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Home Range, Habitat Use, and Activity of Baird's Tapir in Costa Rica[1]

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ABSTRACT

Home range size, habitat utilization, and activity patterns of five adult Baird's tapirs (*Tapirus bairdii*) were studied via radiotelemetry from June 1995 to May 1996 in Corcovado National Park, Costa Rica. Estimates of 4153 animal locations were made. Home range sizes (95% minimum convex polygon) for the entire study period (wet season and dry season) averaged 125.0 ha (SD = 72.7), 94.9 ha (SD = 47.6), and 96.8 ha (SD = 51.2), respectively. Monthly home range sizes averaged 55.5 ha (SD = 32.1) and did not vary between seasons. Across the entire study, secondary forest, the most commonly used habitat type (61.3%) was utilized more than expected as predicted by availability (49.6%), while the second most used habitat, primary forest, was used (25.0%) less than expected (36.2%). The same general habitat selection pattern was observed in the dry season. Wet season habitat utilization values showed tapirs using both primary and secondary forest habitats in proportion to their availability. Diurnal and nocturnal activity levels were estimated at 20.2 and 80.4 percent, respectively. More diurnal and less nocturnal activity was observed during the wet season compared to the dry season.

RESUMEN

El ámbito hogareño, uso del hábitat y los patrones de actividad de cinco tapires centroamericanos (*Tapirus bairdii*) se estudiaron por medio de radiotelemetría desde junio de 1995 hasta mayo de 1996 en el Parque Nacional Corcovado (PNC), Costa Rica. Nuestras estimaciones se basan en 4153 ubicaciones. Los ámbitos hogareños promedio (polígono convexo mímimo del 95%) para todo el periodo de estudio, estación húmeda y seca fueron de 125.0 ha (DE 72.7), 94.9 ha (DE 47.6) y 96.8 ha (DE 51.2) respectivamente. El promedio mensual del ambito hogareño fue de 55.5 ha. (DE 32.1) y no varió entre las estaciones. Durante el periodo de estudio, el bosque secundario fue el hábitat más utilizado (61.3%) a pesar de tener una menor disponibilidad (49.6%); en segundo término le siguió el bosque primario (25%) que fue utilizado menos de lo esperado (36.2%). El mismo patrón de selección de hábitat se observó durante la estación de secas. Los valores de utilización en la estación húmeda indican que los tapires usan el bosque primario y secundario de acuerdo a su disponibilidad. Los niveles de actividad diurna y nocturna fueron 20.2 y 80.4% respectivamente. Durante la temporada húmeda se observó una mayor actividad diurna y una disminución en la nocturna.

Key words: activity pattern; Baird's tapir; Costa Rica; habitat use; home range; radiotelemetry; Tapirus bairdii; *tropical wet forest.*

THE BAIRD'S TAPIR (*TAPIRUS BAIRDII*) is one of four species in the genus *Tapirus*, family Tapiridae. The tapir is an herbivore and the largest native terrestrial mammal in the Neotropics (Emmons & Feer 1990). In addition to being an important food source for many people in rural areas (Freese & Saavedra 1991), the Baird's tapir is an important seed disperser (Janzen 1982, Naranjo 1995b, Fragoso 1997) and a potentially important indicator species regarding the health of Neotropical rain forests (Dirzo & Miranda 1991).

Once common in most vegetation types between sea level and subalpine paramo throughout Central America and northern South America, the Baird's tapir is now extinct in El Salvador and endangered throughout the rest of its range (IUCN 1994, March 1994). Habitat loss and overhunting are cited as the principal causes for the decline in numbers (IUCN 1982, Vaughan 1983, Emmons & Feer 1990). *Tapirus bairdii* was classified as the tenth rarest Neotropical forest mammal by Dobson and Jinping (1993) based on population density and distribution.

Nevertheless, few detailed studies on the ecology of the Baird's tapir exist. Their mostly nocturnal activity, coupled with its secretive behavior in dense tropical forests, make it difficult to study in the wild. Accordingly, habitat use, diet, and abun-

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dance of *T. bairdii* have usually been estimated in short-term studies using methods such as track counts, direct sightings, fecal analysis, and feeding trials with captive animals. Without reliable information on habitat use, spatial requirements, and demographics, developing a strategy for sustaining free-ranging Baird's tapir populations will be impossible. For example, determining size and composition of an area that fulfills critical life history requirements is an important first step in establishing conservation reserves. Disproportionate use of available resources can indicate habitats and areas where conservation efforts should be focused. Here, we report results of the first major radiotelemetry study of space use and activity pattern of the endangered Baird's tapir.

The main goal of this research was to describe the basic ecology of free-ranging Baird's tapir in the forests of Corcovado National Park, Costa Rica. Toward this end, we conducted a radiotelemetry study from June 1995 to May 1996 to monitor the movements of five adult Baird's tapirs. Specifically, our objectives were to determine annual and seasonal variations in (a) habitat use, (b) home range size, and (c) activity patterns.

STUDY AREA

We conducted research in Corcovado National Park (CNP; 41,789 ha; 8°26′–8°39′N, and 83°25′–83°45′W) on the southwestern coast of the Osa Peninsula, Costa Rica (Fig. 1). Created in 1975, CNP represents the largest remaining tract of lowland tropical rain forest in Central America and supports an estimated 500 tree species, 367 bird species, 140 mammals, 51 amphibians, and 64 reptiles (Hartshorn 1983, Boza 1992, Vaughan & Rodriguez 1997). Naranjo (1995a) estimated a population of between 155 and 249 Baird's tapirs in the park. The mean annual temperature in CNP ranges between 23 and 26.5°C depending on elevation. The rainy season extends from May to November (475 mm precipitation/mo), and the dry season from December to April (130 mm/mo; Vaughan 1981).

Base camp was established at the Sirena ranger station, located on the southwest coast of CNP. Two major rivers drain the region: the Rio Claro to the south and the Rio Sirena to the north. The region north and northwest of the Sirena station has alluvial, well-drained soils and vegetation corresponding to tropical wet forest. Vaughan (1981) estimated that *ca* 1800 ha had been deforested in the area (principally in 1 to 17 ha parcels) before it was declared a national park in 1975. The resulting habitat now, 21 years later, is a mosaic of primary and regenerating secondary forests. East and southeast of the station is dominated by primary forests on steep slopes rising to 145 m. Numerous intermittent streams are found throughout the study area.

Six habitat types were identified in the area using a 1992 aerial photograph (scale = 1:20000 Instituto Geografico Nacional de Costa Rica): (a) primary forest, (b) secondary forest, (c) freshwater, (d) beach, (e) coastal grassland, and (f) airstrip/compound (Fig. 1). Phillips (1993) and Naranjo (1995a) have described the structure and dominant species in the primary and secondary habitats. The freshwater habitat included the Rio Claro, Rio Sirena, and the Sirena lagoon, a shallow body of water running parallel to the coast north of the Sirena river mouth. Beach habitats north of the Claro river mouth are primarily sandy, while to the south rocky points separate sandy coves. The coastal grassland is a thin strip of vegetation between the beach and the Sirena lagoon dominated by a tall, coarse grass and interspersed with *Terminalia* sp. (Combretaceae), *Cocos nucifera* (Arecaceae), and *Hibiscus tilleaceus* (Malvaceae). The airstrip/compound habitat included the grassy area of the Sirena ranger station compound and the airstrip.

METHODS

CAPTURE AND MARKING.—Areas used regularly by tapirs were baited in December 1994. A variety of baits were tested for acceptance (salt blocks, apples, bananas, and several local forest fruits). Ripe bananas were found to be the most effective bait for attracting tapirs to capture sites. After three consecutive nights of visitation by tapir(s), rope platforms were constructed 5—10 m high, in trees 10—15 m from the bait site. Most capture sites were located at least 200 m from deep bodies of water to avoid risk of an anesthetized animal drowning. For one site located 100 m from the Rio Sirena, we built a bamboo corral (30 × 20 m) to enclose the bait area. A trip wire in the center of the corral activated two drop doors. Information on darting and anesthetic protocol are documented in Paras *et al.* (1996).

TELEMETRY DATA COLLECTION.—We conducted a three-month pilot study from April to June 1995 to test accuracy (Mean Error) and precision (SD) of bearing estimates on transmitters in known locations using (a) fixed antenna array systems locat-

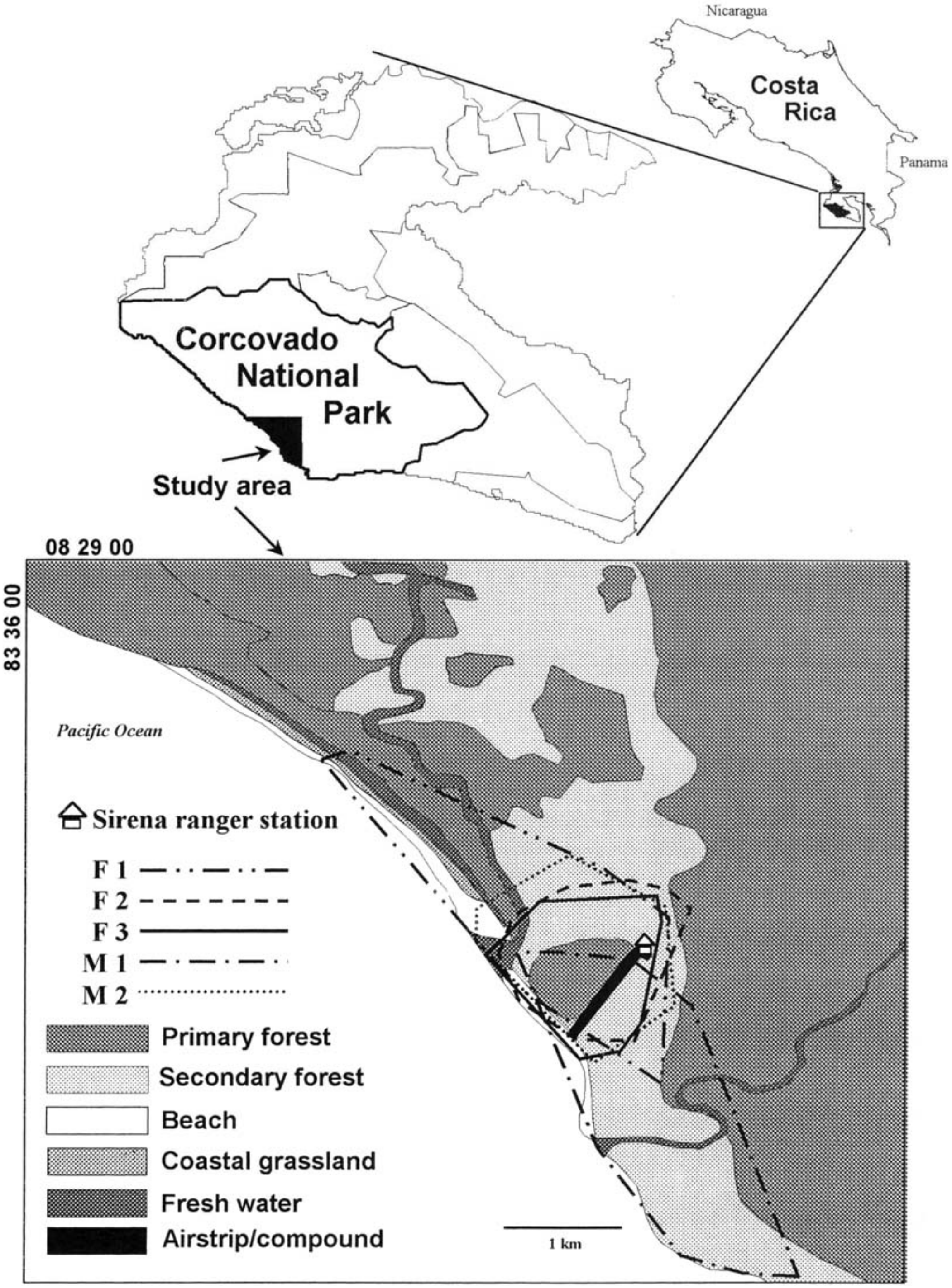


FIGURE 1. Location of Corcovado National Park, habitat map of study area, and annual home range boundaries (95% convex polygon) of each study animal.

ed on hilltops overlooking the study area, (b) fixed antenna sites located in canopy platforms, and (c) handheld antennas at receiving stations along trails transecting the study area. Twenty-five replicates were made on three transmitter locations for each method. Estimates from handheld antennas resulted in more accurate (2.4 ME) and precise (1.1 SD) data compared to antenna array systems (13.3 ME; 4.4 SD) and canopy platforms (9.6 ME; 2.4 SD). Fixed antenna stations did not provide accurate bearing estimates probably due to interference from dense, wet vegetation and the great distance between the animal and receiver.

For the final telemetry sampling design, we used handheld, two-element H-antennas and TR-4 receivers (Telonics, Mesa, Arizona) to locate tapirs by triangulation from two stations along research trails. Bearings were taken either simultaneously or within four minutes of each other. When a marked animal was observed directly, its position (bearing and distance) was recorded relative to the closest telemetry station. The animal's coordinates were estimated using the computer program Telem88 (Dept. of Fisheries and Wildlife, Virginia Polytechnic Institute and State University, Blacksburg, Virginia).

Each tapir was located hourly during diurnal (0600–1759 h) and nocturnal (1800–0559 h) data collection periods. Five diurnal and five nocturnal collection periods were conducted per animal monthly. Mathematical independence of successive nocturnal observations was tested for each month-long data set with the ratio t^2/r^2, where t^2 is the mean squared distance between successive observations and r^2 is the mean squared distance from the center of activity (Swihart & Slade 1985). Independence was assumed when the ratio of t^2/r^2 was 2.0 or greater. Independent locations were used to calculate habitat use and selection.

Activity patterns.—For estimation of animal activity (active or inactive), any pattern of reception other than a consistent pulse intensity was considered an observation of an active animal. We calculated the percentage of active observations (PAOs) for diurnal and nocturnal periods during both seasons and for the entire study period. PAOs were also calculated for each hour and totaled for wet and dry seasons and over the entire study period. The replicated *G*-test (William's correction) was used to compare: (a) wet season diurnal ratios of active observations against dry season diurnal ratios, and (b) wet season nocturnal ratios of active observations against dry season nocturnal ratios.

Home range.—Study-long, seasonal, and monthly home ranges (MHR) (95%) were estimated with the minimum convex polygon method using the computer program Homerange (Ackerman *et al.* 1990). A one-way ANOVA was used to test for seasonal variation in monthly home range size. Data subjected to ANOVA were tested for homogeneity with the log-anova method (Sokal & Rohlf 1995). The computer program Tracker was used to measure (a) seasonal home range overlap for each tapir and (b) study-long and seasonal home range overlap between individuals.

Habitat use.—A habitat map was made using a 1992 aerial photograph (scale = 1:20000, Instituto Geografico Nacional de Costa Rica) and digitalized in the Idrisi computer program for geographic data analysis (Clark Labs for Cartographic Technology and Geographic Analysis, Clark University, Worchester, Massachusetts). Availability of the six habitats (primary forest, secondary forest, freshwater, beach, coastal grassland, and airstrip/compound) was calculated by the percent coverage of each habitat type within each tapir's 95 percent home range boundary using the Idrisi program. Percentage of telemetry locations within each habitat type was calculated to estimate habitat usage by each tapir. Habitat availability and use data for all tapirs were combined to determine an overall habitat selection pattern. The *G*-test (William's correction) was used to determine significant seasonal differences between wet and dry season habitat use. Use of individual habitats more than, less than, or equal to availability estimated for the wet season, dry season, and the entire study period was tested using the program Habuse (Manly *et al.* 1993) which calculates chi-square values and Bonferroni confidence intervals for use versus availability.

RESULTS

Study animals.—Two subadult females (F1 and F2), one adult female (F3), and two adult males (M1 and M2) were immobilized and radio-collared between 15 January and 4 March 1995. Although no established method for estimating tapir age was available, the tapirs were placed in these general age categories based on body size and dental characteristics (size and coloration). Tapirs F1 and F2 were estimated to weigh between 180 and 220 kg. Their incisors and canines were well developed but had very little staining that appears with aging. Tapirs F3, M1, and M2 weighed *ca* 300 kg and had moderate to extreme staining of the incisors and canines. Tapir F2 had a one-month-old (estimated) male calf by her side at the time of capture. This calf disappeared at *ca* 4 months of age and was presumed to have been predated because offspring normally remain with their mother for 12 months (R. Barongi, pers. obs.).

TELEMETRY DATA.—Tapirs F1, F2, M1, and M2 were monitored from June 1995 to May 1996, excluding August 1995. Tapir F3 was monitored until 17 April 1996, when the collar malfunctioned. Estimates of 4153 locations were made (3463 triangulated and 690 visual; Table 1). Wet season and dry season location estimates totaled 2276 and 1877, respectively. Independence between locations was achieved every four hours for tapirs M2 (N = 194) and F2 (N = 192), every five hours for tapirs M1 (N = 146) and F3 (N = 173), and every six hours for tapir F1 (N = 143).

ACTIVITY PATTERNS.—Study-long, wet season, and dry season PAOs for all tapirs combined were 53.9 (N = 4440), 54.9 (N = 2574), and 52.4 percent (N = 1866), respectively. All tapirs were more active during nocturnal hours compared to diurnal hours (Fig. 2). Study-long PAOs during diurnal and nocturnal periods for all tapirs combined were 20.2 (N = 2043) and 80.4 percent (N = 2397), respectively. Wet season PAOs for all tapirs combined during diurnal and nocturnal periods were 24.2 (N = 1134) and 80.3 percent (N = 1440), respectively. Dry season PAOs for all tapirs combined during diurnal and nocturnal periods were 16.7 (N = 909) and 86.5 percent (N = 957), respectively. Tapirs F2, F3, M1, and M2 were significantly more active during diurnal hours in the wet season compared to the dry season (Fig. 3). No significant differences were seen in nocturnal activity between wet and dry seasons for any tapir.

HOME RANGE.—Study-long 95 percent MHR ranges averaged 125.0 ha (SD = 72.7) for all tapirs combined (Fig. 4). Study-long male home ranges ($\bar{x}$ = 159.5 ha, N = 2, SD = 102.88) were larger, but not significantly (t = 0.83, df = 3, P = 0.46) than female home ranges ($\bar{x}$ = 102.0 ha, N = 3, SD = 57.40). Wet season 95 percent MHR ranges averaged 94.9 ha (SD = 47.6, range = 50.5–167.1) for all tapirs combined and did not differ significantly (t = −0.06, df = 8, P = 0.95) from the dry season ($\bar{x}$ = 96.8 ha; SD = 51.2). Male wet season home ranges ($\bar{x}$ = 118.7 ha, N = 2, SD = 68.52) were larger, but not significantly (t = 0.89, df = 3, P = 0.44) than female home

TABLE 1. *Information on age class and radiotelemetry locations collected on each study animal.*

		Number of locations			Total locations		Independent locations		
Tapir	Age class	Calculated	Visual	Error	Diurnal	Nocturnal	Wet season	Dry season	Study-long
F1	Subadult	531	206	13	329	395	79	64	143
F2	Adult	767	134	18	354	529	104	88	192
F3	Subadult	704	158	13	380	469	94	79	173
M1	Adult	817	78	43	368	484	80	66	146
M2	Adult	752	114	21	409	436	104	90	194
	Total	3571	690	108	1840	2313	461	387	848

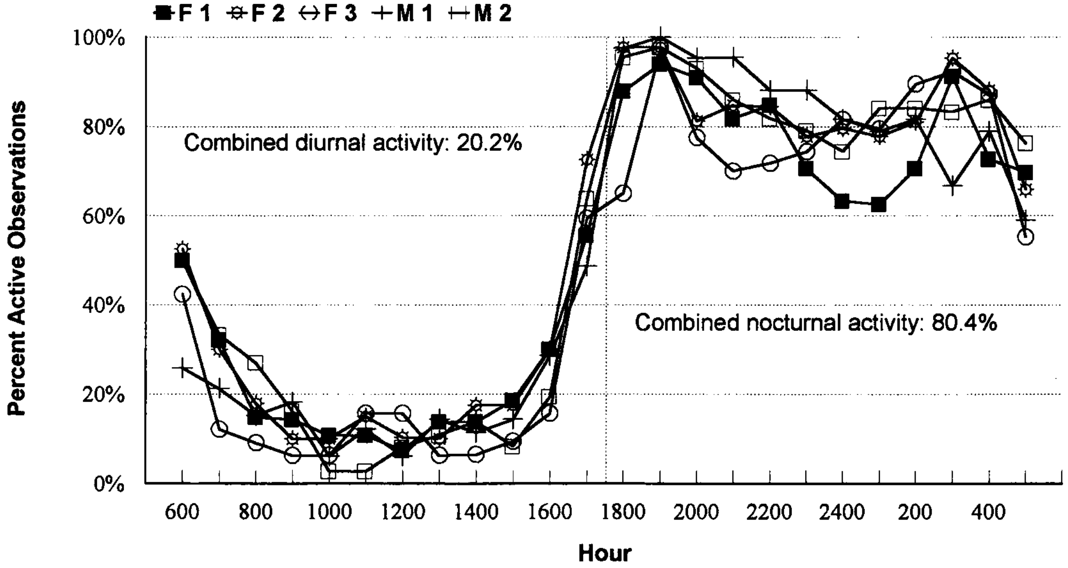


FIGURE 2. Study-long activity pattern for each study animal. Percentage of active observations for each hour interval was calculated from June 1995 to May 1996.

ranges ($\bar{x}$ = 79.1 ha, N = 3, SD = 35.19) in the wet season. Male dry season home ranges ($\bar{x}$ = 123.5 ha, N = 2, SD = 71.49) were also larger, but not significantly (t = 0.93, df = 3, P = 0.42) than female dry season home ranges ($\bar{x}$ = 79.1 ha, N = 3, SD = 38.91). Study-long monthly 95 percent MHR ranges averaged 27.1 ha, (N = 54, SD = 18.4). Male monthly home range sizes ($\bar{x}$ = 35.0 ha, N = 22, SD = 20.2) were larger (t = 2.79, df = 52, P = 0.007) than female home ranges ($\bar{x}$ = 21.6 ha, N = 32, SD = 15.1). Monthly home ranges in the wet season ($\bar{x}$ = 26.7 ha, N = 29, SD = 19.6) were not significantly different (t = −0.152, df = 52, P = 0.880) compared to the dry season ($\bar{x}$ = 27.5 ha, N = 25, SD = 17.2) for all tapirs combined. Based on incremental area plots, which show changes in range size as successive locations are added, approximately four months of data are needed to obtain reasonably stable home range sizes following this data collection schedule (Fig. 5). Tapir F1 required seven months to stabilize because of a slight shift in home range location between September and October.

HOME RANGE OVERLAP.—All tapirs shared a 32.5 ha area of overlap between study-long home ranges (Fig. 6). This represented 19.4, 42.5, 52.5, 14.0, and 37.4 percent of study-long home ranges for F1, F2, F3, M1, and M2, respectively. A 25.9 ha overlap area represented 21.9, 37.9, 51.3, 15.5, and 36.9 percent of wet season home ranges for F1, F2, F3, M1, and M2, respectively. No area was commonly shared among all tapirs in the dry season. All tapirs showed a greater than 70 percent overlap between their own wet and dry season home ranges ($\bar{x}$ = 76.4%, N = 5, SD = 7.26; Fig. 7).

HABITAT USE.—For all tapirs combined over the entire study period, secondary forest was the most utilized habitat type (61.3%), while primary forest (25.0%) was the second most utilized habitat (Fig. 8). Study-long habitat utilization was not as predicted by habitat availability (G_{adj} = 15.18, a = 4, P < 0.05). Bonferroni confidence intervals showed that secondary forest and the airstrip/compound were used more than expected while the primary forest, water, and beach habitats were used less than expected based on availability. Wet season habitat use values did not follow predicted ratios (G_{adj} = 27.31, a = 4, P < 0.001). The airstrip/compound was utilized more than expected during this period while the water and beach habitats were used less than expected. Dry season habitat utilization also was not as predicted by habitat availability (G_{adj} = 32.53, a = 4, P > 0.001). During this period, primary forest and beach habitats were utilized less than expected while secondary forest was used more than expected. Wet season habitat use ratios were significantly different from dry season ratios (G_{adj} = 122.89, a = 4, P < 0.001). Tapirs used the primary forest and airstrip/compound habitats more during the wet season com-

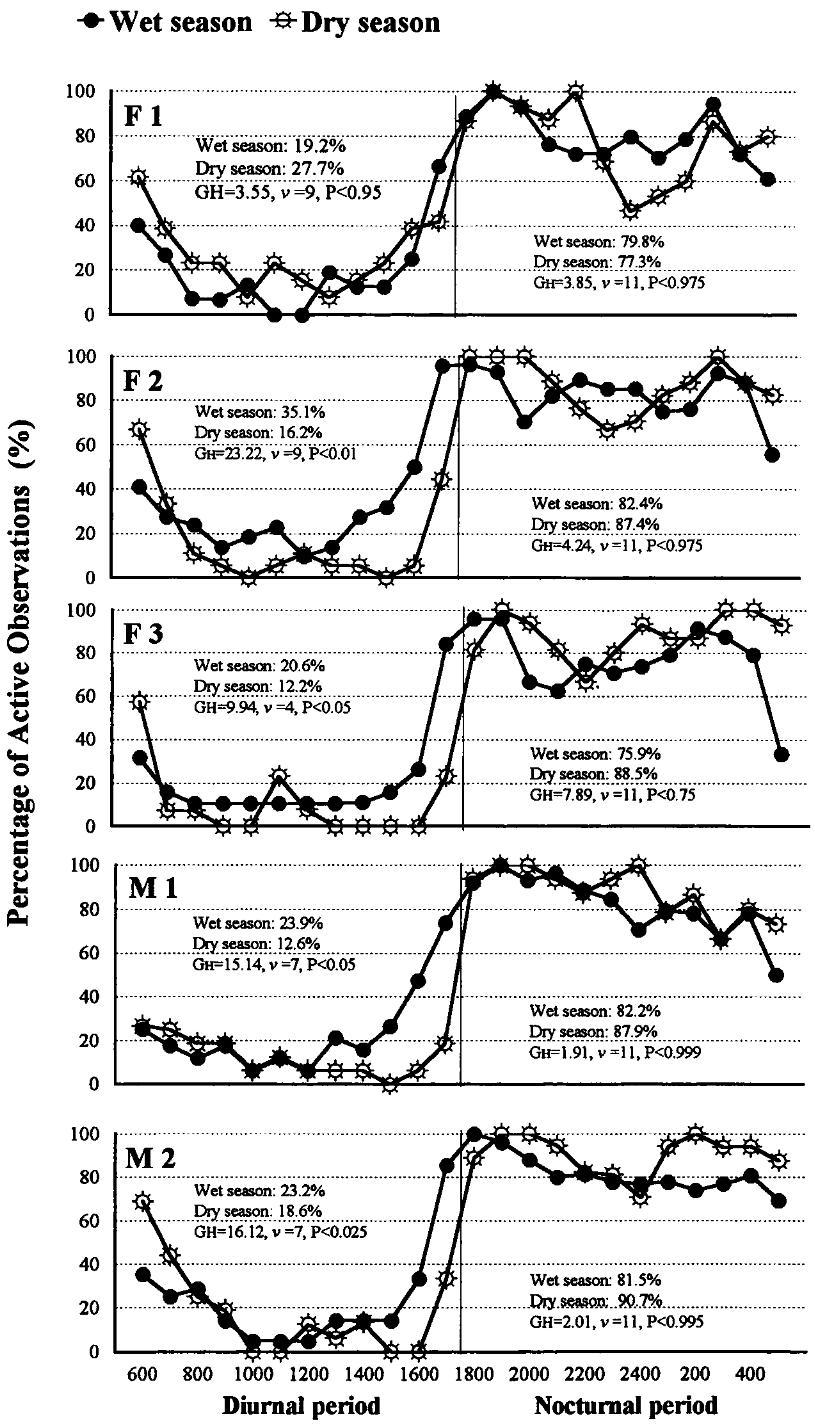


FIGURE 3. Seasonal activity pattern for each study animal. Percentage of active observations during each hour interval was calculated for the wet season (June–November 1995 and May 1996) and dry season (December 1995–April 1996). *G*-test results are given comparing seasonal activity patterns for diurnal and nocturnal data sets.

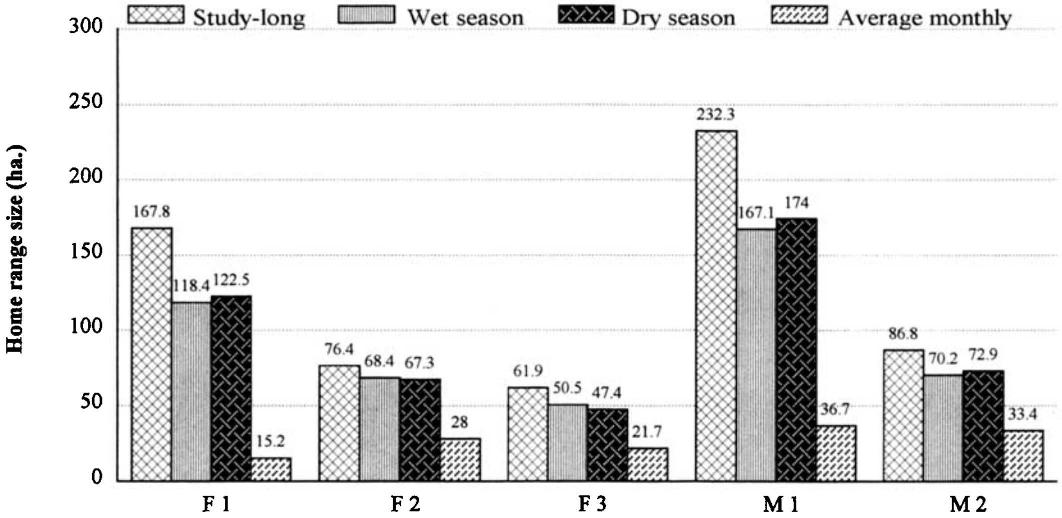


FIGURE 4. Annual (June 1995–May 1996), wet season (June–November 1995 and May 1996), dry season (December 1995–April 1996), and average monthly home range size (95% convex polygon) for each tapir.

pared to the dry season while secondary forest, beach, water, and coastal grassland habitat had higher usage ratios in the dry season.

Individually, secondary forest was the most utilized habitat over the entire study period by all five tapirs (Table 2). All five tapirs used the primary forest habitat more during the wet season when compared to the dry season. Bonferroni confidence intervals showed tapirs F1, F2, F3, and M1 selected against primary forest in the dry season. Only one tapir (M2) selected primary forest in the wet season. Four of the five tapirs utilized the secondary forest habitat more during the dry season than the wet. All tapirs used the secondary forest habitat in proportion to its availability during the wet season, while three tapirs (F2, F3, and M1) selected this habitat in the dry season. The coastal grassland was represented in only one tapir's home range (F1) and it was selected during both seasons and over the entire study period.

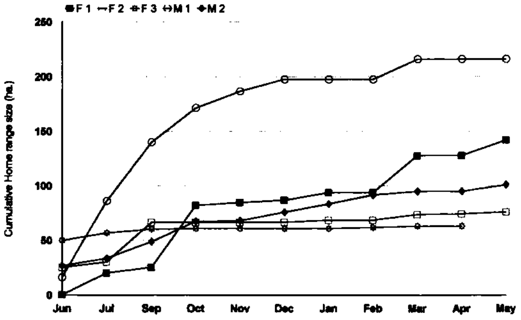


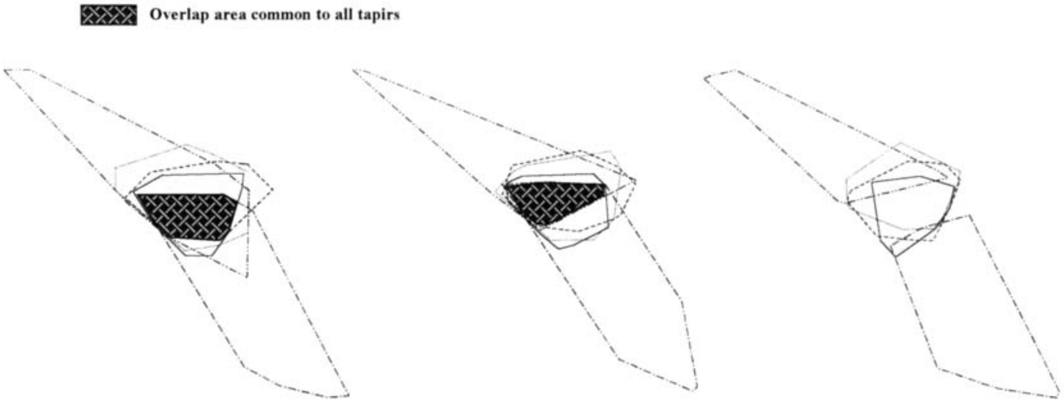
FIGURE 5. Cumulative area versus time plot of 95 percent home range for each tapir.

DISCUSSION

Telemetry data collection.—We believe this study demonstrates the feasibility of long-term telemetry studies for tapir species. The telemetry data gathering technique employed in this study, while labor intensive, resulted in very accurate data. We believe the transmitter bearings estimated from ground level resulted in very reliable animal locations because (a) bearings were usually taken relatively close to the animal (usually <100 m), (b) 690 locations (16.6%) were determined by direct observations, and (c) our ability to choose between many receiving stations allowed us to obtain closer to perpendicular readings.

Fixed antenna stations would probably have been much more desirable for many reasons. We could have constructed insect-free, weatherproof enclosures that would have allowed us to collect data in relative comfort while subjecting our equipment to less damaging conditions. Data entry into computer programs would have also been immensely simplified. Given the right conditions, we would recommend antenna stations to reduce the amount of work involved, but only if the data gathered is reliable.

Capture and immobilization.—The capture and immobilization of the study animals here was rel-



% Study-long home range overlap

	F 1	F 2	F 3	M 1	M 2
F 1		37	28	21	43
F 2	82		69	56	94
F 3	75	85		80	84
M 1	15	18	21		18
M 2	84	82	60	47	

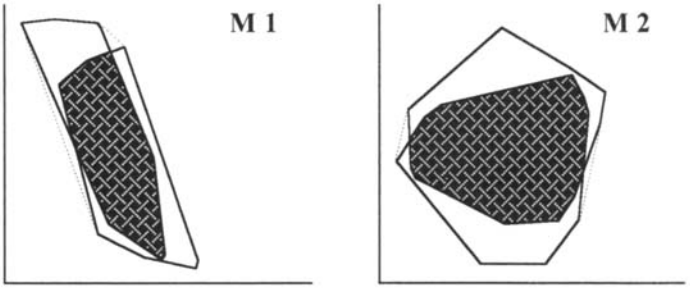
% Wet season home range overlap

	F 1	F 2	F 3	M 1	M 2
F 1		43	28	23	41
F 2	74		62	57	89
F 3	65	84		87	96
M 1	16	23	26		27
M 2	69	87	69	64	

% Dry season home range overlap

	F 1	F 2	F 3	M 1	M 2
F 1		15	5	0	25
F 2	27		64	5	84
F 3	13	91		10	77
M 1	0	2	3		0.2
M 2	42	77	50	0.4	

FIGURE 6. Study-long and seasonal home range (95%) overlap between individuals showing areas in common with all study animals.

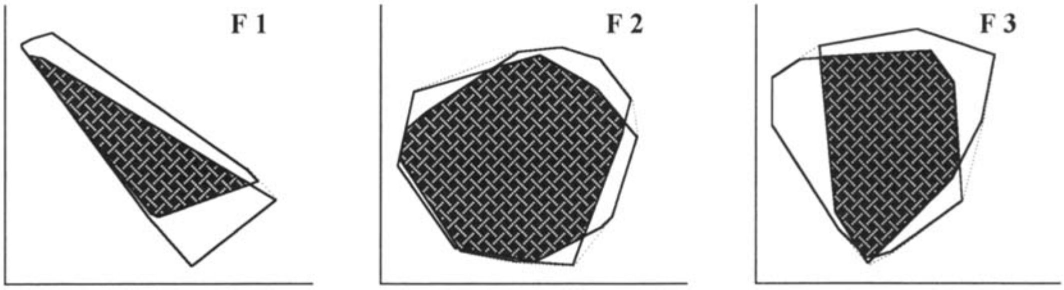


Study-long	Wet	Dry
232.3 ha.	167.1 ha.	174.0 ha.

Seasonal overlap: 74%

Study-long	Wet	Dry
86.8 ha.	70.2 ha.	72.9 ha.

Seasonal overlap: 75%



Study-long	Wet	Dry
167.8 ha.	118.4 ha.	122.5 ha.

Seasonal overlap: 70.2%

Study-long	Wet	Dry
76.4 ha.	68.4 ha.	67.3 ha.

Seasonal overlap: 89%

Study-long	Wet	Dry
61.9 ha.	50.5 ha.	47.4 ha.

Seasonal overlap: 74%

FIGURE 7. Seasonal home range (95%) overlaps for each tapir. Percentages correspond to the percent coverage of dry season range by wet season range.

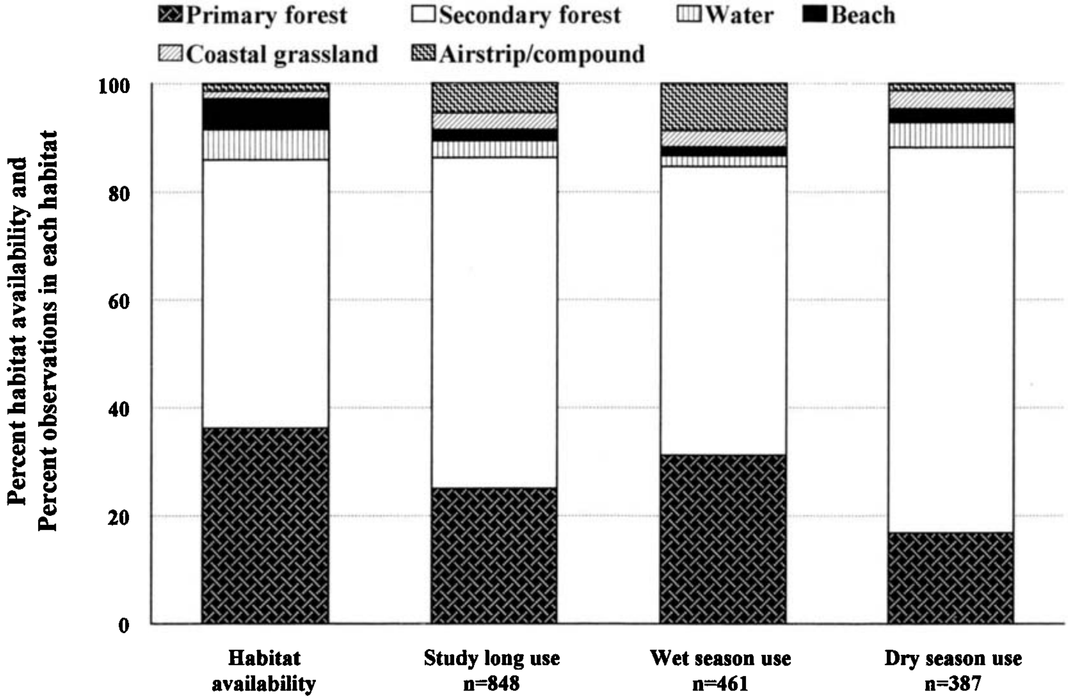


FIGURE 8. Study-long, wet season, and dry season habitat use patterns as estimated by percentage of telemetry locations for all tapirs combined. Habitat availability values represent percentage of coverage each habitat type in the entire study area.

atively easy once we discovered the appropriate bait and darting technique. Although at the time of this study we were still using M-99, recent studies have developed an immobilization protocol that does not involve narcotic agents and thus does not present the level of danger to either tapirs or humans (Foerster *et al.* 2000.).

ACTIVITY PATTERNS.—Downer (1995, 1996) and Acosta *et al.* (1996) have stated that *T. pinchaque* is crepuscular, while Terwilliger (1978) found no pattern in sleeping behavior during her study of *T. bairdii* on Barro Colorado Island. In the tropical dry forest of Santa Rosa National Park, Costa Rica, Williams (1984) reported significantly more nocturnal activity by Baird's tapirs, with peaks between 1800 and 2000 h and between 0400 and 0700 h.

The predominant nocturnal behavior exhibited by the tapirs in this study is probably an adaptation to avoid the hottest times of the day. Large animals such as tapirs (150–300 kg) have a difficult time dissipating excess body heat due to their low surface to volume ratio (Schmidt-Nielson 1990) and thus probably confine their activities to the cooler nighttime hours. The greater diurnal activity during the rainy season is possibly due to an increase in frequency of daytime rains, which produce slightly lower ambient temperatures. The differences in activity patterns between *T. pinchaque* and *T. bairdii* are probably due to temperature differences between the two species distributions. Where *T. pinchaque* is inactive during the colder nocturnal hours of the high Andes (Downer 1996), the Baird's tapir is less active during the hottest part of the day.

Eisenberg (1989) reported that tapirs will become completely nocturnal in regions where they are frequently hunted. Although illegal hunting occurs within the park, it is uncommon near the Sirena ranger station and probably had little effect on tapir activity there; however, human activity in the form of tourists in the Sirena area may have affected seasonal differences in activity patterns observed. More tourists visit the Sirena station during the dry season, and increase human traffic in the study area, especially during the day. It is possible that during months of heavy tourist traffic through Sirena, the tapirs became more nocturnal to avoid confrontations with humans.

n individual habitat availability, use, and selection by each tapir. Avoidance of habitats is denoted by "—." Selection of habitats is denoted by "

F1		F2			F3			M1			
Use	Select.	Avail. (%)	Use	Select.	Avail. (%)	Use	Select.	Avail. (%)	Use	Select.	Avail. (%)
16.8	—	34.9	26.5		35.1	27.4		28.3	13.1	—	24.5
22.9			35.1			34.4			17.5		
10.6	—		15.5	—		17.8	—		7.3	—	
38.9		58.0	69.7	+	55.2	54.7		65.3	74.4	+	64.1
47.9			58.1			41.0			64.0		
29.8			84.5	+		73.3	+		88.9	+	
14.7		0.6	0.8		n/a			2.0	0.9		4.4
6.3			1.4						0.5		
23.4	—		0.0	—					1.0		
10.5		n/a			0.9	0.9		1.9	3.5		1.5
4.2						1.6			3.5		
17.0						0.0	—		2.8		
18.9	+	n/a			n/a			n/a			n/a
18.8	+										
19.1	+										
0.0	—	6.5	3.0		8.8	15.1		2.5	8.1		5.5
0.0	—		5.4			23.0	+		14.0		
0.0	—		0.0	—		4.4			0.0	—	

HOME RANGE.—Mean home range size in this study was considerably smaller compared to *T. bairdii* in a Costa Rican dry tropical forest (1.70 km^2; Williams 1984) and the much smaller mountain tapir in Ecuador (8.8 km^2; Downer 1996). Possibly, tapirs in the Sirena area require less space to fulfill their requirements of water and food. Presently, habitat conditions in the Sirena area appear to provide an excellent balance of diversity to the resident tapir population, resulting in smaller home ranges. The fact that no significant difference in seasonal home range size or location (as shown by seasonal home range overlap) was observed suggests that these tapirs do not need to expand their ranges to meet seasonal deficiencies in habitat quality.

HABITAT USE.—Habitat use results in this study coincide with other tapir research. Based on track counts, Naranjo (1995a) determined that *T. bairdii* in CNP preferred lowland secondary forests and avoided primary forests. Baird's tapirs in Belize prefer secondary forests and floodplains (Fragoso 1990). Williams (1984) found most nocturnal activity of two Baird's tapirs in Santa Rosa National Park, Costa Rica, centered in lowland riparian forest and regenerating riparian forest. *Tapirus terrestris* in Venezuela was found to forage preferentially in lower elevation gaps, keying in on higher biomass of palatable plant species and abundance of certain plants (Salas & Fuller 1996). These authors agree that food and water availability are important factors in habitat selection by tapirs.

In this study, secondary forest was the most utilized habitat during both seasons. We concur with other researchers in that tapirs forage more in secondary forests because it contains high densities of understory plants. Tapirs are strict herbivores (browser/frugivore) and must obtain their forage between the forest floor and *ca* 1.5 m height. In addition to the higher density of plants available in the secondary forest understory, the plant species found there are usually fast-growing pioneer species, which are more palatable and digestible because they tend to invest less energy to forming defensive toxins. We believe the high percentage of secondary forest habitat in the area was a major factor in allowing the study animals to maintain such small home ranges. Based on this assumption, we would expect home range sizes for tapirs in the Sirena area to increase as the regeneration process modifies available habitat.

While we agree that water is an important consideration of diurnal resting site selection (Alger *et al.* 1998), our telemetry data and direct observations convinced us that water plays only a minor role in nocturnal habitat selection. The study animals rarely foraged or rested along creek sides, although streambeds were often utilized for easy travel between feeding sites and for defecation. Dry season diurnal resting sites were almost exclusively in wallowing holes associated with freshwater sources. In the wet season, however, tapirs seldom slept in water, although they were usually less than 20 m from a creek or river.

In this study, primary forest utilization was much higher in the wet season by all tapirs, probably because of increased fruit availability. Tapirs were seen eating fallen fruits during the majority of our direct observations in primary forest, particularly *Licania platypus* (Chrysobalanaceae). This species is found in only two small patches of primary forest in the study area and produces fruit from May through July. During this period, 97 percent of primary forest observations were recorded in these two patches. In following radio-tagged tapirs in these forest patches, they appeared to travel directly from one *L. platypus* to another, circling the bases of the trees in search of fruit while essentially ignoring the remaining vegetation. In a similar manner, Bodmer (1990) reported that *T. terrestris* encountered fruits more frequently when ranging in *Maurita flexuosa* palm forests than in non-palm forests because they changed their searching behavior. The author observed that tapir trails indicated the animals were going from one *M. flexuosa* palm swamp to another via non-palm forests. Naranjo (1995b) also found a disproportionately heavy use of monotypic stands of *Raphia taedigera* (Palmae) by *T. bairdii* in CNP, Costa Rica.

HOME RANGE OVERLAP.—We feel the distribution pattern documented during this study reflects, to some extent, the social behavior of Baird's tapirs. Ecological and evolutionary models predict that tropical forest-dwelling ungulates should occupy monogamous-pair territories because of the seasonal stability of the environment and closed habitat (Geist 1974, Jarman 1974). Tapirs F2, F3, and M2 consistently shared the same area. Although no genetic evaluation of the relationship between the animals was possible, direct observations and subsequent data collection lead us to believe tapirs F2 and M2 represent an adult pair and F1 and F3 were their offspring. During the second half of the study, tapir F2 became increasingly aggressive toward F3 and gave chase whenever they encountered each other, a behavior not observed in the first six months of the study. Tapir F3 left the region two months after this study was completed.

Our observations also indicate that tapir F1 was probably the offspring of F2 and M2 from the previous year. From the time of her capture in January 1995 to September 1995 (2 mo into the study), F1 occupied this same territory with F2, F3, and M2. During this same time period, every interaction between F1 and F3 was hostile in nature, with F2 always the aggressor. In September, F1 shifted her home range 1 km to the north. In addition, prior to this shift, F1 and the other juvenile (F3) spent a great deal of their time together both resting during the day and foraging at night (CRF and CV, pers. obs). This behavior has been noted between known siblings in the years following the study. Similar to tapir F3, tapir F1 dispersed from the area soon after the study was completed. This theory has been strengthened through observations in the five years following this study during which tapirs F2 and M2 have maintained an exclusive territory with no other resident adults. In that time, F2 has produced four more offspring, which have occupied the same area for three to four years prior to dispersal (Foerster, pers. obs.).

The large overlap of all home ranges during the wet season was a function of two factors: (1) the family unit described above and (2) the attraction of the *L. platypus* fruit mentioned above. The wet season included those months prior to the home range shift of tapir F1. These months were also the only time the fruits of *L. platypus* were available in the primary forest patch near the airstrip. During this time, tapir M1 (adult male to the south) made several forays into this area in search of these fruits. At no other time did M1 penetrate the home range of F2 and M2 to any substantial degree.

MANAGEMENT IMPLICATIONS.—Because tapirs inhabit practically all ecosystems from sea level to the subalpine paramo, broad conclusions should not be drawn from individual studies within a restricted area. Several points, however, can be made from this study.

Any management strategy directed toward tapirs should include the protection of water sources. In the majority of areas where tapirs are found, water is not a scarce resource, but the quality of these rivers, creeks, and lakes are often influenced by human activities. Deforestation, pesticide use, and fertilizers can contaminate and/or reduce the quantity of available water. In the case of CNP, gold miners in and out of the park modify the course of waterways and contaminate water sources with mercury. Strict control needs to be enforced on activities that can influence the quantity and quality of water resources.

This study reinforces the importance of "disturbed" habitats (riverbanks, gaps, and secondary forest) for tapirs. This should be taken into account when designating new protected areas. Regions with deforested patches or those that have been selectively logged should not be discounted when considered for protective status. To the contrary, a mixture of primary and secondary forests appears to suit tapirs very well. We believe selective logging may actually benefit tapirs as long as it is not overly extensive and hunting can be controlled. We realize that wildlife managers and park officials rarely have the luxury of making decisions based on the needs of a single species, but in the rare case that tapirs are of major importance to a region and there are few naturally occurring disturbances, it may be a valid consideration to cut down a number of large trees to form gaps. This obviously should be used on a short-term basis, perhaps at the beginning of a reintroduction project.

Finally, more intensive research into the population dynamics is needed to improve our ability to manage and conserve this species. Although radiotelemetry studies can be prohibitively expensive and time-consuming, they offer a unique opportunity to collect data otherwise unattainable with other techniques. Radiotelemetry is an excellent method for collecting data on movement patterns and space use. This can be used to measure the population density in a given area that may be applicable to a larger region. Data on movement patterns could also be combined with simultaneous track counts and direct sightings along transects to formulate correlation factors for these indices to more accurately and reliably estimate population densities. Radiotelemetry can also be used to facilitate direct observations for studies on diet, foraging behavior, social interaction, survival, mortality, and reproduction. Many demographic parameters (e.g., reproductive potential, dispersal, and survival rates) are probably common to all tapir populations, or would be if not for the influence of human activities. Long-term studies of undisturbed, natural tapir populations could provide a database with which to evaluate the pressures exerted by hunting and habitat modification.

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