coating and possibly also for scarification of seed coats.

Germination of *Crescentia alata* seeds was enhanced by passage through the tapir gut (Figure 10). Both dung seeds and fruit seeds exhibited rapid germination rates. Dung seeds germinated more rapidly, however, and more germinated. Within 28 days, 88% of the dung seeds and 58% of seeds taken from ripe fruit had germinated.

Only 2 of 18 (11.1%) *Prosopis juliflora* seeds taken from dung had germinated after 63 days and these did so in the initial two days. Over the same 63 days, no seeds taken from ripe pods had germinated.

F. Tapir captures

The first tapir captured was found resting in an artificial pond ("Laguna Escondida") in the afternoon of May 23, 1981. This female

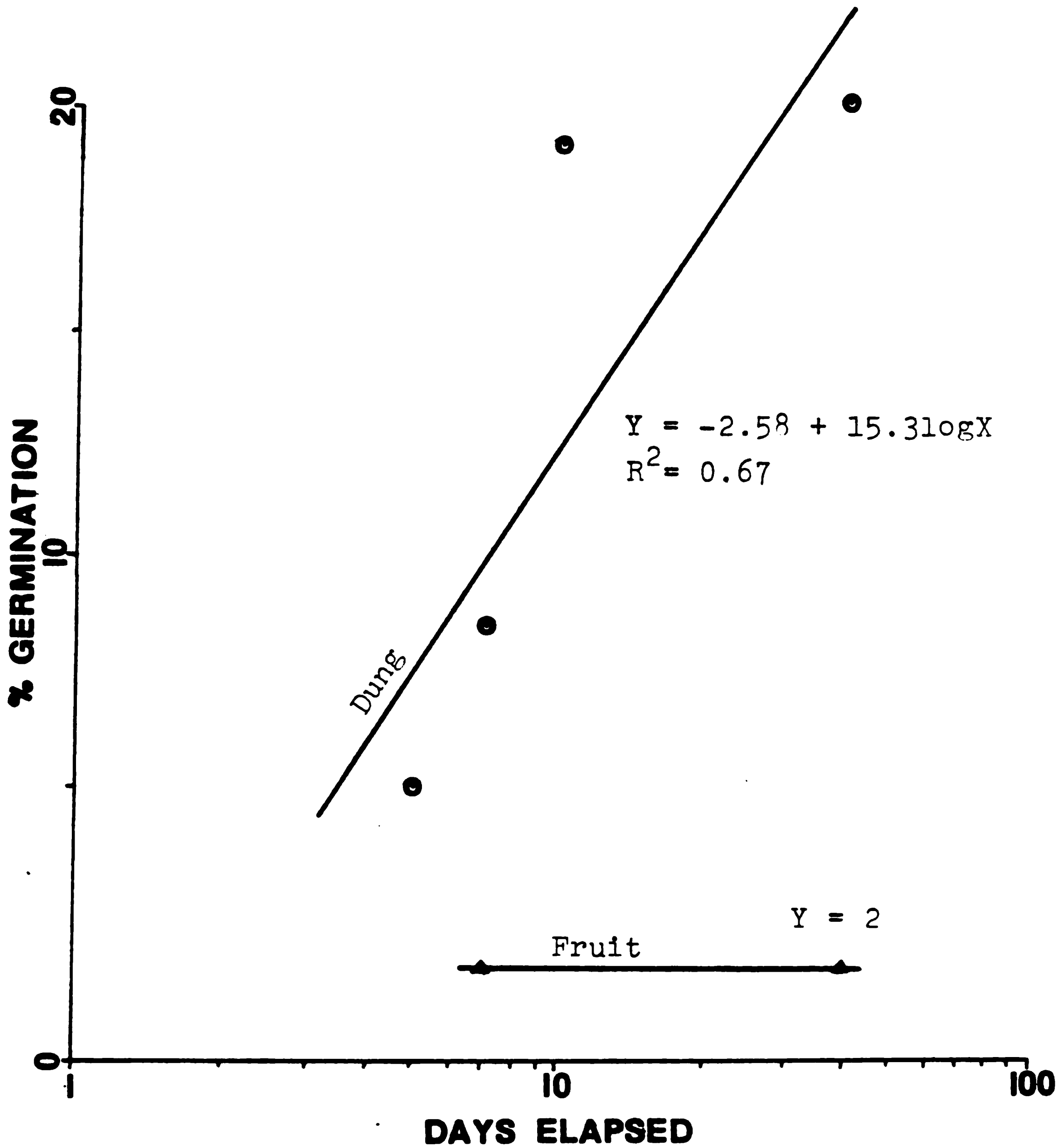


Figure 9. Percentage germination of <u>Guazuma ulmifolia</u> seeds taken from fresh fruits and freshly-collected tapir dung in Santa Rosa National Park, Costa Rica, 1982.

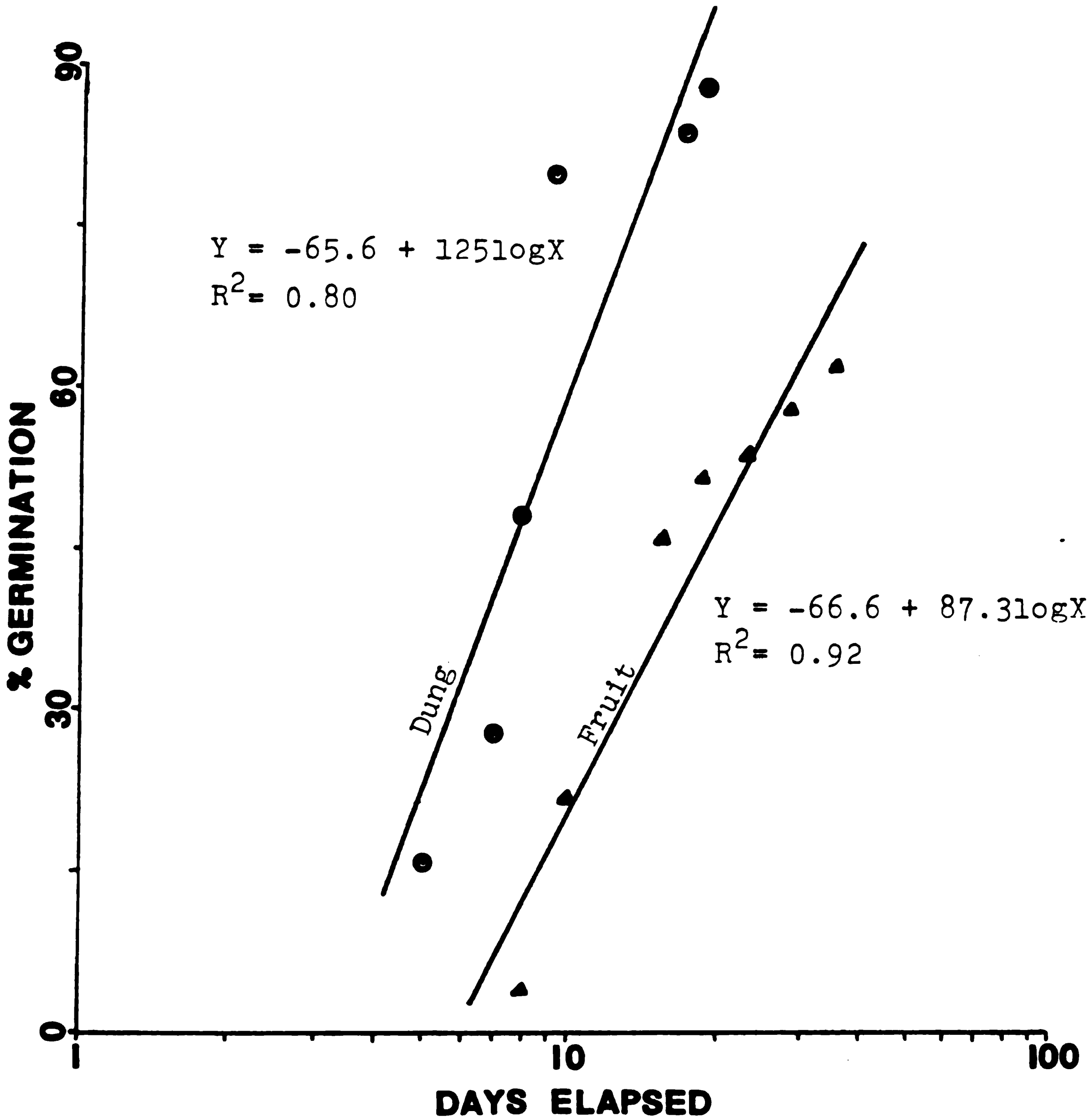


Figure 10. Percentage germination of *Crescentia alata* seeds taken from fresh fruits and freshly-collected tapir dung in Santa Rosa National Park, Costa Rica, 1982.

("Numero Uno") was lassoed around the neck and hind leg and dragged from the pond using two horses. She was tied-up with ropes, a radio-collar fitted and the animal released. She returned to the water and remained there until dark.

An adult male tapir ("Chuck") was found resting in a pool in the bed of the Rio Poza Salada at 4:30 p.m. on March 14, 1982. A projectile syringe, loaded with 2 mg of "Immobilon" (etorphine hydrochloride 2.45 mg ml^{-1} with acepromazine) was fired from a "Cap-chur" gun from a distance of 25 m. It struck the rump and bounced away. A partial injection was effected, however, as the animal exhibited ataxia of the hind legs. The animal was followed into the forest.

Eleven minutes after the first dart was fired the tapir began to walk well and one minute later a second dart (also with 2 mg of "Immobilon") was fired into the rump from 12 m. It penetrated the hide and retained its position. The tapir walked a further 10 m and fell in sternal recumbency. A radio-collar was attached (neck circumference 67 cm), a small red "Rototag" (number 02) punched into the left ear, a blood smear taken, ectoparasites (ticks) collected, measurements taken, 3.5 ml of the antibiotic "Encima" injected, and injuries sprayed with "Larvacid." One millilitre (4.9 mg) of "Revivon" then was injected into an ear vein. Fifty minutes after injection with the second dart, Chuck regained his feet and walked slowly into the forest, urinating frequently.

At 8:30 p.m. on April 17, 1982, two tapirs came together to a pool and commenced drinking 13 m from a blind set in the dried bed of the Rio Poza Salada. This pool was 30 m from where Chuck had been found resting on March 14. Identified as an adult and juvenile, the adult was darted with the aid of a spotlight. This animal was then found to be Chuck, the previously-collared male. He walked to the riverbank and fell in lateral recumbency four minutes after injection. His collar and neck were checked, ticks collected, and the antagonist "Revivon" injected into an ear vein. He regained his feet in one minute. While he was being guided manually away from pools and into the forest the juvenile tapir emerged from the forest and followed.

A dart was prepared as before and the juvenile darted in the rump from a distance of 5 m. Immediately previous to the darting, the juvenile had approached within 1 meter of the operator. The dart bounced out of the rump and some drug spilled on the skin. The animal was immobile 13 minutes later in sternal recumbency. This tapir, a male (called "Pepe"), was treated as was Chuck on his first immobilization, except that a white "Rototag" (number 03) was placed in each ear.

This younger tapir was redarted at 7:25 p.m. on February 3, 1983 at the same location. He entered the forest and was located 20 minutes later in sternal recumbency. One-half of one of the "Rototags" had broken off. The collar was removed, antibiotic injected and "Revivon" injected into an ear vein. A further half-dose of "Revivon" was injected intramuscularly. "Larvacid" was sprayed on wounds. He raised his head within 1.5 min and was on his feet in 3.5 min. He walked slowly away into the forest about 10 min later.

G. Defecation

In SRNP, tapir dung was deposited in running rivers and in pools in dried riverbeds. Droppings also were found on dry land. Tapirs regularly used rivers and pools to drink and to bathe and they entered even shallow (10 cm depth) pools to defecate. There appeared to be three patterns of pool use for defecation. At times tapirs returned to the same pool over several consecutive nights; at other times a series of pools were used. Also tapirs defecated in a pool in a riverbed and (based on an absence of dung and tracks) did not return to that series of pools for several days.

On dry land, dung "dump-sites" were located on 16 occasions. These were found in evergreen forest, deciduous forest, on dry, grass-covered ridges and in grassy patches amongst black mangroves. Only two of these were single deposits (single defecation efforts). Two were dump-sites of two deposits and 2 were of three deposits. Other dump-sites ranged from 5 to 26 deposits. The larger dump-sites covered 12-16 m^2 and were roughly circular.

Fresh deposits (no more than 48 hours old) were found at 4 dump-sites. One site held a deposit about one week old. Other sites contained only old (dried, disintegrating dung-balls) and very old (disintegrated dung-balls) deposits. One dump-site was revisited by a tapir (or tapirs) two times over a 23-day period. Another site with fresh dung, located early in the study, was not re-used by a tapir in the subsequent 20 months. Other old dump-sites were not re-used.

When not deposited in water, dung was poorly covered with soil and surface litter scraped backwards with the hind feet.

H. Urination

Only one urination site was located. Here a tapir had sprayed urine near the base of a tree (25 cm DBH). The strongest urine smell was at a height of 15-20 cm on the tree. Soil had been thrown onto the base of the tree from a 40 cm distance. Scrapings and tracks indicated that this had been done with the hind feet; a similar behavior to that for defecation on dry land.

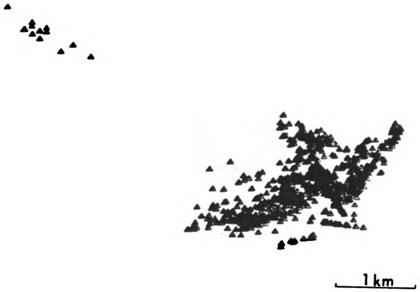
Both females and males are anatomically-equipped to spray urine to the rear. Observations of captive tapirs (all species) indicate that this can be done with considerable force.

I. Radio-tracking

A total of 253 daytime and 885 night-time locations were obtained for Chuck (Figure 11). Pepe was located 418 times during the day and 1372 times at night (Figure 12). The female was located 19 times and only during daylight hours (Figure 13). On many occasions contact was made with tapirs' radio-signals from only one receiving station and triangulations were not possible. At times signal attenuation was severe and no reception was possible at either receiving station.

The number of radio-locations obtained for a male tapir over any one 12-hour period averaged 22 (range 0-53). No readings were obtained for Chuck over four nights (May 6, May 7, June 3, October 21) and over one day (August 6). On two nights (September 9 and October 22), Chuck was located on a ridge between Naranjo beach and Nancite beach (Figure 13a), approximately 2.5 km from the distribution of all other locations. Pepe was always located at least once over a 12-hour period. Contact with the female was lost after July 24, 1981, two months after

(a)



(b)

Figure 11. Radio-locations for male tapir 'Chuck' in Santa Rosa National Park, Costa Rica, March-December, 1982. (a) daytime, (b) night-time.

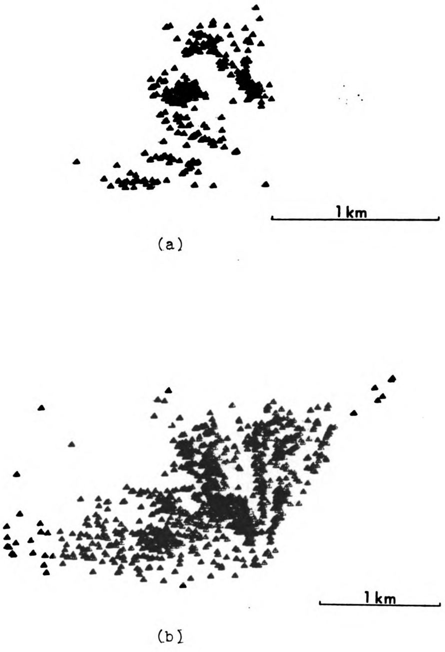


Figure 12. Radio-locations for male tapir 'Pepe' in Santa Rosa National Park, Costa Rica, April-December, 1982. (a) daytime, (b) night-time.

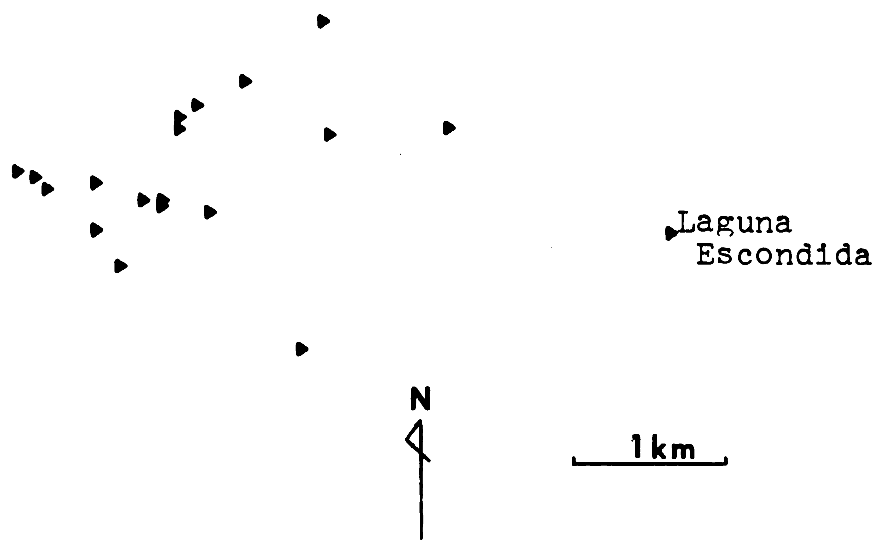


Figure 13. Daytime radio-locations for a female tapir in Santa Rosa National Park, Costa Rica, May 1981-January 1983.

Figure 13a. View of the lower Nancite basin from the dry ridge where a male tapir (Chuck) was located in Santa Rosa National Park, Costa Rica, 1982.

capture and radio-collaring, and was not re-established until 11 months later on July 27, 1982 when she was discovered resting on a ridge above a remote valley in which she had apparently been residing.

Success in locating the instrumented males during the course of the study was greater during the nights than during days (Figure 14). Both tapirs were most easily located between 6:00 a.m. and 7:00 a.m. with the lowest success being recorded between 8:00 - 10:00 a.m. for Chuck and between 10:00 - 11:00 a.m. for Pepe (Figure 14). Only between 3:00 p.m. and 4:00 p.m. was Chuck located with more success than Pepe but the difference was marginal. Success was not well correlated with movement through the forest.

J. Movements

Both instrumented, male tapirs ranged far more widely during the night than they did during the day (Table 4 and Figures 15 and 16). Chuck's nocturnal range at MAP (0.95) was 12 times greater than his diurnal range. At MAP (0.95) Pepe's nocturnal range was 6 times greater than his diurnal range. Several small patches of forest were avoided by these tapirs (Figures 15 and 16). These avoidances could have been either terrain or habitat related.

Two-sample t-tests of the distances traveled by the two males demonstrated that the movements at night were significantly greater ($P < .01$) than those during the day. Daily movements of both tapirs were the same, as were nightly movements. The ratios of average nightly to daily movements, however, were greater than those of night:day ranges (at MAP (0.95)) indicating that there was a much greater concentration of movement during daylight hours.

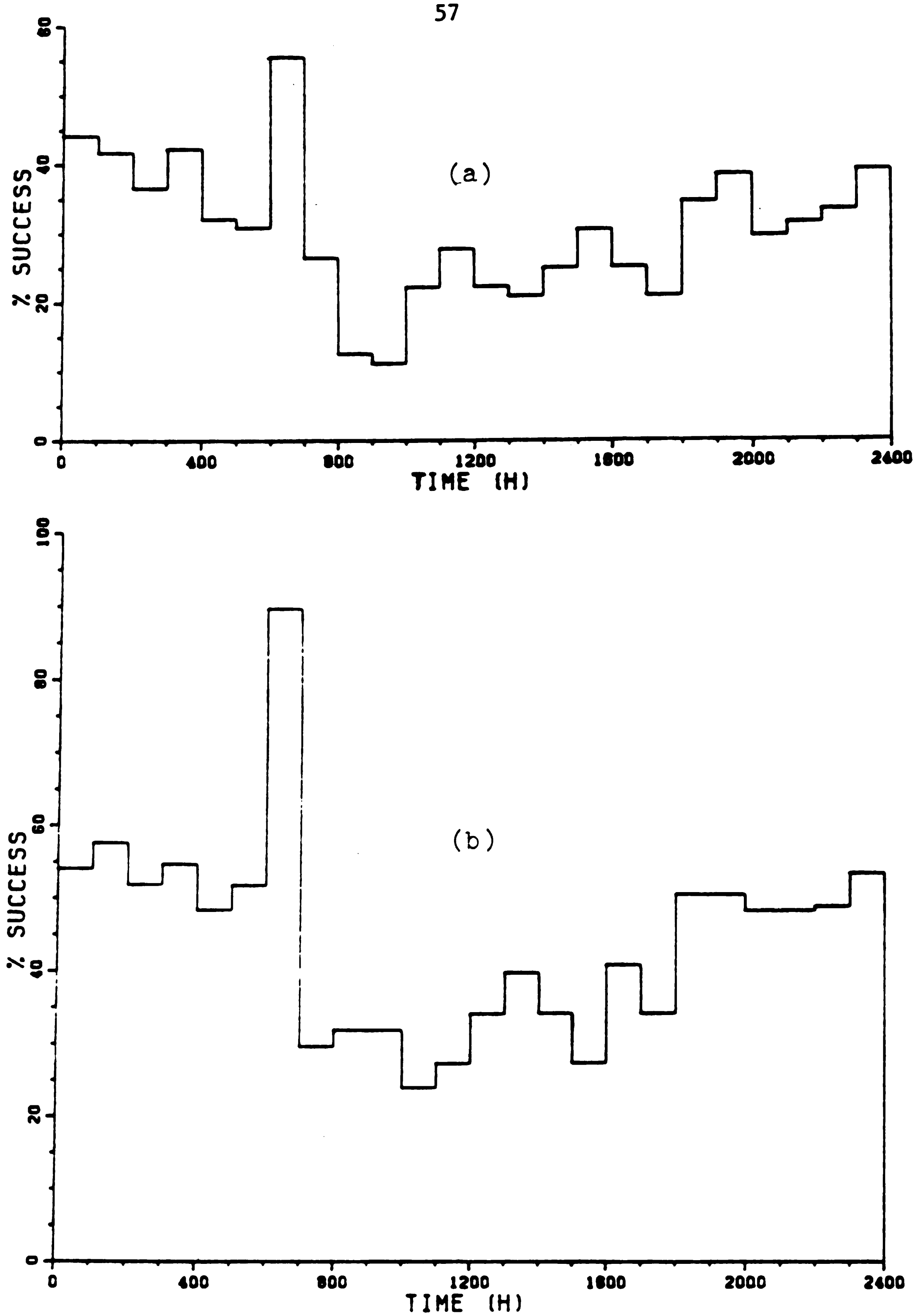


Figure 14. Percentage of successful triangulations per hour for two male tapirs in Santa Rosa National Park, Costa Rica, 1982. (a) Chuck, (b) Pepe.

Table 4. Diurnal and nocturnal activity ranges of two radio-collared male tapirs, Santa Rosa National Park, Costa Rica, 1982.

MAP value*	Diurnal (D) Nocturnal (N)	Range of Chuck (km^2)	Range of Pepe (km^2)
0.95	D	0.15	0.27
0.50	D	0.03	0.07
0.95	N	1.80	1.61
0.50	N	0.48	0.38

*MAP (0.95) = the area enclosed by the contour which delimits 95% of the volume under the utilization distribution.

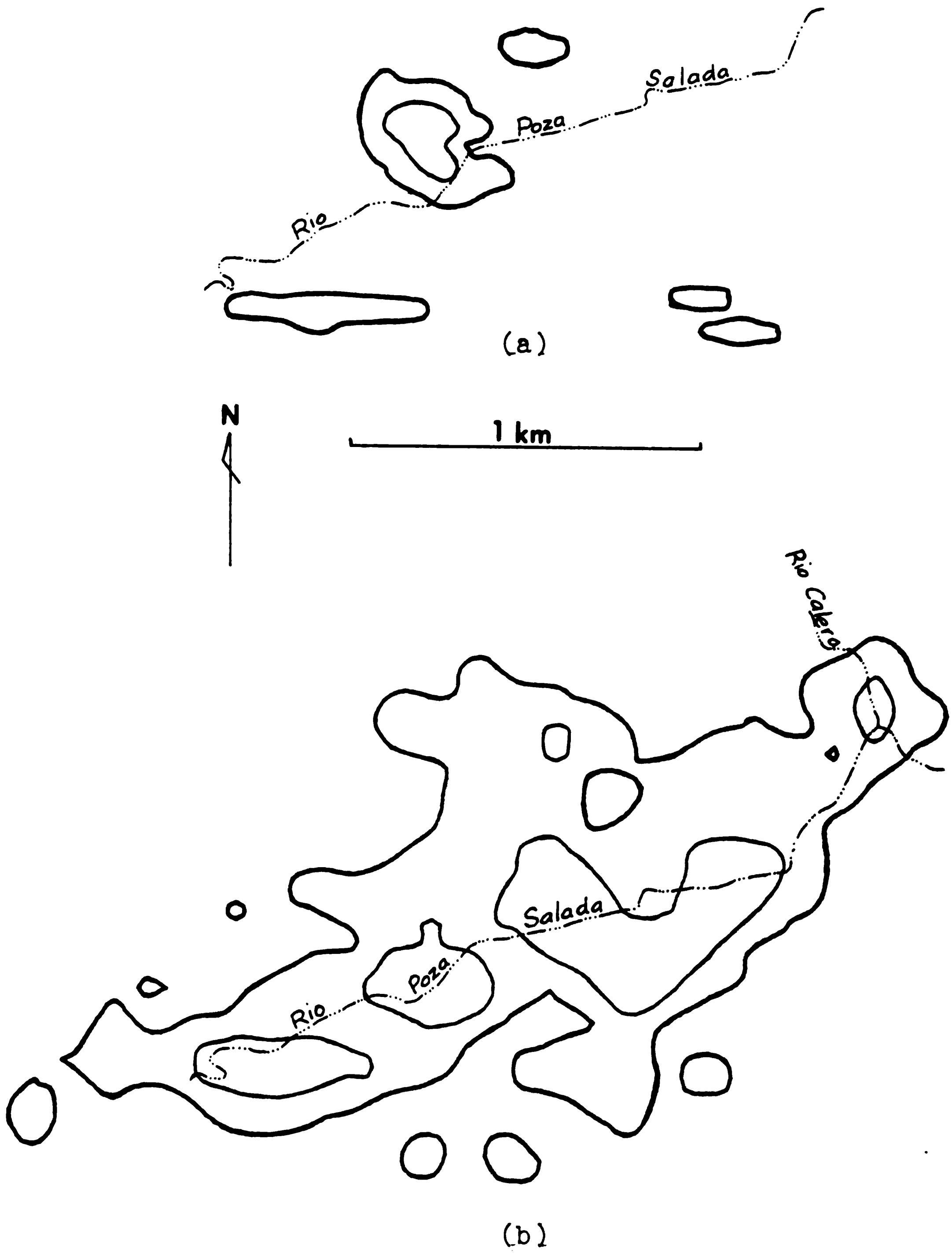


Figure 15. Activity ranges of a male tapir (Chuck) estimated by the MAP (0.95) and MAP (0.50) contours of Anderson's (1982) utilization distribution. (a) daytime, (b) night-time.
—— MAP (0.95) —— MAP (0.50)

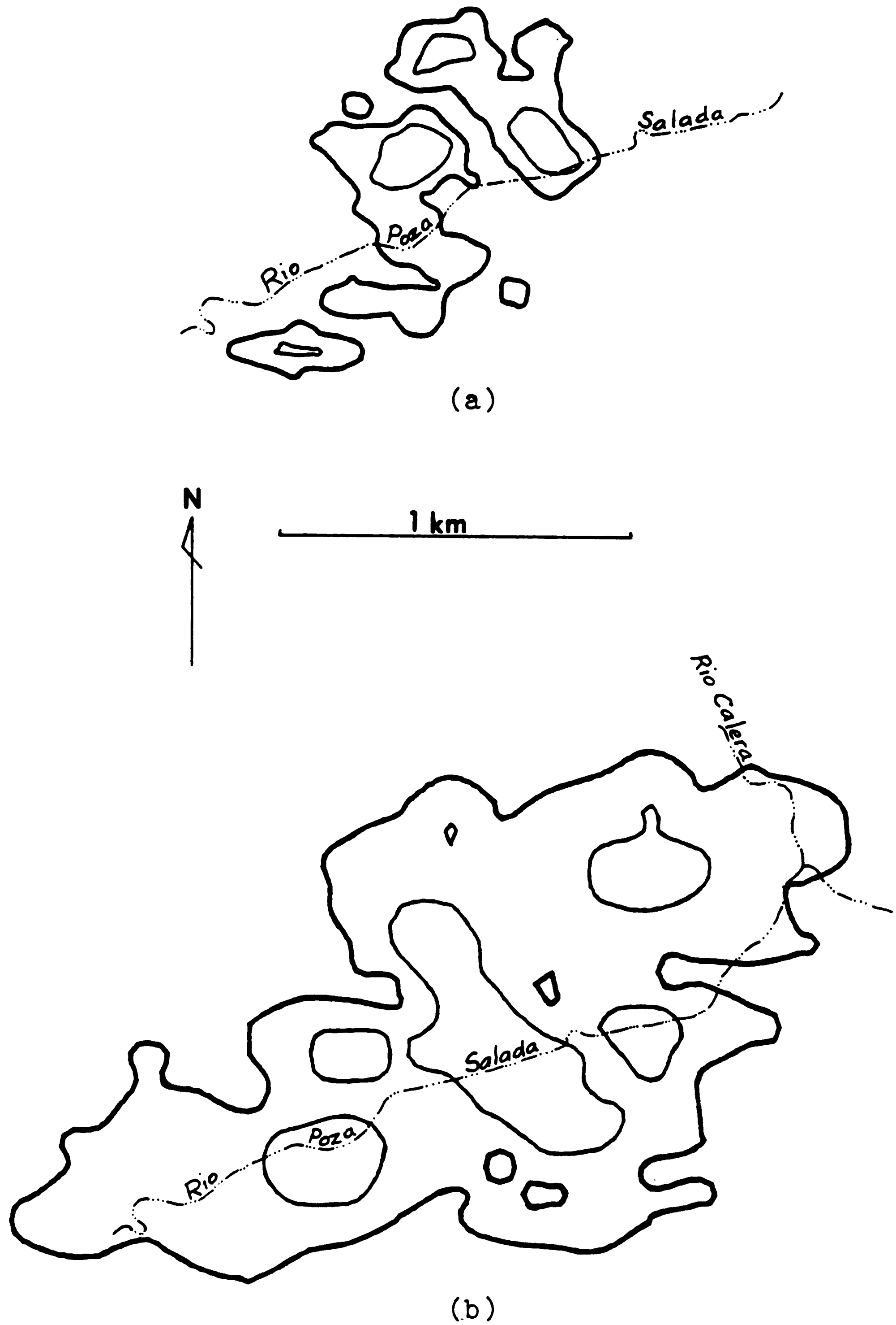


Figure 16. Activity ranges of a male tapir (Pepe) estimated by the MAP (0.95) and MAP (0.50) contours of Anderson's (1982) utilization distribution. (a) daytime, (b) night-time.
—— MAP (0.95) —— MAP (0.50)

The movement patterns of the two males exhibited two common peaks which occurred between 4:00 - 7:00 a.m. and between 6:00 - 8:00 p.m. (Figure 17), corresponding with sunrise and sunset. Additionally, Chuck moved markedly between 9:00 and 10:00 a.m. (Figure 17).

In moving through forests, tapirs have been reported to follow regular trails (Medway, 1969; Fragoso, unpubl. ms.), not to follow regular trails (Lekagul and McNeely, 1977) and to use trails only to traverse difficult terrain and in the vicinity of salt licks (Williams, 1978). Observations of animal trails and tapir spoor in this study indicate that _T. bairdii_ certainly uses trails and that these trails serve to access forest areas either for resting or feeding. Tapirs in SRNP also entered and left riverbeds at the same place and used rivers and riverbeds as trails. These observations concur with those of Fragoso (unpubl. ms.) who observed _T. bairdii_ in Belize.

On one occasion an assistant, Eliecer Monestel, observed two tapirs (possibly Chuck and Pepe) from a distance of 10 m as they walked upstream at 12:45 p.m. in the Rio Poza Salada. They entered a deep pool and continued to walk along the river bottom while completely submerged. They were completely submerged for a distance of approximately 15 m after which they turned and exited the river. Raffles (1822) reported a similar behavior for a captive _T. indicus_ and there are anecdotal reports of _T. indicus_ and _T. terrestris_ crossing rivers in this fashion, making no attempt to swim.

K. Activity range and habitat use

Activity ranges of both instrumented male tapirs were centered along the lower reaches of the Rio Poza Salada and overlapped considerably

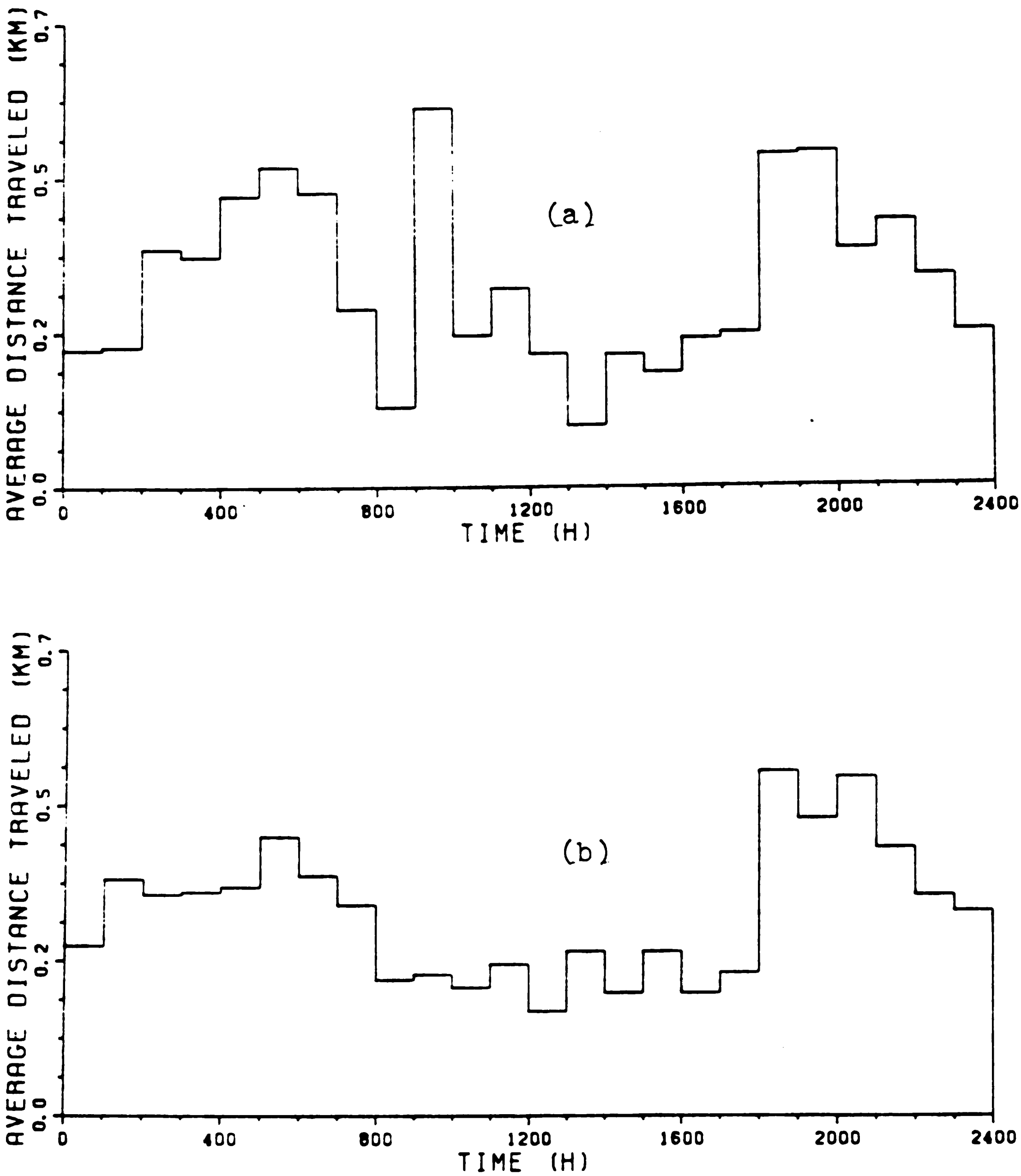


Figure 17. Average hourly movements of two male tapirs, (a) Chuck, (b) Pepe, in Santa Rosa National Park, Costa Rica, 1982.

(Figures 18 and 19). Most of Pepe's (89.7%) and Chuck's (79.4%) daily activities (MAP (0.95)) occurred in lowland riparian and regenerating riparian forests. Their most preferred cover types, as circumscribed by the MAP (0.50) contour, included only these two types (Table 5). Night-time activities displayed similarities except that activity at MAP (0.95) was notably greater in lowland riparian forest for both Pepe (43.8%) and Chuck (46.3%) than in other cover types (Table 5). The most preferred cover types for both males (MAP (0.50)) were, again, riparian lowland forest and regenerating riparian forest. These accounted for 82.5% of Pepe's activity and 85.3% of Chuck's activity at MAP (0.50).

Indicated beach activity (Table 5) by Chuck could have been due to triangulation inaccuracies, although broken and browsed saplings were found only 30 m from the beach sands. It is feasible that Chuck could have left vegetative cover there.

Tapirs were located resting, during the day, in a variety of cover types but always in shade. Dense patches of the vine *Pachyptera hymenaea* were used, as were the bases of trees and liane tangles. One tapir was flushed from tall grass at the base of a forest-edge tree. The instrumented female was located on two occasions resting in dense, woody vegetation (to 3 m) on a dry ridge. She had broken and browsed plants there. This dry ridge, however, was contiguous with evergreen forest which lined the walls and floor of an adjacent canyon. Though very steep, the canyon slopes were passable and tapir tracks and trails were found there. Permanent water was available in the canyon and also at a small spring above the head of the canyon. Both water sources were close to the places where the female was located.

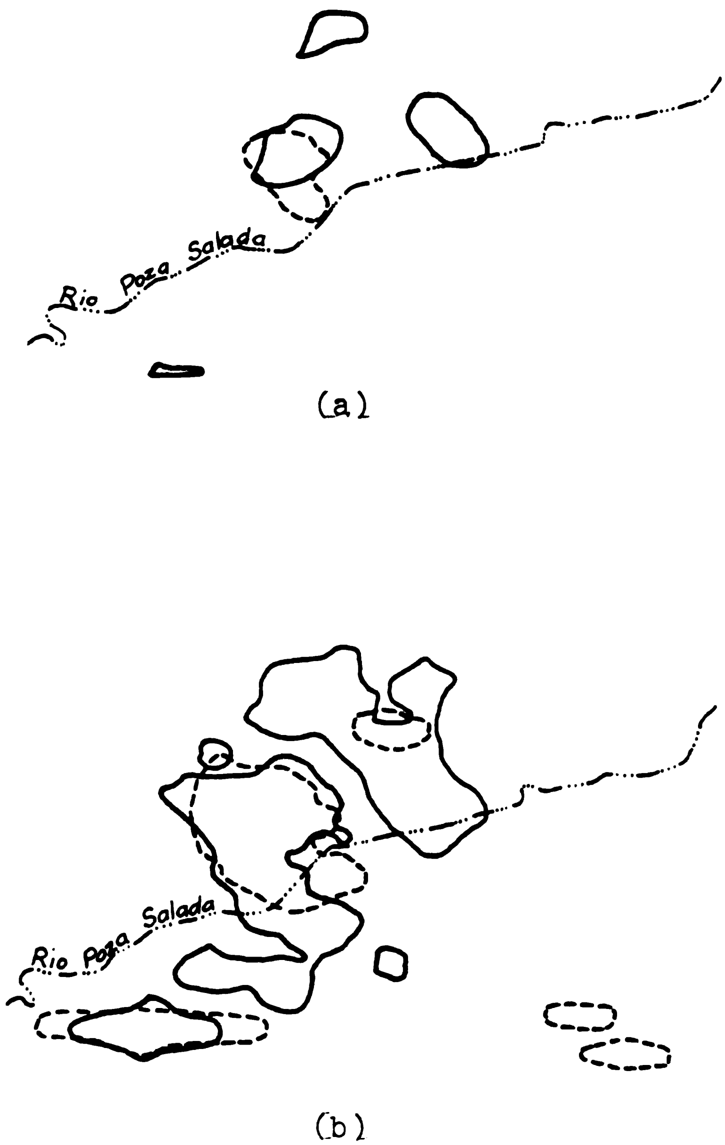
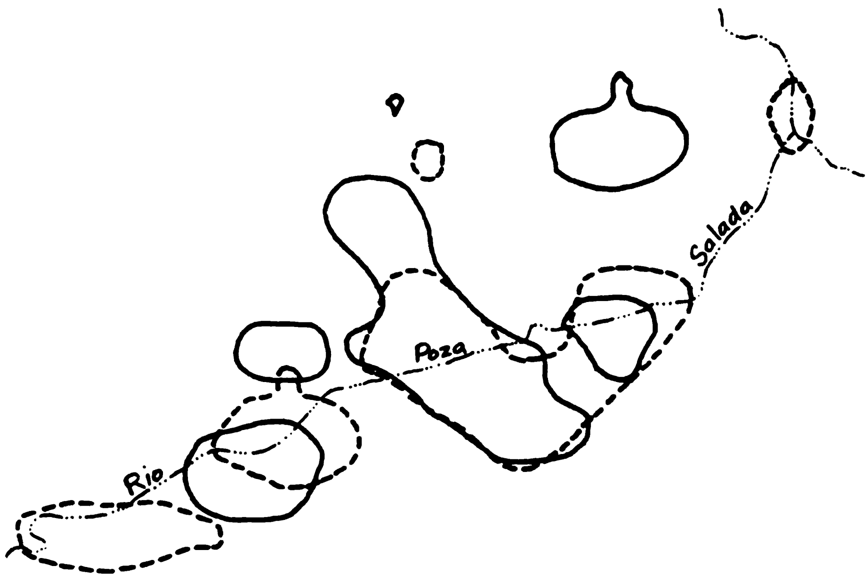
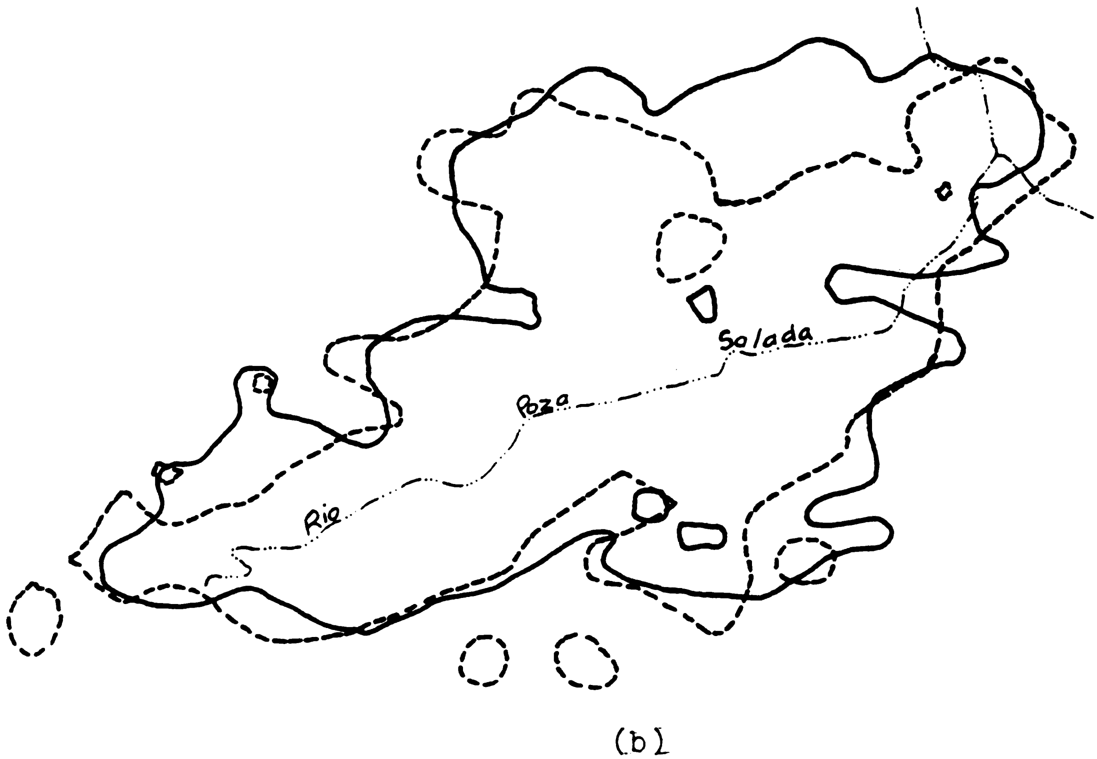


Figure 18. Daytime activity range overlap of two male tapirs in Santa Rosa National Park, Costa Rica, 1982. (a) MAP (0.50), (b) MAP (0.95).



(a)



(b)

Figure 19. Night-time activity range overlap of two male tapirs in Santa Rosa National Park, Costa Rica, 1982. (a) MAP (0.50), (b) MAP (0.95).

Table 5. Use by two male tapirs of interspersed vegetative cover-types in Santa Rosa National Park, Costa Rica, 1982.

Vegetative cover-type number*	Night-time % of total at MAP (0.95)		Night-time % of total at MAP (0.50)		Daytime % of total at MAP (0.95)		Daytime % of total at MAP (0.50)	
	Chuck	Pepe	Chuck	Pepe	Chuck	Pepe	Chuck	Pepe
1	0.59							
2	0.52							
3	4.84	5.60						
4	0.26							
5	0.07							
6	46.34	43.78	39.72	34.84	46.74	48.68	30.00	36.51
7a	20.78	17.75	45.56	47.61	32.61	41.06	70.00	63.49
7b	12.81	11.59	3.61	11.17	7.61	9.38		
8	3.40	3.53			6.52			
9	6.08	11.93	6.67	3.99				
10	1.57	2.63			5.43			
River	2.74	3.19	4.44	2.39	1.09	0.88		negligible
	100	100	100	100	100	100	100	100

* See Figure 3.

DISCUSSION

Forage use

Studies of forage-use by tapirs are few. Only limited information is available for both Tapirus bairdii (Terwilliger, 1978) and T. indicus (Medway, 1974; Williams, 1978; Williams and Petrides, 1980) in moist, tropical forests. These studies indicate that tapirs select specific plant parts from a limited array of the many forages available. The present study strengthened the earlier observations and provided evidence additional to that of Terwilliger (1978) that the consumption of some species is seasonal.

The many differences in plant acceptability shown by the feeding trials using the male zoo tapir of this study and the captive male also studied in Costa Rica by Janzen (1981d) could have been due to individual preferences, previous exposure to foodstuffs, or plant parts fed. Janzen (1981d) fed foliage collected in or near the same areas in which I collected, though in different months. He used samples from the crowns of adult shrubs and trees to obtain a standardized collection technique (Janzen, pers. comm.). "Foliage from young sucker shoots, saplings, and seedlings were generally not offered" (Janzen, 1981d). In my trials, I specifically offered foliage from sucker shoots, saplings and low-growing foliage as these were the plants and parts usually available to and consumed by tapirs in SRNP and elsewhere (Terwilliger, 1978; Williams, 1978; Williams and Petrides, 1980).

Several marked differences were found between the results of my feeding trials and Janzen's (1981d) (Table 6). Janzen's tapir accepted Bursera simaruba only once in 20 trials; my tapir never rejected and eagerly sought out B. simaruba in 76 trials (Table 7). B. simaruba saplings were frequently found broken and browsed by tapirs in SRNP as was Cochlospermum vitifolium, which was accepted only 66.7% (24 trials) of the time by Janzen's (1981d) tapir but never rejected in 58 trials by the San Jose Zoo tapir (Table 7).

Several species that were readily eaten by both tapirs in the feeding trials were not found browsed in SRNP. These included Quercus oleoides, Crescentia alata and Cecropia peltata. As discussed earlier, ants residing in Cecropia possibly inhibited consumption of saplings though dried, fallen leaves may be consumed. The other two species have drooping branches and browse could go undetected. That no branch ends were found browsed on saplings, however, is strange. The San Jose Zoo tapir accepted Alibertia edulis 59.7% of the time, yet Janzen's (1981d) captive eagerly consumed the large mature leaves. A browsed plant of this common understory shrub was located only once in SRNP and appeared to have been taken by a deer.

While both tapirs and deer consume some of the same forage species, their feeding methods are different. By breaking, tapirs are able to utilize understory foliage which is out-of-reach of deer. Deer browse some species that tapirs avoid.

A clear picture of the diets of free-ranging tapirs has not emerged. It seems certain, however, that like Tapirus indicus in

Table 6. Differences in plant species accepted and never eaten by the San Jose Zoo tapir and by Janzen's (1981d) captive tapir.

Species	This study		Janzen (1981d)	
	% Acceptance	Never eaten	% Acceptance	Never eaten
Acacia collinsii	33.3			+
Allophyllus occidentalis	89.2			+
Bursera tomentosa	80			+
Cassia biflora	100			+
Cassia hayesiana	100			+
Cordia alliodora	60.6			+
Genipa americana	73.7			+
Hamelia patans	57.9			+
Inga vera	92			+
Lygodium venustum	38.1			+
Mimosa pigra	100			+
Philodendron scandens	100			+
Piper jaquemontianum	96.2			+
Pithecellobium saman	18.2			+
Serjania schiedeana	66.7			+
Swartzia cubensis	95.2			+
Tabebuia ochracea	53.6			+
Thouinidium decandrum	82.8			+
Trichilia hirta	60			+
Verbesina gigantea	29.2			+
Bauhinia ungulata		+	9.1	
Jacquinia pungens		+	25	
Ipomoea trifida		+	100	

Table 7. Differences in percentage acceptability of plant species offered the San Jose Zoo tapir and Janzen's (1981d) captive tapir.

Species	This study % acceptability	This study Number of trials	Janzen (1981d) % acceptability	Janzen (1981d) Number of trials
Bauhinia ungulata	0	15	9*	11
Bursera simaruba	100	76	5*	20
Byttneria aculeata	100	12	41.6	12
Cochlospermum vitifolium	100	58	66.7	24
Hemiangium excelsum	100	54	9*	11
Jacquinia pungens	0	3	25*	8
Lonchocarpus costaricensis	42.9	14	8.3*	12
Machaerium biovulatum	100	65	28.6	7
Quercus oleoides	100	42	50	8
Tetracera volubilis	63.6	11	50	4

* Tapir "may have learned to reject these species during the feeding trials" (Janzen, 1981d).

Malaysia (Williams, 1978; Williams and Petrides, 1980), T. bairdii is a discriminant browser, consuming variable amounts of the many forage species available and completely rejecting many others. It has been suggested (Freeland and Janzen, 1974) that by mixing its intake an animal more readily can accept toxic compounds consumed. An animal like the tapir, that is capable of assimilating a varied diet, is able to increase greatly the food base on which it can subsist. It is also likely to respond better to unfavorable environmental perturbations than is a species with a more restricted food base.

Defecation and urination

Schauenberg (1969) stated that tapirs use urine for territorial marking. No evidence was presented by him and there is no evidence from other field studies, nor from this one, to suggest that tapirs are territorial. Throughout the period of this study the activity ranges of the two radio-collared males overlapped considerably and, from tapir observations and track measurements, at least two other tapirs occupied the same area.

Terwilliger (1978) found that T. bairdii "urinates frequently during the evening, especially males." Free-ranging male T. indicus also appeared (Williams, 1978) to urinate more frequently than females. That both male and female tapirs can squirt urine backwards implies that this ability is an adaptation for marking. The one instance of a tree used as a urination site in this study was similar to that of T. indicus in Malaysia (Williams, 1978).

What, then, are the functions of urine spraying and dung dump-sites? Are they significant from a behavioral standpoint and do they serve the same, or different, functions?

It has been suggested (Kleiman, 1966; Walther, 1978) that scent marks serve to orientate a resident within its territory (and presumably within its home range). Dung and urine sites could function as olfactory clues; their decay being indicative of the status of residence or use of a particular area. Reports received from local residents from monsoonal forests on the east coast (Tortuguero) of Costa Rica, and the limited data from the radio-collared female in this study, indicate that at least some tapirs utilize their home ranges in a rotational manner. That is, they may intensively use a portion of the annual home range for a period of time before moving to another portion.

Fruit consumption and seed dispersal

Fruits serve as an energy and nutrient source for tapirs and seed defecation provides a means of dispersal. An animal is a successful seed disperser if it moves viable seeds to a favorable germination site away from the parent plant or makes the seed available to a secondary dispersal agent which in turn moves the seed to a favorable germination site. A secondary dispersal agent can be abiotic (water, wind) or biotic (e.g. ants, birds, mammals).

Tapirs are wide-ranging mammals that have the potential to "generate a very complex and remote seed shadow" (Janzen, 1981c). Measurements of the maximum dimensions of tapir home ranges and mobility in this study demonstrates that seeds could be moved by tapirs up to 4.5 km from the parent plant.

In SRNP, tapirs were found to disperse the seeds of Spondias mombin, S. radlkoferi, S. purpurea, Zizyphus guatemalensis, Prosopis juliflora, Guazuma ulmifolia, Pithecellobium saman, Enterolobium cyclocarpum, Cassia emarginata, Crescentia alata, Cochlospermum vitifolium, Acrocomia vinifera, Guettarda macrosperma, Ficus spp., Psychotria nervosa, P. microdon, P. trichotoma, Randia echinocarpa, Ardisia revoluta, and Cordia guanacastensis. Of these, the seeds of Cochlospermum vitifolium are adapted for wind dispersal, Psychotria spp. are suited for dispersal by birds, and Bursera simaruba are adapted for bird or small mammal dispersal.

Of the seeds found to be dispersed by tapirs in this study, Gentry (1942, as noted in Janzen and Martin, 1982) listed Cassia emarginata as well as Bursera simaruba as not having fruits or seeds adapted for large-mammal dispersal. Many viable Cassia emarginata seeds, nevertheless, were encountered in tapir dung. While the small, soft seeds could be crushed during mastication, many are swallowed intact. The small seeds of Ficus spp. and Cordia guanacastensis similarly are transported by tapirs.

Janzen and Martin (1982) hypothesized that the Pleistocene megafauna was an important means of seed dispersal for many of the plant species which still occur in Central American lowland forests. They suggested that horses, cattle and other free-ranging domestic stock may have now, at least to some extent, replaced the extinct fauna in performing this function. They further believed that tapirs act as seed predators as well as seed dispersers with regard to the fruits consumed. In the current study, however, it was found that tapirs in SRNP were only dispersers and not predators of Spondias mombin, S. radlkoferi, S. purpurea, Zizyphus guatemalensis, Guettarda macrosperma and Acrocomia vinifera. Each of these fruits contained a hard nut or seed coat that prevented damage to the endosperm either by molar action or digestion. Only the pulp was digested.

Tapirs are successful seed dispersers. While defecation in water prevents access to seed-containing dung by some biotic elements, those seeds with delayed germination potential (e.g. Acrocomia vinifera, Enterolobium cyclocarpum, Spondias spp., Pithecellobium saman, Zizyphus guatemalensis, Guettarda macrosperma) can be further dispersed by stream and river flooding. Seeds defecated at terrestrial dump-sites can be located favorably for germination. They also are subject to secondary dispersal especially by rodents.

Germinations of Spondias mombin and/or S. radlkoferi (the fruits and nuts were not distinguishable) and of Prosopis juliflora were observed in the field in tapir dung piles. Prosopis germinated within a few weeks of deposition; Spondias spp. sprouted a year after deposition.

The relationship between tapirs and Spondias nuts is noteworthy. The nut is of such a size that smaller consumers (e.g. monkeys, coatis, peccaries) invariably chewed off the pulp and spat out the nut. Tapirs took the whole fruit in large numbers. All nuts swallowed passed through the gut intact and apparently require microbial breakdown to permit water entry for germination. Additionally, they are buoyant and adapted to secondary flood dispersal. Tapirs, thus, may be an important primary dispersal agent for Spondias.

As specific adaptations to tapir dispersal, Spondias nuts (1) are sized to be swallowed by tapirs and rejected by other consumers;

(2) are hard, thus surviving mastication and gut passage; (3) have a long water-immersion life; (4) require decomposition of the nut wall to permit germination; and (5) retain a fibrous jacket that promotes bouyancy even though Spondias spp. are not riparian plants.

Janzen (1981b) and Janzen and Martin (1982) have stated that interpreting the interactions between contemporary native megafauna and plants may be a false approach to plant-animal relationships because such contemporary relationships may have been trivial during the plants' evolutions. As tapirs have changed little since the Pleistocene, however, perhaps they permit a contemporary experience of prehistoric time. It seems not unreasonable to hypothesize that Spondias co-evolved with tapirs or tapir-like species.

The role of tapirs in the dispersal of other seeds is less clear. That this ungulate is one of a coterie of seed dispersers, however, is certain. For many of these ingested seeds, digestion of some seeds may be the price paid for the enhanced distribution and germination of the survivors.

Radio-tracking and habitat use

The activity ranges estimated from radio-tracking the two males demonstrated that the detection of daytime-only locations would severely underestimate the areas utilized. Night-time locations must be incorporated into a radio-tracking program whenever activity over this animal's range is to be studied. Additionally, care must be exercised in collecting night-time data as tapirs leave and return to daytime resting areas around sunset and sunrise, respectively, and are therefore likely to be near those locations at those times.

Tapir locations must be obtained at different times throughout the day and night.

Tapirs wander considerable distances at times. To insure the signal location of distant animals, it is recommended that at least some aerial tracking be planned.

The relatively poor success in locating tapirs during the daytime probably was related to the resting places and positions of the tapirs. Vegetative cover and the above-ground heights of tapir-borne antennas are critical factors, since tapirs sometimes rest on their sides with their antennas near the soil surface. When tapirs rest in rivers and pools the transmitting antenna can be below the level of the river-banks and signals may then be severely attenuated. When tapirs are near large trees signal strength may also be reduced.

Ideal habitat for *T. bairdii* is structurally multi-layered and and is near permanent water. Mature, evergreen trees are needed to supply cooling and shade, young saplings and woody shrubs are required for leafy browse, and patches of dense cover are preferred for day-time retreat. In Belize, *T. bairdii* heavily browsed herbs and shrubs on a floodplain (Fragoso, unpubl. ms.) and the presence of such a flood-plain enhances tapir habitat.

Tapirs do not always require vertical cover and do not need wooded "corridors" to move from one forest patch to another. In Costa Rica, however, their movements probably are restricted by farm fences. Frequently these are constructed with posts spaced two meters apart or less with 5-6 strands of barbed wire. The lowest strand of wire usually is 15 cm or so from the ground. Wire tension and spacing often effectively prevents tapir access; only damaged fences and unfenced watercourses readily permit tapir passage.

Tapir populations

Throughout the period of this study, observations of tapirs, or tapir spoor, anywhere in the park were noted. Temporal and spatial differences indicated that there were between 17 and 26 tapirs resident in SRNP during the course of the study. This translates to an average density of 1 tapir per 6.35-4.15 km^2. For comparison, the population of *T. bairdii* in the 17.2 km^2 tropical monsoon forest of Barro Colorado Island (BCI), Panama, has been estimated at 10 (Terwilliger, 1978), 5 of which were supplementary-fed. It is reasonable to presume that the fed tapirs on BCI received at least 50% of their daily energy requirements from the supplied bread. An estimate of the number of tapirs that BCI was capable of supporting (presuming also that a maximum population existed), then, is about 8 (5 independent tapirs plus half of the 5 fed tapirs), or 1 tapir per 2.15 km^2.

Vaughan (1983) states that in 1977 about 15,901 km^2 of Costa Rica supported dense forest (greater than 80% forest cover) of which 8,479 km^2 was protected against alteration. These areas varied between lowland primary forest and subalpine paramo. If 90% of the densely-forested areas actually was forest-covered, then a maximum tapir population estimate for Costa Rica would be 6,656 (15,901 x 0.9 ÷ 2.15) based on the above BCI density figure. Similarly, the 8,479 km^2 of land in protected areas would support a maximum of 3,549 tapirs. Vaughan's (1983: map 22) reports of tapirs outside areas of at least 45% forest cover were infrequent and generally in isolated or protected patches of the country.

The densely-forested habitats in Costa Rica, though, are highly variable due to differences in altitude, topography, aspect, and weather. For tapirs, many such areas are thought to be inferior to the moist, lowland forests. Because of human disturbances (hunting, settlement, logging) as well, it is judged that Costa Rica may hold as little as half of the maximum estimated number of tapirs. I estimate that the tapir population of Costa Rica is between 3,300 and 6,700. In legally-protected areas of the country, the tapir population is judged to be between 1,800 and 3,500 individuals.

MANAGEMENT RECOMMENDATIONS

National parks are established to preserve natural biotic communities. Manipulation of any part of that community, therefore, should be directed towards the maintenance or restoration of natural ecosystems. Following 200 years of exploitation, SRNP is now largely in a state of forest regeneration. The expansion of forest cover to a semblance of that which existed historically is a local National Park Service goal.

This has been attempted with some success (R. Carlson, pers. comm.) using fire to suppress the savanna grasses. Yet this is still a practice of uncertain benefit in SRNP; personnel currently assigned to burn have been encouraged by a senior officer of the Conservation Foundation of Costa Rica to burn all of the savanna grass each year. No semblance of controlled burning prevails. Fires often have been lit by park personnel and abandoned to become wildfires. Frequently these enter forest edges and destroy regenerating woody plants -- the food of tapirs. An advanced understanding of fire ecology must be learned.

Burns must be controlled. Since personnel in SRNP are limited, burns should be small, frequent and monitored; not big and unconfined. Proper burning will increase tapir forage within the park and decrease the risk of invading blazes from adjacent ranches.

In historic times, severe droughts in Guanacaste must have decimated the tapir population. Recovery, however, would have been possible through immigration from more favorable habitats. Now, such immigration is unlikely because of agricultural development in the region and low tapir numbers in forest isolates there. The maintenance of natural ecosystem function in SRNP requires perpetuation of the local tapir population.

In addition to improving fire control, there are three other specific recommendations for tapir management in SRNP. These are as follows:

1. The repair of the "Laguna Escondida" dam on the upper plateau of SRNP, 2 km from park headquarters. This dam not only has excellent water-storage potential but could serve as a site for an elevated blind for park visitors. Overnight facilities for wildlife viewing would enhance park use and could produce revenue.

2. The lower reaches of the Rio Poza Salada normally provide waterholes for tapirs and other wildlife. Abnormally dry weather as experienced through 1982 and 1983, if continued, could result in a loss of this water source. It is essential that water availability there be monitored and maintained during the dry season. If necessary, these and other waterholes could be deepened.

3. Between 1981 and 1982 there was a marked decline in the quantity of tapir spoor seen in the uplands of the park. While the cause of this decline is not known, it is suspected that free-ranging park horses may be responsible. They frequently muddied the few waterholes and may have affected adversely the tapirs there. Disease transmission from horses to the related tapir also is a possibility.

It is recommended that horses not be permitted to range freely in the national park.

In other parts of the country where dense forest and tapirs exist and the preservation of strictly-natural conditions is not essential, tapir browse availability could be increased by creating openings in the forest where regenerating sapling growth would ensue. For tapirs, such canopy-gaps should best be long and narrow to maximize the edge. Nevertheless, proper selective logging would create light gaps and, if not carried out too extensively, the practice may be beneficial to tapirs. Where logging is permitted, care must be taken to insure that large, contiguous, forest areas, where there is no human disturbance, remain to serve as a refuge. This means that tapir ranges that are to be selectively-logged should be logged on a compartment basis; establishment of sapling regrowth on logged areas is essential before adjacent plots are logged.

Reducing the tension in farm fencing wire and spacing the fence posts at a minimum distance of 4 m would permit the passage of tough-skinned tapirs while still controlling cattle. This plan should be encouraged where uncleared farmland and tapirs co-exist.

As tapirs reproduce slowly (Williams, 1978) even moderate hunting pressure can affect adversely the fecundity of a population. Extension efforts directed towards removing the apathy of law enforcement personnel and improving wildlife law enforcement should be encouraged.

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