

Habitat Use, Foraging Behavior, and Activity Patterns in Reproducing Western Tarsiers, *Tarsius bancanus*, in Captivity: A Management Synthesis

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As the only obligatorily predatory primates, tarsiers are notoriously difficult to keep successfully in captivity. Here we report empirical and experimental results from a 5-year study of behavior and life history in captive *Tarsius bancanus*. Four reproducing adult tarsiers used space nonrandomly, preferring small-diameter vertical or near-vertical locomotor substrates at midlevel enclosure heights (1.2–2.1 m) for sleeping, scanning, and prey capture. The tarsiers were completely nocturnal, and spent 78% of the scotophase scanning, 13% sleeping, and 9% in prey capture and other activities. Only live crickets were eaten; prey capture rates were highest in the first hour after waking, but overall activity rates were highest later in the scotophase. Adult males and nonpregnant or lactating females ingested approximately 44.7–49.7 kJ/day. Growing and lactating individuals ingested approximately 84.4–94.1 kJ/day. An energetically conservative, sit-and-wait predatory strategy was employed, in which 88% of capture attempts were successful. Most successful prey captures involved reaching for, or leaping from, 90° or 60° supports in a horizontal or downward direction onto prey less than 0.6 m away. Virtually all prey captures were in arboreal locations, despite much higher densities of crickets on enclosure floors. Prey capture rates during the first hour of the nocturnal activity period were positively correlated with arboreal cricket densities. At constant arboreal cricket densities, capture rates were negatively correlated with ambient light intensity, with optimum levels for prey capture ranging from 0.1 to 2.0 Lux. In terms of social behavior, these *T. bancanus* were nongregarious. Females enforced interindividual spacing by chasing and displacing males. Chase/displacement rates increased significantly during late pregnancy and lactation, apparently in an attempt to keep males from harassing infants. There was no direct male parental care. Infants were precocial at birth, and grew at a rate of 0.35–0.5 g/day, until nutritional weaning at approximately 60 days of age. The implications of specialized predatory morphology and behavior for management are discussed. Published 1993 Wiley-Liss, Inc.

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INTRODUCTION

At a maximum weight of about 150 g, tarsiers are among the smallest primates and, like many other small prosimians, are nocturnally active in open tropical forests (see Musser and Dagasto [1987] and Niemitz [1984a] for recent reviews of tarsier biology). Vertical clinging and leaping is maximally developed in tarsiers through modification of forelimb, hindlimb, cervical, and caudal anatomy, enabling them in a single bound to leap many times their own body length with great power and accuracy [Grand and Lorenz, 1968; Niemitz, 1984a; Peters and Preuschoft, 1984]. Tarsiers have spectacularly large and sensitive eyes for nocturnal bifocal vision [Castenholtz, 1984], acute directional hearing for locating and pinpointing prey, specialized interlocking incisors for piercing and firmly gripping prey once located [Maier, 1984], and efficient sit-wait-and-ambush predatory tactics. In short, tarsiers are superbly outfitted as the only specialist primate predators [Bearder, 1987; Niemitz, 1985].

As adaptive as these dietary and foraging specializations might be for wild tarsiers, they have proved formidable constraints to successful captive management because, more than any other primate, tarsiers must rely on wild foraging skills to survive in captivity [Wright et al., 1989]. Although zoo records indicate almost two dozen attempts to keep *T. syrichta* and *T. bancanus* in captivity in the last 50 years [M. Jones, personal communication; see also Wright et al., 1987, 1989], no consistently successful formula for sustained management or reproduction has emerged. In fact, the record for captive reproduction can only be described as dismal. While copulations and conceptions have been reported several times [e.g., Harrison, 1963; Hill et al., 1952; Schreiber, 1968; Ulmer, 1963; Wright et al., 1986a,b, 1987], live-births are rare. Miscarriage and/or death of the mother are too often the outcome of pregnancy. When live infants have been born, they have usually died within 1–3 days from injury or maternal neglect [Haring and Wright, 1989; Harrison, 1963; Hill et al., 1952; Schreiber, 1968; Ulmer, 1963; Wright et al., 1987]. The only reported instances of captive born *T. syrichta* being reared to weaning are a mother-reared infant at the Frankfurt Zoo [Wright et al., 1987], two mother-reared young at the Cincinnati Zoo [M. Dulaney, personal communication], and a hand-reared infant at the Duke University Primate Center [Haring and Wright, 1989]. The only successfully reared *T. bancanus* have been at the National Zoological Park, where four mother-reared infants survived to weaning between 1984 and 1988 [Roberts, 1993].

The purpose of this report is to present a quantitative description of the behavioral, habitat, and husbandry factors most pertinent to successful long-term captive management and reproduction in this colony of *T. bancanus*. In particular, we focus on space and substrate use, foraging behavior, and activity patterns.

MATERIALS AND METHODS

Housing

Each of the two pairs was initially housed in an indoor room 5.1 m × 3.6 m × 4.5 m (length × width × height) with a concrete floor and solid partition walls. A complex network of branches of varying diameters, bamboo poles (mean diameter of ≈2.5 cm) and wooden dowels (5 cm diameter) was installed from floor level to a height of approximately 4 m in each enclosure [see Roberts and Cunningham, 1986,

for precise details of substrate configuration and the methodology used for substrate/space use surveys]. After being in residence for about 12 months, each pair was given access to two such interconnected rooms.

Two cardboard “nest” boxes, each measuring 61 cm × 61 cm × 30.5 cm, were situated approximately 2 m from the floor within the substrate network. The bottom of each box was completely open to enable the tarsiers to “shimmy” up and down vertical poles leading into it. Additional bamboo poles originating from the substrate network protruded into the cardboard boxes through a ≈15 cm × 15 cm entry hole cut in its side. The tarsiers frequently slept on the branches or on poles inside these boxes, with each adult using a separate box. Wooden and fiberglass boxes situated approximately 4 m above the floor were never used.

Floors were initially covered with sand to cushion falls and retain moisture for increasing the humidity. The sand, being difficult to sanitize, was removed completely after 6 months. For the remainder of this study, no floor covering was used in the enclosures, except following a birth, when a 5 cm-thick layer of wood shavings was added to cushion falls. Wood shavings were removed approximately 3 months postpartum, when the risk of infants’ falls became negligible.

Temperature and Humidity

A forced air-heating/ventilating/air-conditioning unit maintained temperature at 25.5°C–29.4°C (usually 26.6°C–27.7°C) year-round. A high relative humidity, 60–90%, was maintained throughout the year by misting the floors and branches with warm water three times a day. We believe that high and consistent temperature and humidity were responsible for preventing the skin, respiratory and “ringtail” problems encountered elsewhere [Wharton, 1950; Ulmer, 1963].

Rooms were illuminated with three 120-W incandescent white bulbs, providing approximately 60 Lux at floor level. The photophase was 12L:12D (i.e., 12 h light and 12 h dark), with the scotophase (active period) starting at 1600 to accommodate observation and keeper schedules. A single 40-W incandescent blue bulb provided a “moonlight glow” of approximately 2 Lux at floor level during the scotophase.

Diet (Food and Watering)

Despite being offered a variety of live and prepared food, the tarsiers subsisted almost entirely on live crickets (*Acheta domestica*). Live *Anolis* lizards were provided regularly for the first few weeks, but were rarely eaten. Live Haitian cockroaches (*Blaberus discoidalus*) were occasionally eaten when first introduced, then ignored. Live and dead mouse pups and mealworms were offered, but never eaten.

Crickets, the preferred food, are extremely low in calcium and trace minerals, and have an unfavorable Ca:P ratio of approximately 0.14:1 [Allen, 1989]. To provide the tarsiers with a nutritionally balanced diet, we maintained the crickets, in both the holding bins and tarsier enclosures, exclusively on an ad lib granulated alfalfa pellet diet enriched with calcium, phosphorus, trace minerals, and vitamin D (Cricket Diet 53-9000-00 available from Ziegler Brothers, P.O. Box 95, Gardners, PA 17324). While crickets incorporated very little of the supplement into their own body tissue [Allen, 1989], some supplement was retained in the gut and was subsequently ingested by the tarsiers. Supplemented crickets sampled in the enclosure had a markedly improved Ca:P ratio of approximately 1.64:1 [Allen, 1989]. We added 200–300 additional presupplemented crickets daily to each enclosure, just before the onset of

the scotophase, to replace those that died, escaped, or had been eaten; approximately 6,000 crickets per week were required to maintain a resident population of 50–300 crickets in each tarsier enclosure.

The tarsiers often licked water from branches after they were misted, but three types of watering devices were also available. The one used almost exclusively was a dripper system, consisting of a plastic 1 gallon water bottle with a 30–60 cm long, 0.5-cm diameter dripper hose projecting from the bottom. The free end of the dripper hose was fitted with an aquarium valve to adjust the flow from the bottle from draining too quickly. The bottle was suspended from a branch with the hose tied to a branch below it, so that the tarsier could lick water dripped onto the branch or directly from the valve. Water was treated with 6 ml of 1 N hydrochloric acid per 4 L of water to prevent bacterial growth. A ceramic crock on the floor and a small glass jar in a bracket attached to a tree branch were used only when the dripper system malfunctioned.

Daily Care

Tarsier rooms were cleaned once a day, and enclosure walls were wiped clean twice a week with a dilute disinfectant solution in hot water to retard fungal and bacterial growth. Keepers recorded room temperature, humidity, and the location of each animal three times a day. Fecal deposits were counted and weighed each morning as a crude estimate of food intake.

Capture and Restraint

Tarsiers can be injured easily and require care in handling. We caught tarsiers during the photoperiod, when they were sleepy and appeared slightly torpid, by simply wrapping a cloth bag around them. To reduce the risk of injury, we never caught tarsiers either by their tails or with nets. Tarsiers were weighed in bags, and morphometric measurements were easily obtained by gently pressing a bagged animal ventrally against a horizontal flat surface, and gradually peeling the bag away from its lower body, while keeping the head covered.

Tarsiers were transported in small cardboard or wooden boxes (approximately 30 cm × 20 cm × 20 cm) with bamboo pole perches. The small size of the boxes limited the animals' movements, and they remained calm when placed in them. Holes cut in the sides of the boxes provided ventilation and a means of introducing food and water.

Medical/Pathology

On arrival, the tarsiers were heavily parasitized with cestodes, capillaria, acanthocephalans, and a variety of unidentified larvae. Tarsiers refused medications offered in food and tube feeding and/or injecting anthelmintics was ruled out as too stressful. After some experimentation, we arrived at the solution of mixing medications with a thick pleasant-tasting paste carrier and smearing this paste on the tarsiers' hands or legs just before their activity periods began. Being fastidious animals, the tarsiers would immediately groom the paste off, thereby ingesting the medication. Subsequent fecal screens indicated that intestinal parasites were virtually eliminated within three months of the implementation of this protocol.

TABLE 1. Synopsis of reproduction

Female	Birth date	Sex	Interbirth interval (d)	Death date	Age at death (d)	Comments
4	3/26/84	M		4/13/84	10	Fell
4	11/2/84	M	221	—	—	
4	9/8/85	M	310	9/8/85	0	Stillbirth
6	12/28/83	M		1/16/84	19	
6	1/11/85	M	380	4/28/88	1,203	
6	8/15/85	M	216	10/23/85	69	
6	4/21/86	M	249	4/21/86	0	Stillbirth
6	11/1/86	F	194	—	—	
6	6/10/87	M	221	6/13/87	3	
6	2/21/88	M	256	2/21/88	0	Stillbirth
6	9/15/88	F	207	—	—	

Reproduction

Eleven singleton litters were born to two females during the course of this study (Table 1). Three of these were stillbirths, and the rest were full term. Details on growth and development, parental care, and the ontogeny of behavior are given elsewhere [Roberts, 1993].

Behavior

Behavioral observations were conducted for 2–7 days/week for 1 h/day, concentrated in the 2 weeks before and 15 weeks after birth (observational methodology is described by Roberts and Cunningham [1986] and Roberts [1992]). Six 24-h observations were also conducted over the course of the study. In all, approximately 700 h of direct observation were made, and more than 42,000 sample data points were collected. Hourly activity rates were determined as the percentage of 1-min scans in which animals were moving or engaged in nonscanning or nonsleeping behaviors. Jump distances were recorded for 1,191 jumps, and jump launch substrates noted for an additional sample of 1,081 jumps.

Arboreal cricket densities were experimentally manipulated by ringing trees with Vaseline or Tanglefoot, so that crickets could not move between strata. As this material was applied in very thin layers, crickets almost never became stuck in it and in fact appeared to be deterred from contacting it. Arboreal and floor cricket densities were calculated by averaging preobservation densities and postobservation densities after subtracting the number of crickets captured during the observation period. Light levels were altered rheostatically, and were measured at floor level with a Gossen Luna-Pro light meter.

RESULTS

Space and Substrate Use

The tarsiers used locomotor substrates and vertical space in a distinctly non-random manner. Bamboo poles were used significantly more than expected, based on their distribution in enclosures; trees were used significantly less than expected, and dowels were used at approximately the expected frequency ($\chi^2 = 66.8$; $df = 2$;

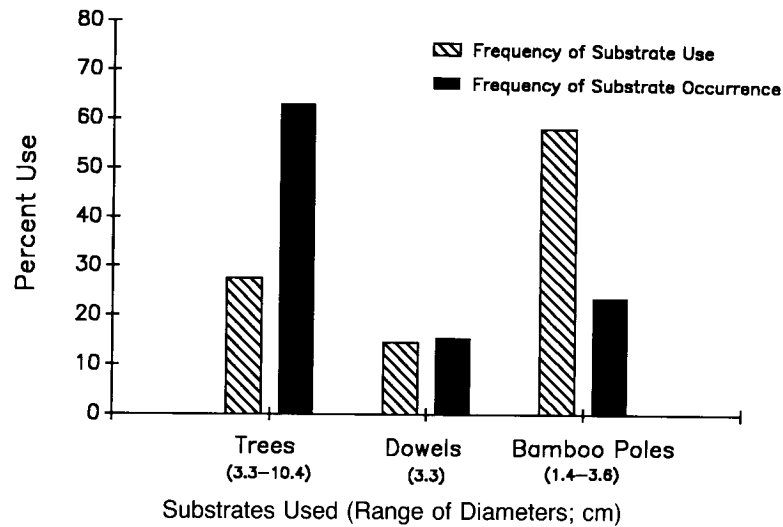


Fig. 1. Rate of use of three major substrate types by adult *T. bancanus*, compared with frequency of occurrence in enclosures ($N = 4$ adults).

$P < 0.005$) (Fig. 1). Vertical substrate supports of all sorts were used significantly more than expected; based on their distribution in the enclosures, 60° supports were used in approximately the proportion expected, and 45° , 30° , and horizontal supports were used significantly less than expected ($\chi^2 = 35.2$; $df = 4$; $P < 0.005$) (Fig. 2). The tarsiers also exhibited a strong preference for each substrate type at heights between 1.2 and 2.1 m above the floor ($F_{10,33} = 3.45$; $P = 0.003$) (Fig. 3).

Behavior and Substrate Use

All four adults showed a strong preference for vertical and 60° bamboo substrates in the 1.2- to 2.1-m height band for scanning, grooming, prey capture, eating, and scent marking ($\chi^2 = 94.6$; $df = 3$; $P < 0.005$). Vertical and 60° bamboos and dowels were used significantly more than other substrate types and angles as substrates from which to launch jumps ($\chi^2 = 143.6$; $df = 3$; $N = 1,081$; $P < 0.001$) (i.e., for “traveling” locomotion, as well as positioning during prey capture runs).

The modal jump distance of adults was 0.6–1.0 m, with approximately 80% of all jumps being 0.3–1.3 m (Fig. 4). The distribution of jumps was significantly skewed to the right (Kolmogorov–Smirnov $D = 0.902$; $N = 1,191$; $P < 0.005$). However, extremely short jumps (< 0.3 m), primarily employed in prey catching, were almost as infrequent as extremely long jumps (> 1.6 m).

Activity

The tarsiers were almost completely sedentary during the photoperiod (inactive period), with changes in location recorded on only 5% of 1,576 position checks during the photophase on 408 randomly selected days. The tarsiers generally awoke within 15 minutes of the onset of the scotophase, and virtually all activity occurred during the scotophase. Although there was no significant difference in hourly activity

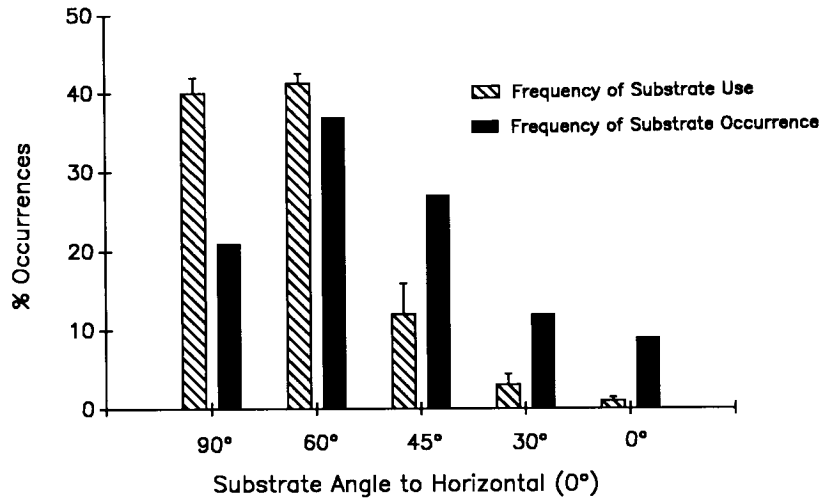


Fig. 2. Rate of use of substrate inclinations by adult *T. bancanus*, compared with frequency of occurrence in enclosures (N = 6 adults; vertical line = 1 SE).

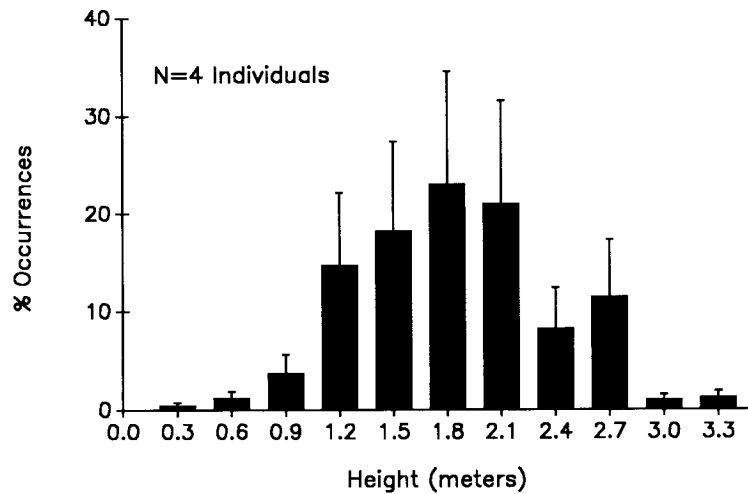


Fig. 3. Rate of use of substrates at different heights by adult *T. bancanus* (N = 4 adults and 8,640 scan samples; vertical line = 1 SE).

rates ($F_{11,89} = 1.61$; $P = 0.111$), activity did exhibit a phasic pattern, with periodic activity peaks gradually increasing in magnitude over the course of the scotophase (Fig. 5). The first activity peak occurred immediately after the onset of the scotophase, and was associated with foraging and patrolling. Later peaks tended to be associated more with elevated rates of travel and patrolling than with foraging.

Time budgets for four adult tarsiers over six 24-h observation sessions are shown in Figure 6. During the photoperiod (the inactive period), the tarsiers slept during 98% of all samples and other activities, such as scanning, grooming and

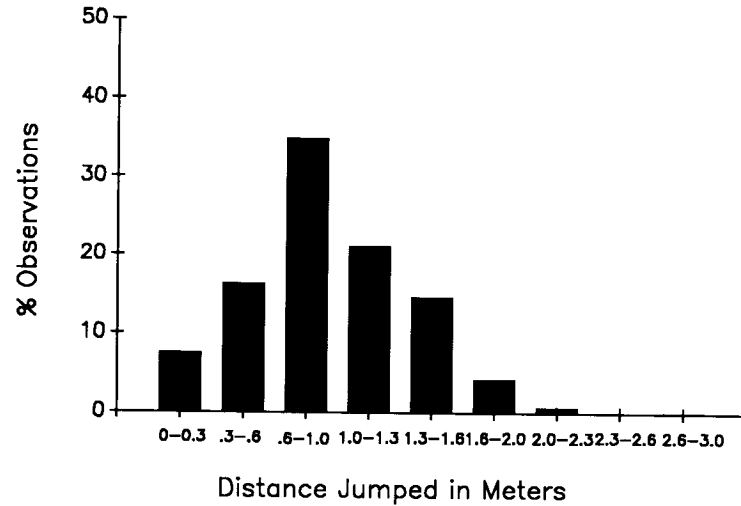


Fig. 4. Jump distance distribution for adult *T. bancanus* (N = 4 adults and 1,191 jumps).

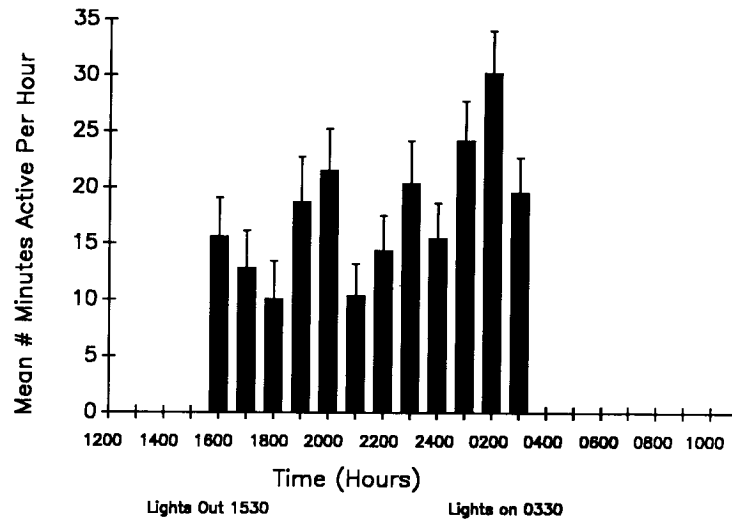


Fig. 5. Activity rates for adult and subadult *T. bancanus* (N = 4 adults, 2 juveniles and 8,640 scan samples; vertical line = 1 SE).

jumping, accounting for only 2% of all activity. During the scotophase, sleep accounted for only 13% of all samples, scanning accounted for 78%, and grooming, eating, and moving for a combined total of only 9%. Thus, in an average 24-h period, the tarsiers slept for approximately 13.3 h (55% of the period), scanned for 9.4 (39%), and spent 1.3 h (6%) engaged in other activities such as eating, grooming, playing, and moving.

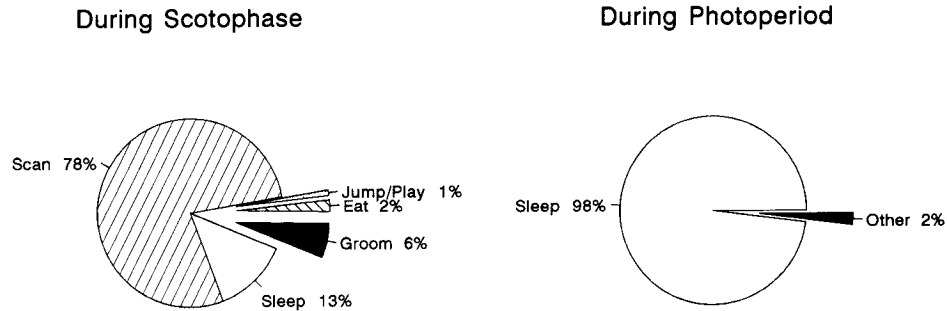


Fig. 6. Activity budgets for adult *T. bancanus* (N = 4 adults and 8,640 scan samples over six 24-h continuous observation periods).

Foraging Behavior

Prey capture rates for six 24-h observation periods for four adults are shown in Figure 7. The prey capture rate during the first hour of the scotophase (approximately 5.25 crickets/hour) was higher than during other hours, but not significantly so ($F_{11,91} = 1.84$; N = 4 individuals; $P = 0.065$). Subsequent hourly prey capture rates ranged between 1.5 and 3.3 crickets/hour, with a second peak of approximately 4.25 crickets/hour occurring in the second hour before the onset of the photoperiod. On average, adult males ate 33.6 crickets per night, nonlactating females 25.3 per night, lactating females 34 and juveniles (<110 g) 33.2 crickets. Mean intake differences between adult males and nonlactating females and between lactating and nonlactating females were significant ($t = 2.1$; $df = 5$; $P < 0.05$ and $t = 2.05$; $df = 5$; $P < 0.05$, respectively).

Because we were able to count precisely the total number of crickets eaten per day during continuous 24-h observation periods, we could also estimate approximate average daily tarsier energy intake. Average cricket weight was calculated as 0.368 g (SD = ± 0.02 g; CV = 5.4; N = 50), dry matter content was estimated at 25–30% and energy content at 22.3 kJ/g [Allen, 1989]. Hence, males consumed 82.76 kJ/day, nonlactating females 62.2 kJ/day, lactating females 83.7 kJ/day, and subadults 81.7 kJ/day. These estimates are undoubtedly high as they assume zero waste, total digestibility and absence of preferential feeding on unusually small or large crickets.

Attacks on prey fell into three categories: (1) *reaches*, where immobile tarsiers reached out and captured prey that passed nearby; (2) *single leaps*, where tarsiers made single, short leaps onto passing prey out of immediate reach; and (3) *multiple leaps*, where prey were spotted at a sufficient distance to warrant at least one preceding leap prior to the final attack leap. Twenty percent of 313 capture attempts were by reaches, 29% by single leaps, and 51% by multiple leaps.

Approximately 88% of the 313 capture attempts were successful. Seventy-two percent of all attack leaps were ≤ 0.6 m, and virtually all were from ≤ 1.2 m. Most of the 12% unsuccessful capture attempts occurred either when tarsiers attempted captures on the floor or when the attempted attack leap was > 1.2 m.

Sixteen percent of 276 successful captures occurred when tarsiers reached or made attack leaps in an ascending trajectory (i.e., when the prey was located above the tarsiers' initial resting position), 36% when descending, and 48% resulted from

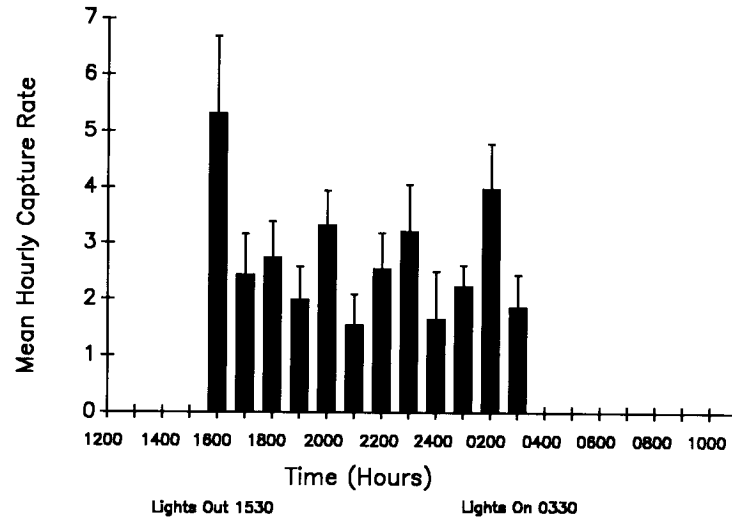


Fig. 7. Hourly foraging rates for adult *T. bancanus* (N = 4 adults and 8,640 scan samples; vertical line = 1 SE).

horizontal captures. During their orientation maneuvers just before launching an attack, tarsiers frequently moved up or down a support to position themselves preferentially for horizontal or descending attack leaps.

Prey were virtually always captured in arboreal locations despite the vastly greater abundance of crickets on enclosure floors. Approximately 85% of resident crickets were concentrated on enclosure floors and the remaining 15% in the branch network (Fig. 8). Adult tarsiers did not forage on the floor even when arboreal cricket densities were experimentally reduced to 1% or less of the total. The rate of arboreal cricket captures was significantly correlated with arboreal cricket densities ($Y = (8.0 + 0.0545 X) \cdot 100$; where Y = hourly capture rate, and X = number of arboreal crickets); $r = 0.50$; $df = 20$; $P < 0.05$) (Fig. 9). When arboreal cricket densities were experimentally reduced, arboreal capture success rates declined, and the average number of jumps required per capture increased markedly, but capture attempts on the floor did not [Roberts, unpublished observation].

When arboreal cricket densities were experimentally maintained at relatively high levels over 26 days (mean = 159.6 arboreal crickets, SE = 7.4; N = 26), and scotophase light levels were experimentally varied between 0.1 Lux and 15 Lux, cricket capture rates correlated negatively with light intensity ($Y = 0.61X^{-0.54}$, where Y = hourly cricket capture rate, and X = ambient light levels in Lux; $r = -0.66$; $df = 28$; $P < 0.01$) (Fig. 10). These data suggest that optimum light levels for tarsier foraging are approximately 0.1–2 Lux, with an inhibitory effect above this illumination level.

Reproduction

Nine full-term offspring and three late gestation stillbirths were born to two females between December 1983 and September 1988, when the colony was effectively disbanded. Three of the full-term infants died soon after birth, two others died

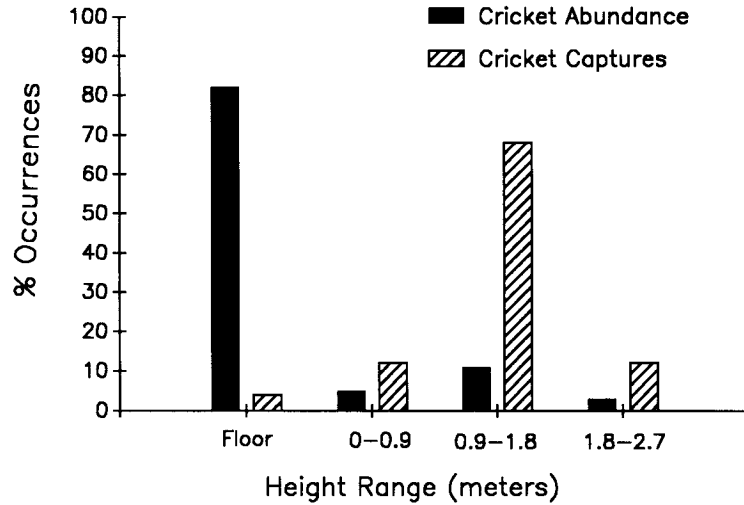


Fig. 8. Cricket capture rates at different height strata for adult *T. bancanus* (N = 4 adults and 313 captures).

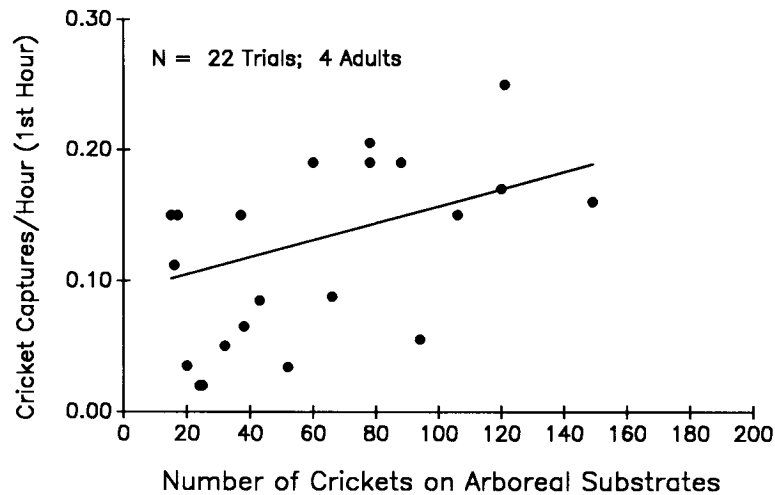


Fig. 9. Hourly cricket capture rates relative to experimentally manipulated arboreal cricket densities for adult *T. bancanus* (N = 4 adults and 22 1-h trials).

at days 18 and 19, and the remaining four infants survived beyond sexual maturity (Table 1). All litters were singletons. The mean weight of the four surviving full-term infants was 23.0g (SD ± 2.35 g). The average interbirth interval in this colony was 250.5 days, with a range of 191–380 days; there was no evidence of seasonality in births.

DISCUSSION

While the status of tarsier husbandry remains fairly rudimentary, the results of this study suggest that some success can be achieved, at least in *T. bancanus*, if the

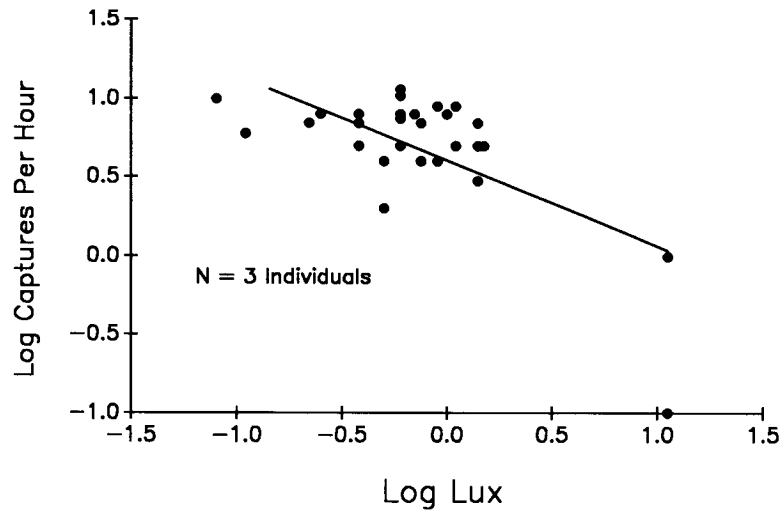


Fig. 10. Cricket capture rates relative to ambient enclosure brightness by three adult *T. bancanus* (N = 3 adults and 27 1-h trials).

species' basic biological requirements are recognized and accommodated. Three areas require special attention: nutritional, social, and space/substrate management.

The obligate predatory nature of tarsiers, combined with their highly selective and sometimes idiosyncratic tastes for prey, demands that special attention be given to nutrition. In nature, tarsiers may enjoy "balanced" diets by eating a wide variety of invertebrate (and occasionally vertebrate) prey which are of varied (i.e., "balanced") nutritional composition [Niemitz, 1984b]. In zoos, the range of invertebrates useful for food is limited by commercial availability, culturing requirements, and expense. Those typically used to feed captive animals are often deficient or unbalanced in one or more critical nutritional elements [Allen, 1989].

In this study, tarsiers self-selected crickets as their exclusive diet, despite being offered a wide range of alternatives. Unsupplemented crickets are low in calcium and have an unfavorably skewed Ca:P ratio [Allen, 1989], characteristics potentially contributory to metabolic diseases [Fowler, 1986], such as poor bone mineralization [Allen, 1989], in animals fed crickets exclusively. However, the vitamin and mineral composition of whole crickets can be significantly altered by dietary supplementation with a vitamin/mineral mix [Allen, 1989]. This alters the composition of cricket gut contents rather than their body tissue per se [see also Bilby and Widdowson, 1971].

Under such a supplementation regimen, the tarsiers in this study not only maintained excellent body condition and health, but also successfully reproduced and weaned offspring. Infant growth rates were roughly comparable with those of other highly (but not exclusively) insectivorous prosimians of similar body size [Roberts, 1993], suggesting that the cricket diet was appropriate for the nutritional demands of lactation and growth. While it is not possible to evaluate precisely the nutritional composition of diets fed to tarsiers elsewhere, supplementation appears to have been either absent or inappropriate suggesting that most tarsier diets may have been nutritionally inadequate for successful reproduction [e.g., Cook, 1939; Evans, 1967; Hill et al., 1952; Lewis, 1939; Schreiber, 1968; Ulmer, 1963; Wharton, 1950].

The basal metabolic rate of adult *T. syrichta* has been estimated at approximately 65% of Kleiber [Kleiber, 1961; McNab and Wright, 1987], or

$$67.6 M^{0.756} \text{ kcal} \cdot 0.65 = 9.67 \text{ kcal} = 40.42 \text{ kJ},$$

where M = mass (in kg).

In this study, estimated daily energy intake of nonreproducing males and non-lactating females was only 205% and 154%, respectively, of their estimated basal rates. This suggests that locomotion in general, and prey catching in particular, may be relatively inexpensive energetically [see also Niemitz, 1984b]. In fact, tarsiers appear to have evolved an energetically conservative foraging strategy in which they remain immobile, while scanning the environment for prey in the near vicinity, and attack only when prey is first auditorily, then visually located [Niemitz, 1984d]. The high capture success rate reported here (88%) appears due largely to high selectivity of capture attempts and close approaches before committing to a final attack leap.

Despite what appears to be a conservative energetic strategy, these tarsiers did not appear to accumulate much body fat [T. Grand, personal communication; see also Clarke, cited in Wharton, 1950] and may have limited energy reserves in the event that illness or injury disrupts normal foraging. Increased energetic demands during thermal stress and reproduction may further tax slim reserves of even healthy and normally foraging animals [Ulmer, 1963; Wright et al., 1989]. For example, we determined that lactating tarsiers ingest approximately 136% of the energy of normally active, nonreproducing females or approximately 207% of estimated basal requirement (as estimated for *T. syrichta* [McNab and Wright, 1987]). Clearly, establishing a high plane of nutrition and an appropriate thermal environment (i.e., preferably within thermalneutrality) are crucial for successful management.

In our opinion, successful reproduction in captive *T. bancanus* is also dependent on strategic social management. Whereas other species of *Tarsius* may be socially tolerant, and even gregarious, *T. bancanus* is not [Haring et al., 1985]. Outside the mating and mother–infant context, *T. bancanus* exhibit almost no gregarious behavior. Adults sleep separately, forage independently, do not allogroom, and maintain distinct interindividual spacing during all activities [Roberts, 1993]. Spacing is maintained principally by females directing a low level of chases and displacements (typically 0.5–1.0 chases/displacements per hour) toward males [Roberts, loc cit.]. The rates remain relatively constant throughout the reproductive cycle until approximately two weeks before parturition when there is more than a doubling of the chase/displacement rate. Distinct peaks in the chase/displacement function also occur just after parturition and again when infants attain locomotor independence [Roberts, 1993]. Concomitantly, average male–female proximity increased from approximately 1.6 m 3 weeks or more prepartum to well over 3 m between 4 weeks prepartum and 8 weeks postpartum [Roberts, 1993].

Increased female agonism is clearly a tactic to minimize male contact with infants [Roberts, 1993]. One of the two breeding males in our colony consistently attacked his own infants, and was responsible for at least two deaths of otherwise healthy and (maternally) well-cared-for infants. The second breeding male was less inclined to harass infants, but was also closely monitored and chased by the female.

Infants are nutritionally dependent on their mothers for approximately 60 days postpartum. Maternal foraging rates doubled between birth and 60 days, and declined

to near-parturition levels by approximately 70 days [Roberts, 1993]. Infants began independent foraging at approximately 45 days, and were completely nutritionally weaned by 70 days. Prey capturing was learned independently by infants, as there was no parental assistance or provisioning. Infants concentrated their early foraging efforts near the enclosure floor, where crickets occurred in greatest abundance. As foraging skills matured, juveniles gradually adopted the adult strategy of foraging principally in arboreal locations. Male *T. bancanus* contributed no direct parental care. Other details of maternal care are given elsewhere [Roberts, 1993].

T. bancanus is polyestrous [Wright et al., 1986a]. While females may resume sexual cycling within 2 weeks of parturition (loc cit.; this study), the mean interbirth interval of 250 days suggests that most fertile postpartum copulations occur well after infants are weaned. As males provide no direct parental care and may harass and may even injure or kill their own offspring, little benefit is lost, and much can be gained, by separating the sexes before parturition.

As vertical clingers and leapers [Napier and Walker, 1967], tarsiers have specific habitat and positional preferences for locomotion, sleep, and other behaviors [Crompton and Andau, 1986; MacKinnon and MacKinnon, 1980; Niemitz, 1984c; Roberts and Cunningham, 1986]. In this study, as in the wild [Niemitz, 1984d], the tarsiers exhibited strong preferences for small-diameter vertical and near-vertical substrates approximately 1–2 m from the ground for locomotion, resting, and foraging. Tarsiers avoided small twig substrates probably because they provided insufficient support for launching jumps. Interestingly, enclosure floors were avoided by all adults despite cricket densities, as these are many times greater than in arboreal substrates. This is somewhat in conflict with the observation that 2–11% of all leaps by semiwild tarsiers were to the ground [Niemitz, 1984d]. This may be due in part to avoidance of hard rough-textured floors, but we believe it more likely a reflection of an extremely strong preference for arboreal substrates of certain types when arboreal prey were available. However, infants learning to forage showed a marked tendency to forage on or near the floor, probably because higher cricket densities enabled greater foraging success [Roberts, 1993].

Given these preferences, it is clear that complex enclosure furnishings with appropriate substrate diameters/orientations, and an array of jump-gap distances must be provided to accommodate the wide range of adult and ontogenetic behaviors. All too often in the past, however, tarsiers have been housed in small enclosures with minimal furnishings incompatible with normal behavior [e.g., Cook, 1939; Evans, 1967; Hill et al., 1952; Reason, 1978; Schreiber, 1968; Ulmer, 1963; Wharton, 1950, but see also Harrison, 1963; Niemitz, 1984a; Wright et al., 1989, for examples of more suitable habitats].

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