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Space and Substrate Use in Captive Western Tarsiers, *Tarsius bancanus*

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Tarsiers are considered "vertical clingers and leapers" but there are few empirical data available concerning actual substrate- or space-use patterns in any of the three species. In this paper we examine these patterns in four wild-caught, captive Tarsius bancanus *maintained in large enclosures designed to promote natural behavior. We find that this species uses space in a distinctly nonrandom manner, exhibiting a preference for midlevel heights and upright, small-diameter substrates. The observed space-utilization pattern was best explained by strong preferences for specific heights and not by the distribution of prey items, preferred substrate types, or substrate angles. Unlike wild* T. bancanus, *which reportedly forage consistently on the ground, these tarsiers did not forage on the floor of the enclosures despite the abundance of food there.*

KEY WORDS: *Tarsius bancanus;* space use; substrate use; captive behavior.

INTRODUCTION

Anatomical and biomechanical studies have shown that tarsiers are well adapted for vertical clinging and leaping (Pocock, 1918; Napier and Walker, 1967; Grand and Lorenz, 1968). However, with the exception of a study of *Tarsius spectrum* on Sulawesi (MacKinnon and MacKinnon, 1980), there are no empirical data describing how tarsiers actually use space or supports in their environment.

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It has been suggested that tarsiers are dependent on small-diameter, vertical substrates and may be restricted to habitats having an abundance of these support types (Niemitz, 1979, 1984a,b). The available field data do not unequivocally support these assumptions. Tarsiers live in a variety of habitats differing greatly in structural architecture—in primary forests (Fogden, 1979), secondary forests (Niemitz, 1979), and "urban gardens" (MacKinnon and MacKinnon,1980)—within which they may use an equally diverse array of substrates, including tangled underbrush, vines, grasses, and the boles of large trees, for locomotion and support (Cook, 1939; Fogden, 1974; MacKinnon and MacKinnon, 1980).

It has been argued, primarily on the basis of limb morphology, that the three extant species of tarsier exhibit a continuum of adaptations for vertical clinging and leaping and arboreality. According to morphological predictions, *T. spectrum* is the least specialized and least arboreal, *T. bancanus* is the most specialized and most arboreal, and *T. syrichta* is intermediate (Niemitz, 1979b). Field studies suggest that both *T. bancanus* and *T. spectrum* travel and hunt almost exclusively on vertical supports and forage approximately 10% of the time on the ground (MacKinnon and MacKinnon, 1980; Niemitz, 1984a). These findings do not reflect the differences in substrate preferences or foraging behavior predicted by morphology. Furthermore, the differences in arboreality that do occur might be explained by differences in forest architecture rather than by tarsier anatomy, and any differences in terrestrial foraging may be due to spatiotemporal variation in food availability, as suggested by Fogden (1974).

Unfortunately, no empirical data on habitat architecture, support orientation, or the spatial distribution of prey are available to determine the influence of these potentially important variables on space-use patterns. This is probably due to the obvious sampling difficulties involved in the field. The only empirical study of space and substrate use in captive tarsiers suggests that *T. syrichta* may prefer large-diameter, horizontal substrates to others (Reason, 1978), while anecdotal reports support the notion that *T. bancanus* and *T. syrichta* prefer small-diameter, vertical substrates (Cook, 1939; Lewis, 1939; Wharton, 1950; Harrison, 1963; Ulmer, 1963). However, data from these studies should be interpreted with caution because the small, sparsely furnished enclosures invariably used to house animals undoubtedly constrained locomotion and substrate selection (Roberts *et al.*, 1984).

In light of these ambiguities, we examined space- and substrate-use patterns in captive *T. bancanus* given access to large enclosures designed to promote a full range of natural behaviors. The study was designed to test four prevailing assumptions about the space- and substrate-use patterns of tarsiers in general and this species in particular: (1) vertical inclinations will be used more than others; (2) small-diameter substrates will be used more than large-diameter substrates; (3) heights in the 0- to 2-m range will be used more than others; and (4) animals consistently and regularly forage on the ground.

MATERIALS AND METHODS

The four animals used in this study were captured as presumed pairs in mist nets approximately 3 km from the Sepilok Wildlife Reserve, Sabah, Malaysia (Patricia Wright, personal communication). Following capture, the tarsiers were held in field enclosures for a short period, to ensure that they were adjusted to captivity, and were then transported by air and placed directly into their permanent enclosures at the National Zoological Park.

The animals were housed in two identical 5.1-m-long, 3.6-m-wide, and 4.5-m-high rooms at the Department of Zoological Research. A one-way mirror at one end of each enclosure permitted undetected observations. A forced-air heating/ventilating/air conditioning system and misting three times a day maintained the temperature between 25 and 30°C and the relative humidity at 60–70%. The 12.5-hr photoperiod began at 0400, illumination being provided by two 200-W incandescent white bulbs. During the scotophase, a 20-W blue bulb provided a "moonlight glow" which aided observation and proved necessary for the animals to conduct normal foraging activities. The two enclosures were separated from one another by a similar room, thereby reducing olfactory and auditory contact between the two pairs.

Live crickets (*Acheta domesticus*), maintained on a vitamin/mineral supplement, were available *ad libitum*. Live lizards (*Anolis carolinensis*) and Haitian cockroaches (*Blaberus discoidalus*) were also provided but were rarely eaten.

Three types of climbing substrates were presented in each enclosure: smooth wooden dowels, 180–240 cm long and a uniform 3.3 cm in diameter; bamboo poles, 180–300 cm long and 1.4 to 3.6 cm in diameter; and rough tree branches, 120–400 cm long and 1.0–10.4 cm in diameter. Tree substrates were classified as "twigs" 1.0–2.1 cm in diameter or "trees" 3.3–10.4 cm in diameter.

A catalogue of substrates and inclinations at 31-cm (1-ft) intervals from the floor was made using a horizontal transect system (these catalogues are available from the senior author on request). A similar sampling technique was used to determine the distribution of crickets, essentially the sole food source (Cunningham, 1984).

For the majority of the duration of the study, the floors of both enclosures were left bare. At various times the floors were covered with a 2-cm layer of sand, a 5-cm layer of pine bark mulch, or a 5-cm layer of pine shavings.

Data were collected between 1600 and 1800, that is, within the first 2 hr of the scotophase. Animals were observed with Javelin Model 301 light amplification goggles through the one-way mirror of each room. Data were tape-recorded in real time and later transcribed onto standardized checksheets. A 1-min-scan sample technique was employed using a 1-min-interval tone system. Each minute, a variety of data was recorded for each animal, including the type of substrate it was on (tree, bamboo, dowel, or twig), the height from the floor (to the nearest 0.3 m), and the inclination of the substrate to the horizontal (each substrate was classified as vertical, 60, 45, or 30°, or horizontal). In addition, the principal activities of the animal and the location and number of food items taken per minute were recorded in an *ad lib.* fashion. Approximately 142 hr of direct observation was conducted in this fashion.

Space and substrate use for the most frequently observed categories of behavior was also recorded. These behaviors were as follows.

1. Scanning. The animal was perched on a substrate while surveying the enclosure, a potential food item, the other animal, or a potential landing site. Each animal spent more waking time scanning than in any other activity.

2. Grooming. This category consisted entirely of autogrooming. Allogrooming was never observed.

3. Scent-Marking. The animal was applying and rubbing the circumoral, epigastric, or perianal glandular areas on a substrate.

4. Prey Catching. This category consisted primarily of captures of crickets. Captures of lizards and cockroaches were too rarely observed to be included in the analysis.

5. Eating. This category included behaviors involved with the actual consumption of food. Since no tarsier ever ate prey items where they were caught, sites for eating differed from capture (prey-catching) sites and were accordingly classified separately.

6. Jumping. This category consisted of leaping from one substrate to another.

Correlations and partial correlations were conducted with the appropriate SPSS program (Nie *et al.*, 1975). The chi-square test was used to determine the significance of overall substrate, angle, and height usage (Dance, 1983). Expected values were calculated from the overall abundance of each variable or the height-specific abundance of the variables unless otherwise stated. Where appropriate, chi-square analyses were subdivided following Zar's (1974) technique. Interroom and intraroom comparisons of substrate, angle, and height use were compared using the Mann-Whitney *U* test (Sokal and Rohlf, 1973). Significance levels are $P < 0.05$ unless otherwise stated.

RESULTS

Angle and Substrate Use

The floor was avoided by all animals. During the first week after arrival, before the beginning of the study period, the animals regularly foraged on the bare floor but soon abandoned this practice. We added pine-bark mulch to the floors of the enclosures to see whether animals might forage there if a "softer" substrate was available, but they did not. We initially felt that this might have been because crickets were not readily visible against the dark pine bark, but no increase in floor foraging was seen when white wood shavings were substituted for the pine bark.

As no animal was observed on twigs or on the floor at any scan, we consider substrate use on bamboo, dowels, and trees only in the following analysis.

Table I shows the correlation patterns of individual height use with substrate and angle densities.

The data indicate no consistent pattern of correlation of height use with any of these variables. Most of the significant correlations between individual height preferences and substrate height densities were reduced to nonsignificant levels when angle effects were removed, with vertical or 60° angles having considerably more influence than the other angles.

There were no significant correlations between height-use patterns and angle height density in three of the four animals. For the fourth animal the significant correlations with 60, 45, and 30° supports were all reduced to nonsignificant levels when the effects of substrate were removed.

Each animal used bamboos significantly more, and trees significantly less, than expected based on their overall abundance in the enclosures (Fig. 1, Table II). Dowels were used at approximately the expected rate. Each animal used verticals and 60° supports significantly more than expected, and the remaining angles significantly less than expected, based on their overall abundance in the enclosures (Fig. 2, Table III). There were no significant differences between or within rooms in angle or substrate use patterns.

Three of four animals used all substrates combined, and each substrate separately, significantly more between 1.2 and 2.1 m than at other

Table I. Correlations of Height Distribution with Height Density for Each Individual

		Tree	Bamboo	Dowel	Vertical	60°	45°	30°	Horizontal
Room 2 M[a]	r	0.67	0.59	0.47	0.13	0.23	0.21	0.23	0.29
	P	< 0.05	<0.05	—[b]	—	—	—	—	—
Room 2 F	r	0.92	0.74	0.62	0.41	0.40	0.31	−0.02	0.29
	P	< 0.01	<0.01	<0.05	—	—	—	—	—
Room 4 M	r	0.53	0.49	0.28	0.42	0.24	0.64	0.25	−0.14
	P	—	—	—	—	—	<0.05	—	—
Room 4 F	r	0.86	−0.28	−0.51	0.05	−0.54	0.71	0.87	0.32
	P	< 0.01	—	—	—	—	<0.01	<0.01	—

[a]M, male; F, female.
[b]Dashes indicate nonsignificant correlations.

Table II. Scan Frequencies for Each Animal on Each Substrate Type[a]

	Tree	Bamboo	Dowel	
Room 2 M	1206 (−)	1707 (+)	738 (+)	χ^2 = 1806.3, $P < 0.001$
Room 2 F	871 (−)	2561 (+)	225 (−)	χ^2 = 3986.1, $P < 0.001$
Room 4 M	143 (−)	630 (+)	242 (+)	χ^2 = 1025.7, $P < 0.001$
Room 4 F	329 (−)	497 (+)	144 (−)	χ^2 = 442.0, $P < 0.001$

[a](+) Significantly greater than expected; (−) significantly less than expected. M, male; F, female.

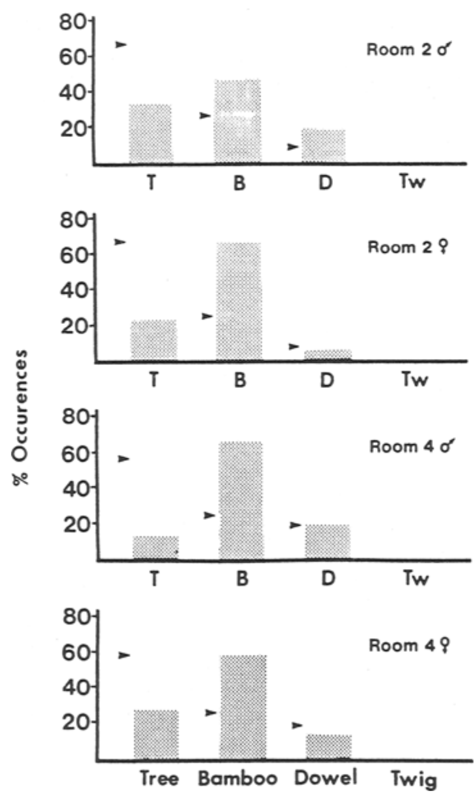

Fig. 1. Rate use of substrate types by four *Tarsius Bancanus*. Shaded areas indicate actual percentage use. Arrowheads indicate expected use rate. T, tree; B, bamboo; D, dowel; Tw, twig.

Table III. Frequencies of Scans for Each Animal on Each Angle Type[a]

	Vertical	60°	45°	30°	Horizontal	
Room 2 M	1712	1457	444	35	11	$\chi^2 = 2387.0$, $P < 0.001$
	(+)	(+)	(−)	(−)	(−)	
Room 2 F	1406	1651	191	355	32	$\chi^2 = 1643.5$, $P < 0.001$
	(+)	(+)	(−)	(−)	(−)	
Room 4 M	363	399	237	11	7	$\chi^2 = 194.4$, $P < 0.001$
	(+)	(+)	(−)	(−)	(−)	
Room 4 F	384	432	108	17	24	$\chi^2 = 278.7$, $P < 0.001$
	(+)	(+)	(−)	(−)	(−)	

[a]See Table II, footnote *a*.

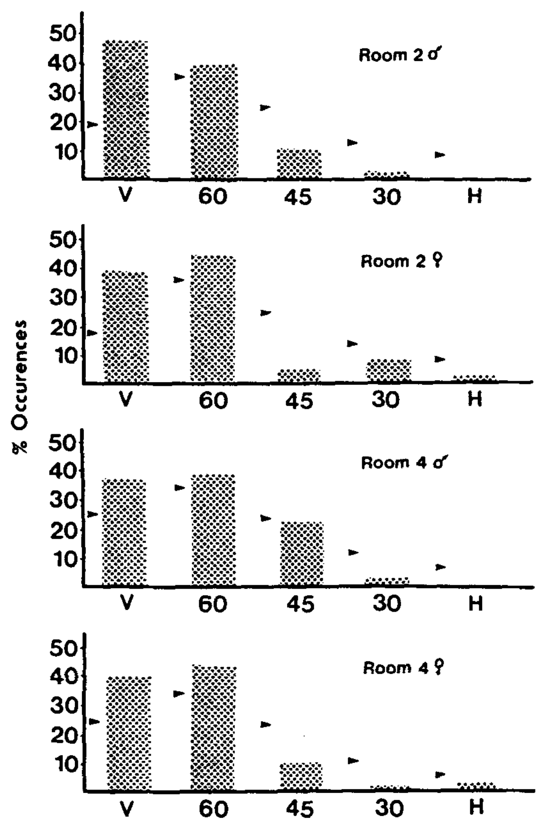

Fig. 2. Use rate of angle types (vertical, 60°, 45°, 30°, horizontal) by four *Tarsius bancanus*. Shaded areas indicate actual percentage use. Arrow heads indicate expected use rate.

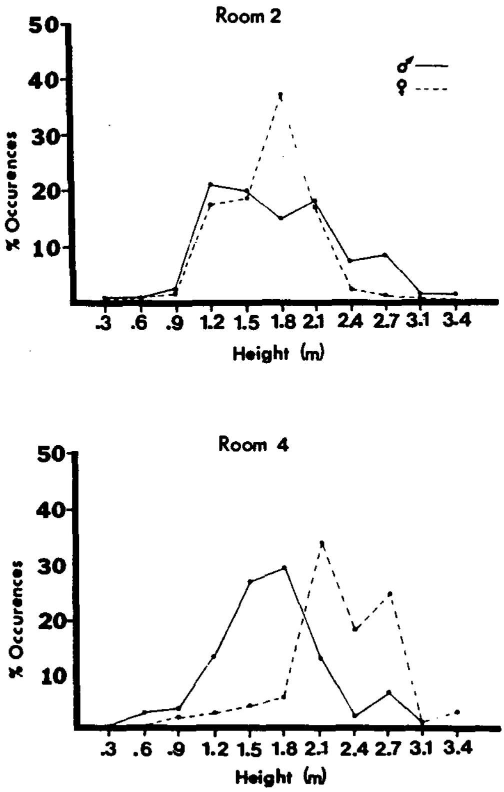

Fig. 3. Height use rates by four *Tarsius bancanus*.

Table IV. Frequency of Height Use, on All Substrates Lumped Together, for Four *Tarsius bancanus*[a]

Height (m)	Room 2 male	Room 2 female	Room 4 male	Room 4 female
0.3	5	1	0	1
0.6	9	7	31	0
0.9	106	80	51	19
1.2	778	662	171	33
1.5	727	715	317	64
1.8	576	1396	360	85
2.1	677	662	172	402
2.4	292	107	21	219
2.7	333	32	91	311
3.1	29	20	1	21
3.4	52	0	0	49
	χ^2 1509.2	2891.9	1101.4	1502.7
	$P < 0.001$	<0.001	<0.001	<0.001

[a]Boxes indicate the height ranges used significantly more than any other by each animal.

heights (Fig. 3, Table IV). These same animals also used verticals and 60° angles significantly more in this height range. The fourth animal, the Room 4 female, used these same substrates and angles significantly more in the 2.1- to 2.7-m height range.

These data suggest a weak association of substrate density and angle density with each animal's height-use pattern. Substrate, bamboo in particular, had a stronger correlative effect than angle, in which verticals and 60° supports appeared to have the strongest effect. Perhaps most significant is the finding that each animal was using vertical space in a distinctly nonrandom, density-independent manner. These results underscore the significant effect of height, per se, on the space distribution pattern of each animal.

Behavior and Substrate Use

The frequencies of four categories of behavior are shown in Figs. 4 and 5.

Scanning. Three of four animals used 1.2–2.1 m and the fourth 2.1–2.7 m significantly more than expected. The Room 4 male and the Room 2 female used bamboo significantly more than expected based on the abundance of substrates in the enclosures. The Room 4 female used trees and bamboo equally, and the Room 2 male used all three substrate types at the expected rate. Verticals and 60° supports were used significantly more by all animals.

Grooming. The height range for grooming for each animal was similar to that for scanning and each showed a strong preference for bamboo. Trees were used less than expected, while dowels were virtually unused. Both Room 2 animals used verticals significantly more than 60° supports for grooming, while the reverse was true for the Room 4 animals.

Scent-Marking. The height range for scent-marking for each animal was similar to that for scanning and grooming. Both Room 4 animals scent-marked significantly more on trees. The Room 2 male scent-marked equally on trees and bamboos, while the Room 2 female scent-marked exclusively on bamboos. Both males and the Room 2 female scent-marked significantly more on verticals than on other inclinations, while the Room 4 female marked significantly more on 60° supports.

Prey Catching. Substrate preference experiments showed that crickets perched on the walls and floor much more more than on the elevated substrates. Of the elevated substrates, crickets used trees significantly more than any other substrate, presumably because of a preference for rough-textured surfaces (Cunningham, 1984). Crickets used all substrate angles in approximately equal proportions (Roberts and Baker, unpublished data).

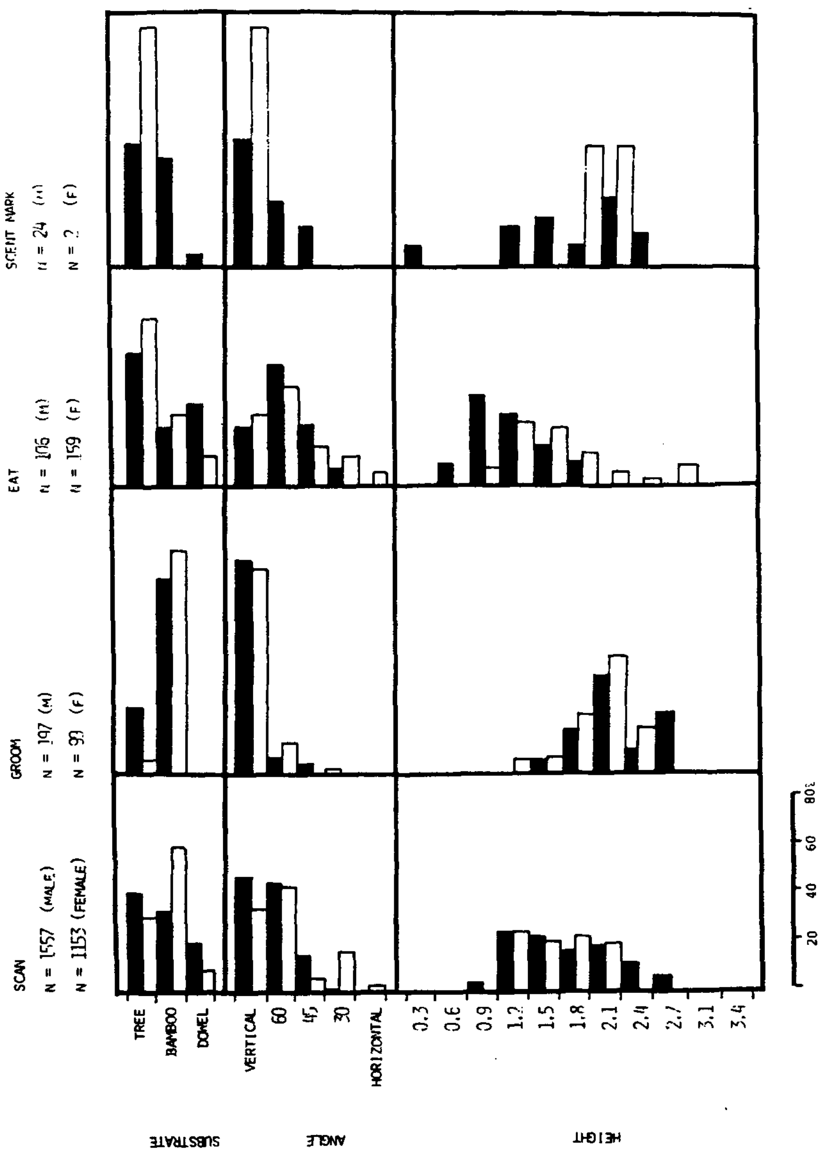

Fig. 4. Use rates of substrates, angles, and heights for four behavioral categories for male and female *Tarsius bancanus* in Room 2. Filled histograms represent the male; open histograms, the female.

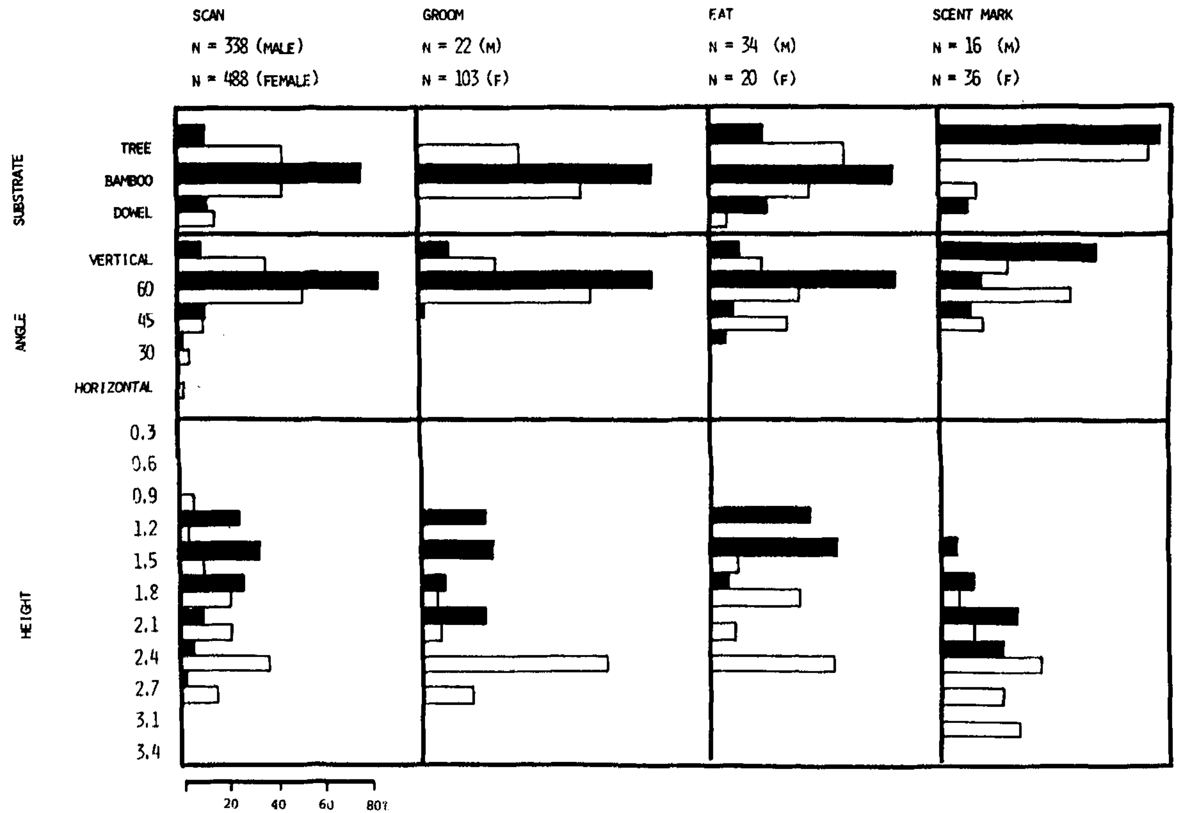

Fig. 5. Use rates of substrates, angles, and heights for four behavioral categories for male and female *Tarsius bancanus* in Room 4. Filled histograms represent the male; open histograms, the female.

Table V. Frequency of Jumps from Each of Four Substrate Types for the Four *Tarsius bancanus*

	Tree	Bamboo	Dowel	Twig	
Room 2 M	195	92	49	0	χ^2 = 23.1, $P < 0.005$
Room 2 F	102	104	63	5	χ^2 = 109.3, $P < 0.001$
Room 4 M	119	196	71	0	χ^2 = 177.2, $P < 0.001$
Room 4 F	98	73	101	5	χ^2 = 68.76, $P < 0.001$

In Room 2, crickets were most abundant on the floor and at heights of 0.3-2.1 m. In Room 4, the greatest abundance was on the floor and at heights of 1.5-2.1 m.

No tarsier was seen catching prey on the floor. Each animal tended to catch prey at 0.9-2.1 m heights, with the exception of the Room 4 female, which did so in the 0.9- to 1.8-m range, well below her emphasized height range. Each animal caught prey on trees significantly more than on either of the other substrates. The Room 2 male also caught prey on dowels significantly more than expected. Each animal caught prey on verticals significantly more than on substrates of any other inclination. Other inclinations were used at or below the expected rate.

These results indicate that the tarsiers avoided the floor, where crickets were most abundant overall, but caught prey significantly more on the elevated substrates where crickets were most abundant. Prey-catching heights tended to be slightly lower than the emphasized heights; in the case of the Room 4 female, they were significantly lower.

Eating. Each animal used the same height range as for scanning, grooming, and scent-marking. Both Room 2 animals used trees significantly more than the other substrates. The Room 4 male used bamboo significantly more and the Room 4 female used trees and bamboos approximately equally.

Sixty-degree angles were preferred for eating, but animals also used a substantial number of verticals and 45° supports. Only the Room 2 female used 30° and horizontal supports to any appreciable degree.

Jumping. We recorded the height, the substrate jumped from and to, the angle jumped from and to, and the distance jumped for 1081 jumps, which were divided approximately equally among the four animals. Each

Table VI. Frequency of Jumps from Each Angle Type for the Four *Tarsius bancanus*

	Vertical	60°	45°	30°	Horizontal	
Room 2 M	118	188	24	5	2	χ^2 = 179.3, $P < 0.001$
Room 2 F	63	161	26	16	8	χ^2 = 84.8, $P < 0.001$
Room 4 M	103	245	23	12	3	χ^2 = 183.4, $P < 0.001$
Room 4 F	127	124	11	14	1	χ^2 = 126.8, $P < 0.001$

animal jumped significantly more within its emphasized heights, and used bamboo and dowels significantly more and trees significantly less, than would have been expected from the overall abundance of substrates in the enclosures (Tables V and VI). Verticals and 60° supports were used significantly more and 45°, 30°, and horizontal supports significantly less by all animals. Jump distances ranged from 0.3 to approximately 2.7 m, with the mean jump distance for all animals being 1.0 m.

DISCUSSION

Each animal concentrated its activities in a specific height-range band. These "emphasized heights" ranged from 1.2 to 2.1 m for three animals and from 2.1 to 2.7 m for the fourth. Supports at heights below 0.6 m and over 3.0 m were rarely used by any animal, despite the abundance of suitable substrates and inclinations. Foraging was the only behavior to occur to any degree outside of the emphasized heights. Foraging occurred primarily on trees, the arboreal substrate used significantly most by crickets. The floor was avoided by all animals despite the abundance of crickets there.

These data concur with the observation that wild *T. bancanus* spend 95% of their time in the 0.3- to 1.8-m height range and rarely use the ground (Niemitz, 1979b). They conflict with Fogden's (1974) and Niemitz's (1984a) findings that this species forages extensively on the ground when suitable foods are concentrated there. The data do not support the hypothesis that tarsiers use a narrow height range because of increased food density or greater abundance of preferred substrates. We believe that specific heights were emphasized because others were avoided. The ground was probably avoided because of the difficulties of locomotion there, while canopy supports were probably less suitable for locomotion because of the inherent flimsiness of terminal branches. In the wild, the risks of predation from terrestrial and arboreal predators are probably significantly increased near the ground and canopy, so avoidance of these heights could be adaptive for this reason alone. We suggest that observations of tarsiers foraging and moving extensively on the floor in previous captive studies are a consequence of the extremely small size of the enclosures, the paucity of perches, and the placement of food items on the enclosure floors (Lewis; 1939; Harrison, 1962; Ulmer, 1963; Schreiber, 1968), promoting an exaggerated use of the floor for all activities.

In a subsequent study on the tarsiers that are the subject of this report, Roberts and Baker (1985) were unable to induce foraging on the floor even by reducing arboreal cricket densities almost to zero. The effect of reducing the arboreal cricket density was to increase the arboreal search rate and reduce the capture rate, suggesting a strong disinclination to forage on the floor. Floor foraging occurred only when crickets were completely eliminated in arboreal locations.

The ontogeny of foraging behavior was followed in the same study. It was found that infant tarsiers spent considerable time very close to the floor tracking moving insects before making their first prey capture. Almost all captures up to the age of approximately 10 weeks of age were made on the floor, but gradually, arboreal catches occurred and increased in frequency until virtually all crickets were caught in the trees by the age of 16 weeks. The transition from floor to arboreal catches seemed to coincide with the juveniles' maturing visual-muscular coordination. These data suggest that both age and insect abundance may influence the rate of terrestrial prey capture in *T. bancanus*. The tarsiers that Fogden (1974) and Niemitz (1984) observed catching prey on the ground were presumably adults, thereby ruling out the simple ontogenetic explanation mentioned above. Fogden (1974) noted that tarsiers scanned for insect prey attracted to ripe fruits on the forest floor in a year when fruit was abundant. Animals in the same population moved to a higher vertical distribution when the fruit crop was poor. This finding supports the idea that the vertical prey abundance can influence the vertical habitat distribution. Additional longitudinal data on prey distribution, prey density, and the location of prey capture in the wild are needed to clarify this point.

We believe that the predominant use of bamboo as a substrate was not a result of selection for bamboo per se but, rather, for characteristics of bamboo lacking in the other substrates. One potentially influential characteristic, substrate texture, was subjectively similar in all the substrates, so we found no reason to believe that it had a significant influence on substrate use. Two lines of inference suggest that tarsiers were selecting for the relatively small diameter of bamboo.

Cartmill (1974) has suggested that vertical clingers that manually hunt prey among branches require a fine-tuned control over jumping movements, best achieved through using relatively small-diameter substrates as jump-off points. The more secure grip possible on smaller substrates is undoubtedly also beneficial (Dykyj, 1980). In this study, twigs were a smaller substrate than bamboo, but bamboo was the smallest-diameter substrate that was stable enough to be an effective launch site. Indeed, bamboo was used significantly more than other substrates for jumping.

Cartmill (1974) also estimated a contact arc of 136° as being the minimum necessary for a clinging animal to be able to maintain sufficient frictional force to allow it to stay on a vertical or near-vertical perch. Using the digit-length measurements of Niemitz (1979c) and the foot contact data of Preuschoft *et al.* (1979), we estimated that a support diameter of 2.6 cm would allow each hind foot of *T. bancanus* to subtend this 136° arc. Only twigs and bamboo had diameters that consistently fell within this range; dowels were approximately 33% greater in diameter and trees were consistently much larger in diameter. Significantly, the larger-diameter trees were used only for short-term clinging, whereas bamboo was used for long-term clinging. A preference for this approximate substrate diameter has also been shown for wild *T. spectrum* (MacKinnon and MacKinnon, 1980) and a reanalysis of Reason's (1978) data indicates that his captive *T. syrichta* also exhibited this preference.

All tarsier species have enlarged digital pads with prominent friction ridges (Pocock, 1918), friction pads at the base of the tail (Hill, 1953), and structural modifications of the musculature of the hands and feet (Day and Iliffe, 1975) that improve gripping ability. Tarsiers are clearly well adapted for the friction gripping required for the use of vertical substrates, and our observations tend to confirm that upright substrates are selected. However, our observations also show that tarsiers are capable of long leaps from, and prolonged clinging to, substrates of any inclination, so it is not immediately clear why they would exhibit a behavioral preference for vertical substrates. We suggest two possible explanations.

The mechanics of bipedal leaping in primates suggest that the most efficient leaps are executed perpendicular to the support axis (Jouffroy and Gasc, 1974; Charles-Dominique, 1974). In this study, and in wild observations of this species (Niemitz, 1979), tarsiers clearly preferred to be within a relatively narrow height band. Leaps within this band could most easily be accomplished from substrates roughly perpendicular to the preferred direction of travel, i.e., vertical substrates for horizontal travel. Also, Preuschoft *et al.* (1979), Sprankel (1965), and our own observations indicate that the principal load-supporting and friction-producing surfaces of *T. bancanus* are the hind foot and tail pads. In order for this support system to work effectively, body weight must exert a torque force against the support surface. This is best accomplished on near-vertical surfaces, given the limb structure of this species (Niemitz, 1979b). Clinging on substrates subtending less than an approximately 60° angle to the horizontal may tend to neutralize the friction/torque support mechanism and place an unacceptably high support burden on limb musculature.

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