International Journal of Primatology, Vol. 8, No. 1, 1987

Ranging, Activity Rhythms, and Sociality in Free-Ranging *Tarsius bancanus*: A Preliminary Report

Robin Huw Crompton[1,2] and Patrick Mahedi Andau[3]

Received May 1, 1986; revised November 3, 1986

Two male and two female western tarsiers were followed in primary and secondary lowland rainforest using radiotelemetry. Home ranges were determined to be at least 8.75 and 11.25 ha for two adult males and 9.5 and 4.5 hectares for two adult females. Sleeping sites tend to be clustered, and the study animals did not sleep with any other individuals. Tarsiers also hunt alone and were never seen with other tarsiers during the study period. However, calling is common and, with scent marking, probably represents the major mode of social communication outside of courtship and mating. Activity shows distinctc cyclicity, the exact pattern of which varies with the behavior under examination. The present evidence suggests that the social organization resembles that of Lorisinae and some Galaginae, but with much less direct or close contact, and does not tend to support arguments for the existence of monogamy or pair bonding in this species.

KEY WORDS: home range; ecology; *Tarsius;* social behavior.

INTRODUCTION

The biology of *Tarsius* is crucial to any analysis of primate phylogeny. Yet despite recent symposia devoted to *Tarsius* (see Chivers and Joysey, 1979; Niemitz, 1984a), and despite a substantial corpus of knowledge about its

---

[1] Department of Human Anatomy and Cell Biology, The University, P.O. Box 147, Liverpool, L69 3BX, United Kingdom.

[2] To whom correspondence should be addressed.

[3] Wildlife Section, Forest Department, P.O. Box 311, 90007 Sandakan, Sabah, East Malaysia.

anatomy, the behavior of free-ranging *Tarsius* remains largely unknown. Our knowledge rests primarily on three contributions: a paper by Fogden (1974) reporting the results of mist-netting operations at Semongok Forest Reserve, Sarawak, Niemitz's (1979a, b, 1984a-f) careful and detailed studies of *Tarsius bancanus* held in a cage enclosure in the same forest, and MacKinnon and MacKinnon's (1980) field study of *Tarsius spectrum* in Sulawesi. On the other hand, our knowledge of the ecology and behavior of the other nocturnal prosimians is at a reasonably advanced stage: in particular, we have a good knowledge of the West African (Charles-Dominique, 1977) and South African (Bearder and Doyle, 1974; Bearder and Martin, 1979; Harcourt, 1980; Crompton, 1980, 1982, 1984) Galaginae. Harcourt and Nash (1986) are now beginning to expand our knowledge about the East African forms. We thus have a good comparative and theoretical background for a study of a group which is morphologically comparable to some Galaginae (especially *G. senegalensis* and *G. alleni*) and may, judging from recent karyological (Poorman *et al.*, 1985) and DNA studies, be more closely related to galagines than has hitherto been accepted. The poor conservation status of the living tarsiers makes such a study particularly urgent.

Unfortunately, tarsiers' lack of a tapetum lucidum, rather cryptic habits, and small size conspire with the physical characteristics of their natural rainforest habitat to make observation far more difficult than it is for bushbabies and most other nocturnal primates. The development of miniaturized radiotelemetry equipment, however, now makes systematic observations of tarsiers in their natural habitat possible, if not easy.

We report some preliminary findings of a study of free-ranging *Tarsius bancanus* in Sepilok Forest Reserve, Sabah, using radiotracking techniques. Locomotion and habitat use are described elsewhere (Crompton and Andau, 1986).

STUDY SITE

Sepilok Forest Reserve (Fox, 1973) is a gazetted protected forest of 2300 ha with surrounding protected areas adding up to a total of 4000 ha. It is situated near Sandakan, on the north shore of Sandakan Bay in Sabah, East Malaysia (Fig. 1).

The area has an equatorial climate subject to two monsoons, the greater being in December and January, and the lesser in July. Over 46 years, the Sandakan area has had a mean annual rainfall of 123.93 in. The heaviest rainfall is experienced during the two monsoons, particularly that in December to January, but rainfall patterns vary considerably from year to year, drought years being experienced at least once every 10 years and resulting in con-

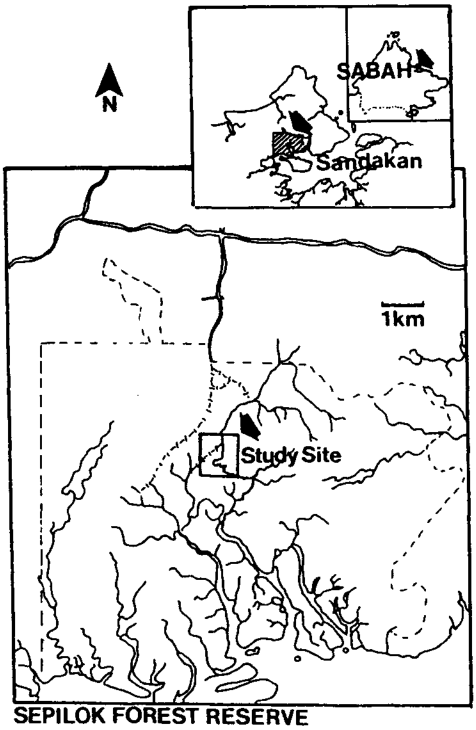

Fig. 1. Location of Sepilok Forest Reserve and study site.

siderable defoliation and even death of trees. The year of this study (1985) appears to lie in the lower part of the range for summer rainfall but was by no means a drought year (Fig. 2). The flowering pattern, and hence the seed product of the predominant trees, the dipterocarps, does not correlate well with rainfall (Wood, 1955; quoted by Fox, 1973). The mean relative humidity is usually over 80% and rarely under 70%, and mean daily temperatures in open conditions are around 80°F. The outstanding topography is formed by sandstone ridges reaching to 100 m above sea level. These ridges are dissected by rivers draining south through mudstones of Miocene age and, in their lower reaches, forming extensive alluvial flats often covered in mangrove.

The forest is composed primarily of dipterocarps. Within the study site itself, primary lowland evergreen dipterocarp forest, ridge dipterocarp, and secondary forest (pole forest to near-climax) can be found. The most common large trees in the study area are *Shorea xanthophylla, S. multiflora, S. smithiana, S. glaucescens, S. gibbosa, Dipterocarpus grandiflorus, D. acutangulus, Parashorea tomentella, Hopea* spp., and *Eusideroxylon zwageri*

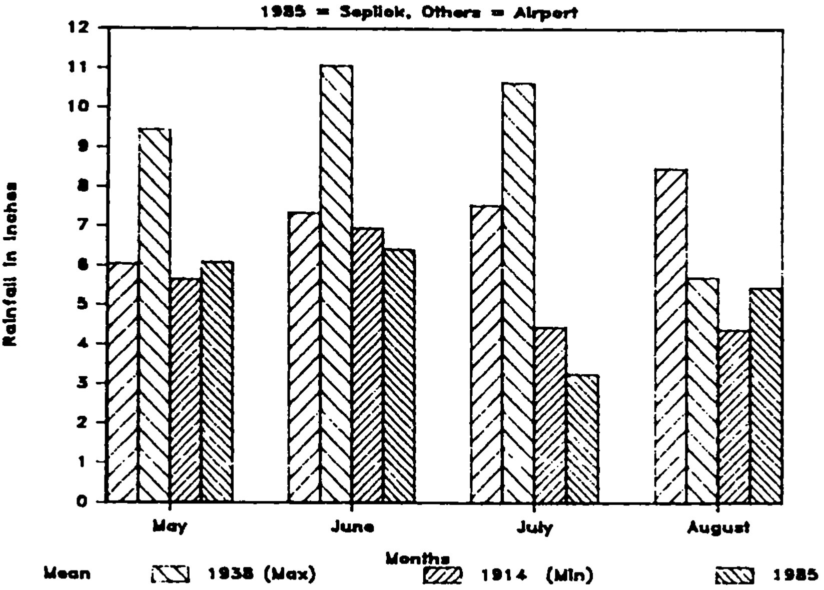

Fig. 2. Rainfall in the Sandakan area.

(A. Moad, personal communication). The most common fruiting trees are of the genera *Macarangus* and *Ficus* (dipterocarps do not produce a fleshy fruit and thus provide little food for arthropods or mammals). No fully developed *Kerangas* (Whitmore, 1984) was present but some forest over poor soils showed tendencies to transition towards *Kerangas*. The high canopy of the lowland primary evergreen forest is generally about 40 m high, with emergents to 60 m or more. The young regrowth in early stages of regeneration (such as pole forest) has a broken canopy about 10 m high, with a dense and tangled undergrowth including many creepers and rotan palms. The primary forest has a much more open aspect in the understorey.

METHODS

We present our method here in some detail since this is the first study of free-ranging tarsiers in which continuous all-night following has been successfully performed.

We selected a study area (Fig. 3) in a relatively flat area containing primary, secondary, and near-climax secondary forest. Narrow paths were

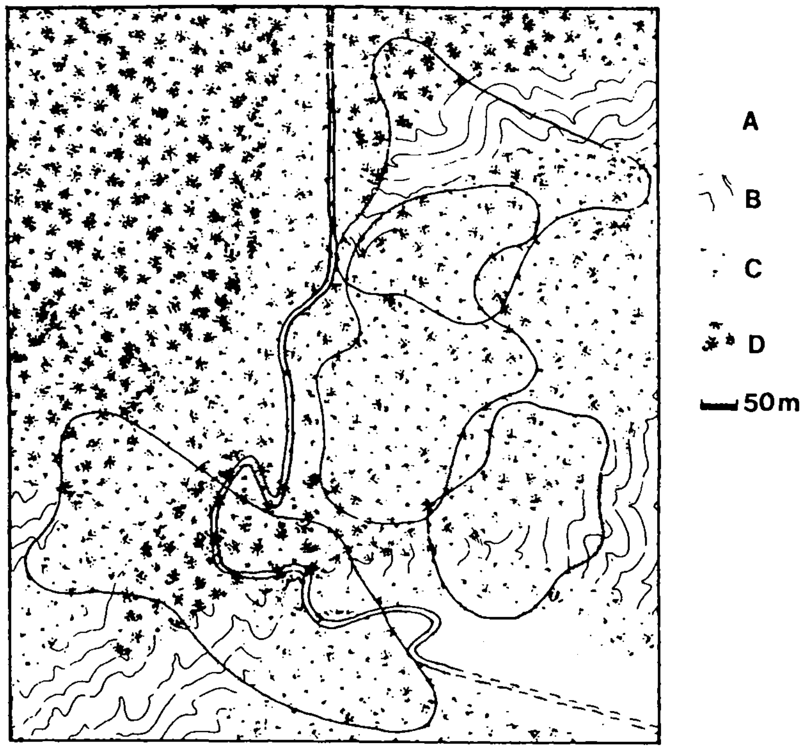

Fig. 3. Map showing approximate extent of various forest types in the study site. A, seasonally flooded areas; B, high-relief and ridge dipterocarp forest; C, secondary forest; D, primary or near-climax secondary dipterocarp forest.

cut on compass bearings at 50-m intervals to form a grid 300 × 300 m in size, with its southern base on a large east–west path forming part of the Forest Reserve's 1-km-square grid system. The paths were marked at 10-m intervals with nylon forestry flagging to facilitate route plotting and to establish a quadrat system. The grid was greatly enlarged later. The initial size of the grid was determined on the basis of Niemitz's reports of a 1.5-ha home-range size for *T. bancanus* in Sarawak. Mist nets, 12.5 × 2.5 m in size, were set up, 12 to 20 at a time, in areas where tarsiers had been caught in test trappings or in locations where calling or marking by tarsiers was observed. No attempt was made to randomize the location of nets. Nets were opened at 1830 hr, checked four times during the night, and closed at 0530 hr. No tarsiers died or were injured during our trapping operations.

Trapped tarsiers were weighed, standard measurements on body and limbs were taken, and the margin of the pinna was notched for permanent identification. Ear notching is standard practice with African *Galago* studies and does not seem to cause distress to the tarsiers. Bleeding is minimal. Adult tarsiers (weighing over 110 g and sexually mature) were selected and fitted with a radiocollar.

The radiocollars utilize Austec KG80 transmitters, operating in the 216-MHz band [a higher frequency than usual is regarded as advisable in dense foliage (AVM Instrument Co., 1979)]. Seven channels were spaced at 0.02 kHz, with either of two pulse frequencies. The transmitters use lithium cells, GE CR1/3N, which were found to give a maximum useful life of about 55 days under rain-forest conditions. The transmitter/battery assembly was sewn onto a narrow leather belt and sealed onto it with transparent dental repair acrylic (DeTrey RR). The aerial was left on the outside of the belt and passed through loops of linen thread after the belt was fitted. Given the 7- to 8-cm waist circumference typical of *Tarsius bancanus*, it is not possible to seal the aerial inside the belt. It was found essential to line the inside of the belt with satin to avoid abrasion of the delicate abdominal skin of the tarsier. The completed assembly weighed 11 to 12.8 g, which appears tolerable for a 110- to 140-g species, if placed near the center of gravity. Following release, all tarsiers were left for several days to allow settling down before tracking began. The effective range of the transmitter, combined with a receiver and preamplifer (Austec Models 31 and 22) and a miniature antenna, was 100 to 300 m, depending on the terrain, density of foliage, humidity and weather. It was found that heavy rain decreased the directionality of the signal. The density of the undergrowth makes it impossible to use a normal-sized antenna for tracking.

Tracking started at 1830 hr and sleeping sites were located and tarsiers tracked from there. Two two-man teams were used. One tracked and made observations and laid out numbered route markers of brightly colored flagging every 5 min. The next morning the other team measured distances and bearings between all markers with reference to the established grid system.

Observations were recorded on sighting the animal according to the schedule in Table I, and the direction, number, and (if possible) identity of any animals calling was recorded. No attempt was made to use a particular behavior sampling method (see, e.g., Altmann 1974), as we believe such methods are more appropriate for diurnal, easily observed species. We located a focal animal and followed it for as long as possible, using cap-lamps (Petzl) covered with red celluloid (Southern 1955) for all observations. It was soon apparent that *Tarsius bancanus* habituate to an acceptable level after a few hours or, at most, a couple of evenings, and it was possible (subject to equipment failure due to high humidity and conditions of the terrain) to follow an individual animal from a distance of 5 to 10 m for the whole active period. No attempt was made to approach closer, lest the subject be disturbed. However, low visibility and the frequent immobility of tarsiers when foraging often meant that much closer approaches were accidentally made.

Table I. Schedule of Locomotor Observations

1. Date
2. Time
3. Animal number
4. Locomotor/postural mode: sit, stand, cling, leap, climb, walk, cantilever, hop
5. Initial support type: sapling trunk, climber/vine, buttress, branch, tree trunk, tree root, twig, ground
6. Initial support diameter (cm)
7. Initial support orientation vertical (80–90°), angle (45–80°), slope (10–45°), horizontal (0–10°)
8. Terminal support orientation (same categories as 7)
9. Terminal support type (same categories as 5)
10. Terminal support diameter (cm)
11. Initial height (m)
12. Terminal height (m)
13. Distance traveled (m)
14. Activity: foraging, feed, rest, travel, groom
15. Continues from previous observation: Y/N
16. Number, direction, and identity of any *Tarsius* calling

Having first established the location of sleeping sites for each collared animal by radiotracking, we carried out at least 40 contact hr of tracking for each of four animals (three dusk-to-dawn sessions for each plus extra hours for males 1 and 2 and female 2; two dusk-to-dawn sessions and extra hours for female 1).

These generated 1321 usable positional records. In addition, 722 associated observations on locomotion and habitat use were made when sightings allowed precise determination of behavior, and these results are reported elsewhere (Crompton and Andau, 1986).

The diet of tarsiers appears to be largely insectivorous (Niemitz, 1979a, b, 1984b; personal observation), with occasional consumption of small vertebrates: orthopterans (see Davis, 1962) are particularly common dietary elements. It follows that an assessment of the differential arthropod activity in the forest types present in the study site would be a reasonable measure of the potential of local variations in forest type to influence ranging patterns. Leaf damage (Proctor *et al.*, 1983) is a simple and reasonably accurate indirect method of measuring the relative density of arthropods. We therefore assessed the relative insect damage to leaves in seven locations in the study sites. A sample of 100 leaves under 20 cm in length was taken at 0.5-m intervals along a 50-m transect, at a height of 0.5 m [about the normal height of hunting activity in tarsiers (Niemitz, 1979 *et seq.*)]. Sites for transects were selected within the known ranges of tarsiers, to sample the various forest and soil types present in the site (forest types are shown in Fig. 3). Line 1 lay in the northern part of the range of male 1, in the typical ridge variant of primary lowland dipterocarp forest. Line 2 lay in the shared part of the range of male 1 and female 1, in lightly logged forest with many large trees of the primary growth remaining. Line 3 lay in the southwestern

Table II. Trapping Records at Sepilok, 1985

Animal	Weight at capture (g)	Height captured (m)	Time of capture	Location	Recaptured
Male 1: collared	140 (recapture, 137)	0.2 (recapture, 0.5)	0600 2115	Southern boundary of own range	Mist net, 50 m north of capture site
Male 2: collared	119	0.5	0315	Souther part of range of female 1, *outside* own range	By hand
Male 3: collared	120	0.5	0130	Northern part of range of female 2	Lost
Male 4: collared	135	0.15	0545	Southeastern part of range of female 1	Mist net, 100 m north of capture site; lost

Male 5	127	0.6	0320	Eastern part of range of female 1	Not re-captured
Female 1: collared	123 (recapture, 115)	1.2	06.00	Middle of own range, c. 50 m south of capture site of male 1	Mist net, 50 m southwest of capture, then by hand
Female 2: collared	112 (recapture, 117)	0.5	2300	Northern part of own range, c. 50 m from male 3	By hand
Juvenile female	74	0.05	2115	1.5 m from recapture site of male 1	Not re-captured
Juvenile male	73	0.5	0130	Near capture site of female 2	Not re-captured

part of the range of female 1, in secondary regrowth over an area clear-cut some 20 years ago. Such forest typically has densely tangled vegetation and very low and broken canopy. Line 4 lay on less cut-over secondary regrowth with a ridge-growth aspect, on rather better soil than line 3, inside the range of female 2. Line 5 lay in partly logged riverain secondary regrowth in the home range of male 2. Line 6 lay in pole forest (young regrowth with little tangled undergrowth and better soils) on the western margins of the range of female 2, and line 7 lay on the northern margins of the range of male 5, in very old near-climax regrowth.

RESULTS

Trapping Records

The results of mist-netting are summarized in Table II. In 13 nights of mist-netting, only nine individual tarsiers were caught. This low figure contrasts with a record of five tarsiers caught on one night in the same area in preliminary trials.

Two adult female tarsiers weighing 123 and 112 g, one infant male weighing 75 g, an infant female (74 g) and five adult males (119, 120, 127 135, and 140 g) were captured. Of 12 captures and recaptures, only 2 tarsiers were caught above 0.5 m (0.6 and 1.2 m, respectively). The location of capture sites is marked in Fig. 4, which shows that most capture sites lay in close proximity to sleeping-site clusters. [However, captures (Table II) were not particularly patterned in time.] It should be noted that both subadult tarsiers were caught with 2 m of the site of capture of an adult. The female subadult was captured at the same place and at the same time as male 1. The male subadult was caught at the same location as female 2, but 3 hr later. We do not regard the skewed sex ratio as significant; Fogden (1974) found a balanced ratio in a much larger sample.

Sleeping Sites

The tarsiers generally spent the daylight hours clinging to branches or vines angled from 50 to 90° to the horizontal, about 2 cm in diameter. The heights of sleeping sites usually lay between 4 to 5.5 m, but tarsiers were found sleeping as low as 2.5 m on occasion. Vine tangles and naturally formed "platforms" of creepers were the most common sleeping sites; they provided both shelter from rainfall and camouflage. Perhaps because of the rarity of such tangles in primary forest, the tarsiers were seen to sleep only in secondary forest, treefall zones, or riverine margins of primary or near-climax secondary forest. On *no occasion* did we see more than one animal at a sleeping site.

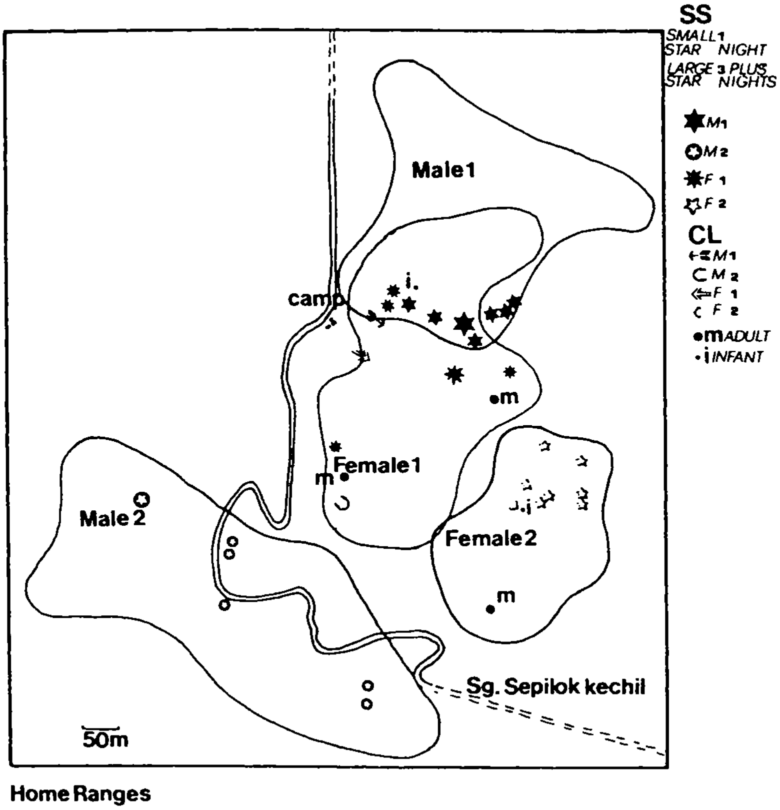

Fig. 4. Map of study site, showing capture locations (CL), sleeping sites (SS), and home-range boundaries.

Recorded sleeping sites are marked in Fig. 4. They are notably clustered and, for three of the animals, are essentially grouped in a small part of the range. Male 1 and female 1 were frequently found to be sleeping in trees less than 100 m, sometimes less than 50 m, apart. Three of four animals were found to return to the same cluster of trees or undergrowth, within a 10-m square quadrat, on three or more occasions. It was not, unfortunately, possible to mark the exact location in these cases for fear of disturbing the undergrowth too close to the sleeping site.

Home-Range Size and Population Density

Determination of home range (Mohr, 1947; Layne, 1954) is an essential basis for ecological study of any species, and equally essential for efforts directed at conservation and management. Bearder and Martin (1979) distinguish two alternative methods for estimating home range in nocturnal prosimians. First, an envelope can be constructed to enclose all known sleeping sites. Bearder and Martin term this the "minimum sleeping area" or a_1. Second, an envelope can be established to surround all known sightings: this is the "minimum home range" or a_2 in Bearder and Martin's terminology. An envelope surrounding sleeping sites (a_1) in our study site gives approximate range sizes of 0.3 ha for male 1, 1.4 ha for male 2, 1.9 ha for female 1, and 0.4 ha for female 2. A total of 1321 surveyed records of position was used to determine a_2, the minimum home range (excluding from "home range" any "prereproductive" or exceptional migrations), for two adult male and two adult female tarsiers. The home ranges were 8.75 ha for male 1, 11.25 ha for male 2, 9.5 ha for female 1, and 4.5 ha for female 2 (see Fig. 4).

Unless our radiotracking results are gravely inaccurate, a_1 would evidently be a gross underestimate of the home range of *T. bancanus* at Sepilok.

Overlap and Arrangement of Home Range

From Fig. 4 it can be seen that, while the two female ranges do not overlap greatly, the home ranges of male 1 and female 1 have a considerable overlap. The overlap zone represents 31% of the male's range and 28% of the female's. While one adult male (male 3, 120 g) and one juvenile were trapped in female 2's range, four adult males (male 1, 140 g; male 2, 119 g; male 4, 135 g; and male 5, 127 g) and one juvenile were all captured within the range of female 1. Male 2 was observed within her range only on trapping. No further range information is available for the uncollared male, male 5. However, male 4 (135 g) was captured a second time in female 2's range and tracked to two separate sleeping sites within her range before disappearing. So two males of relatively heavy body weight at least temporarily shared part of her range. Note (Fig. 4) the proximity of one of her sleeping sites to the capture sites of both male 2 and male 4. It is also certain that male 3 had at least one sleeping site within the range of female 2, about 30 m south of its capture site.

Utilization of Home Range: Distance Traveled and Clustering of Observations

The animals studied hunt and move alone: not one visual observation was made of two animals together in over 120 hr of close following.

The mean distance traveled in a normal, full activity period is 1800 m. Males move farther per night than do females, with a mean of 2081.6 m for males and a mean of 1448.1 m for females (t = 3.67, df = 6.53, one-tailed

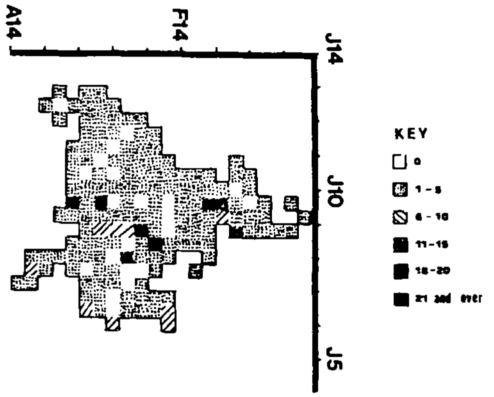

Fig. 5. Density of observations in each 20 × 20-m quadrat: male 1.

P = 0.0045). Each night the males utilized an area corresponding to between one-half and three-quarters of their total home range. Female 2 utilized between two-thirds and all of her small (4.5-ha) home range every night. Female 1, however, whose home range was nearly twice as large, utilized about a third of her home range each night. A useful measure of the pattern of home-range utilization may be derived by quadrat analysis (Greig-Smith, 1964), which Pollock (1979) applied to *Indri*, and Harcourt (1980) to the two South African bushbabies. Figures 5 to 8 show the number of observations

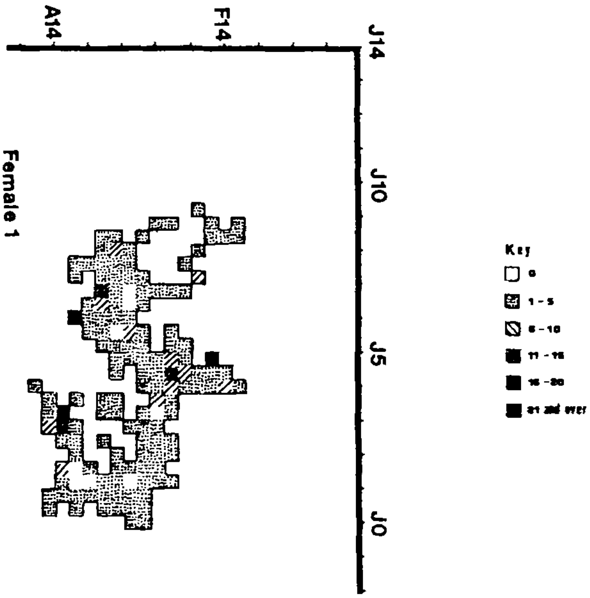

Fig. 6. Density of observations in each 20 × 20-m quadrat: female 1.

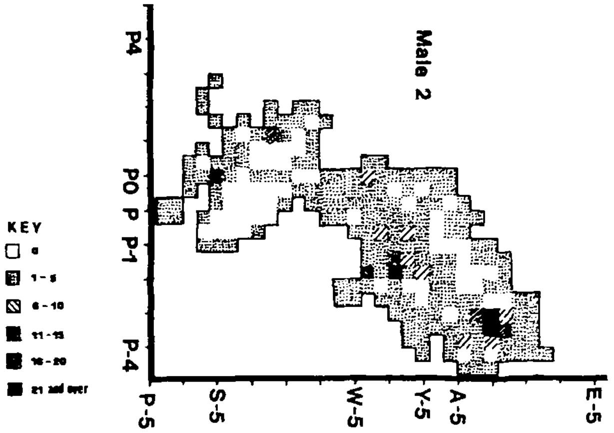

Fig. 7. Density of observations in each 20 × 20-m quadrat: male 2.

in every 20-m-square quadrat. (Using a 10 × 10-m quadrat was thought inadvisable because of unavoidable errors in plotting.) Clearly, all four figures show clustering of observations. Greig-Smith's measure of clustering, $S^2/\bar{X}$ (see also Harcourt, 1980), where the higher the ratio, the more clumped the observations, gives an overall mean of 11.1. Comparing individual home ranges, there is a clear, but nonlinear correlation ($r = 0.775$, $P = 0.01$) between range size and clumping as measured by $S^2/\bar{X}$ (male 2, 22.5; female 1, 8.91; male 1, 7.4; female 2, 5.59).

A different and more intuitive assessment of clumping may be estimated by the percentage of time (measured in 5-min units) that the tarsiers spent in each quadrat.

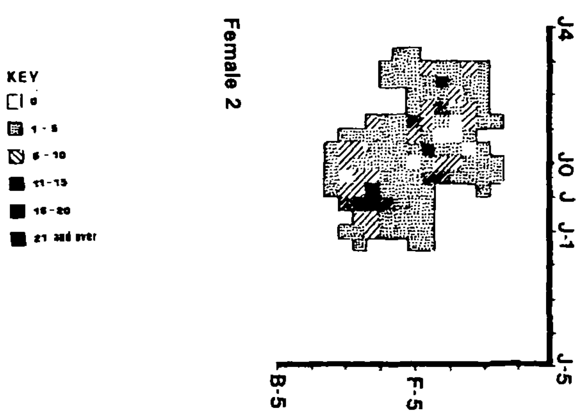

Fig. 8. Density of observations in each 20 × 20-m quadrat: female 2.

Our tarsiers spent a mean of 45% of their time in 10% of their home ranges. Male 1 spent 51% of the time in 10% of his range; male 2, 42% of the time in 9% of his range; female 1, 53% of the time in 10% of her range; and female 2, 51% of the time in 11% of her range. (The figures include some quadrats only because they lie inside the smoothed curve that was used to enclose the minimum-home range envelope. No observations were made in them, nor are they surrounded by quadrats with observations. The more irregular the envelope accepted, the less this error factor. We have chosen to prefer the known errors resulting from a smooth envelope to the unknown errors that may result from a very irregular envelope.)

Arthropod Productivity of Different Forest Types – Line Transects

Our results were as follows: leaves on Line 1 had 20.2% arthropod damage; Line 2, 19.8%; Line 3, 16.4%; Line 4, 19.9%; Line 5, 23.6%; Line 6, 23.3%; and Line 7, 20.1%. The differences were tested with Duncan's multiple-range test. The only line showing significant differences from others was Line 3. This (see Methods) was secondary forest on a site that had been clear-cut some 20 years previously. It contrasted significantly with primary-ridge dipterocarp (Line 1), riverain secondary regrowth (Line 5), and pole forest (Line 6). While our results show little difference between most forest types (cf. Proctor *et al.*, 1983), regrowth over previously clear-cut forest appears arthropod-poor by this measure and, hence, may be a marginal habitat for tarsiers.

Communication in *Tarsius bancanus* at Sepilok

The two major modes of communication in most nocturnal prosimians appear to be urine-marking and vocalization (Charles-Dominique, 1979). Niemitz (1979a) systematically recorded numerous sites of deposition of urine on trees. Such marks were usually at about a 1.5-m height. He found that sites were frequently reused and that tree roots and other sites were also marked with the secretion of the epigastric gland.

While we confirm that both activities are part of the communication repertoire of *Tarsius bancanus*, we recorded very few urine-marking sites in our study area. However, since urine marks will not usually be detectable by humans beyond 4 to 5 m, we may very well have missed sites that were not associated with sleeping trees, as the prime direction of our study was toward active following of animals. On the basis of our observations, most sleeping sites do not seem to be systematically urine-marked. Epigastric gland rubbing on a tree root was observed once, however, as male 5 returned toward a frequently used sleeping site.

However, while Niemitz (1984e) appears to agree with earlier writers [Le Gros Clark, (writing about *T. spectrum*), 1924; Harrisson, 1962, 1963; Fogden, 1974)] that *Tarsius bancanus* is "ordinarily silent," we heard numerous clear calls while following tarsiers at Sepilok – so numerous that we feel that vocal communication is at least as important at Sepilok as urine-marking may be at Semongok.

Niemitz reports that tarsier calls are difficult to distinguish from the background of forest sounds. Indeed, cicada and some small-bird calls rather resemble tarsier calls. However, once recognized, these calls are relatively easy to distinguish, although they are high in frequency.

Three calls were heard repeatedly during tracking. The first was a whistle of unknown motivational association; the second, a repeated, rapid "chick-chick-chick" call that might indicate disturbance, as tarsiers sometimes made this call when we approached too close before they were well habituated. But most common by far was the third call, a clear "tsit--tsit-tsit" that was heard again and again while following tarsiers or in areas where tarsiers are present. As far as possible, we recorded the occurrence of this call when tracking. (Unfortunately, our radiotracking receiver uses headphones and therefore we had to rely on our accompanying rangers, some of whom did not so easily recognize the call at every occurrence; some tracking sessions, therefore, definately underestimate calling frequency.)

A remarkable feature of our observations of calling was the "calling concerts" (cf. Charles-Dominique, 1979). Three to five tarsiers may be heard calling (always with the tsit--tsit-tsit call) within a radius of perhaps 50 m of the observer. The calling in one case lasted for over 4 hr. Most calls are single, however. Of 91 records of calling retained for analysis, 68% are single calls, and a further 18.7% are of two tarsiers calling simultaneously. There are six cases each of three and four or more tarsiers calling simultaneously. This "concert" calling is quite distinct from the duetting reported for *T. spectrum*: there is no obvious audible structural difference in the calls, however, many animals may be calling. Figure 9 shows the location in relation to home ranges.

Activity Rhythms: Onset and Cessation

Niemitz (1984c) provides detailed descriptions of the cycle of behavior in *Tarsius bancanus*, and here we intend only to supplement his precise and extensive observations on captive animals with data available from field observations.

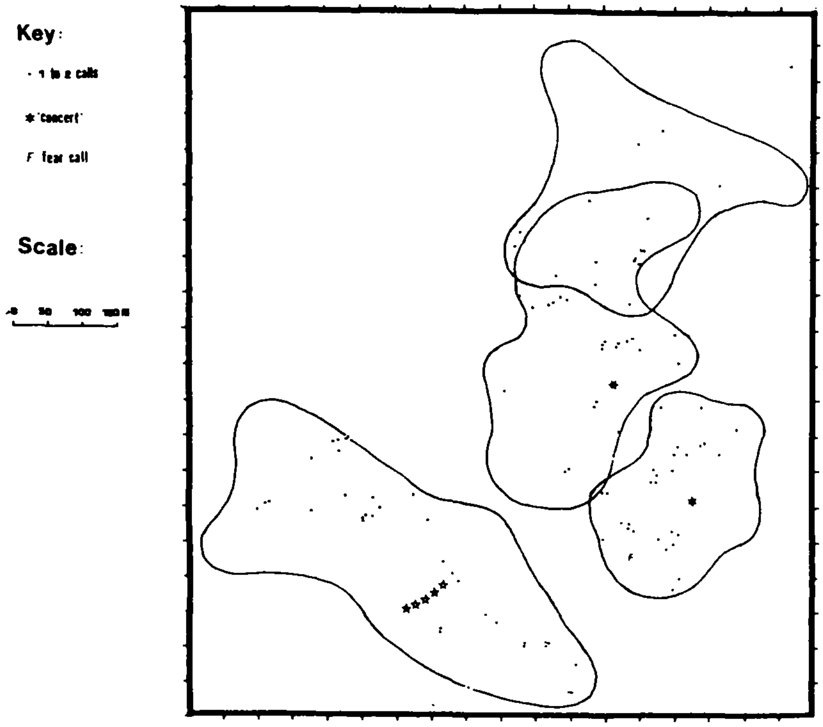

Fig. 9. Plot of locations of calling behavior in relation to ranges.

Tarsius bancanus is entirely nocturnal: but calling from the sleeping site has been heard as early as 1600 hr. The time tarsiers began to move from the sleeping site (rather than waking time, which could not be determined under field conditions) varied between 1805 and 1910 hr but, in most cases, lay between 1830 and 1845 hr. Animals stopped traveling between 0555 and 0615 hr. The luminosity range at the commencement of travel was 15 lux (1.5 footcandles) to 1.4 lux, with a mean of 6.8 lux. Activity ceased again at dawn in light levels of about 12 lux. (These approximations are obviously true only for the observer's position and may not closely estimate the light reaching the subject animal.)

Cyclicity

Distance traveled varies with hour of the night. The graph (Fig. 10) shows a rise in the second hour, falling off to the fourth hour, rising somewhat in the fifth and sixth hours, then dropping markedly to the eighth hour before

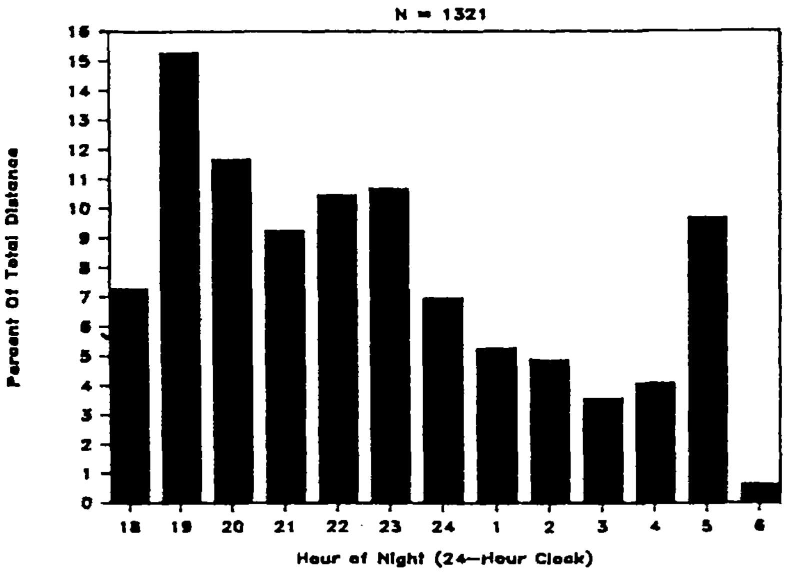

Fig. 10. Variation in distance traveled in an hour by time of night.

a large peak in the twelfth hour, and falling off sharply immediately afterward. The overall difference is significant (one-way ANOVA $F = 6.8$, df $= 12$, $P = 0.0000$; Kruskal-Wallis nonparametric one-way ANOVA $\chi^2 = 71.23$; $P = 0.0000$). A Duncan's multiple-range test ($P = 0.05$) indicates that the peak at 0500 hr is significantly different from all means between 1800 and 0400 hr; a peak between 1900 and 2200 hr is also distinguished from a trough between 2400 and 0400 hr. (Other significant results are less meaningful.)

The mean number of animals calling also varies significantly with the hour (one-way ANOVA, $F = 3.37$, df $= 12$, $P = 0.001$). A Duncan's multiple-range test ($P = 0.005$) demonstrates peaks at 1900 and 0100 hr, different from the following trough and from that at 0500 hr, and shows that the peak at 0300 hr is different from all other hours in which calling occurred.

A further analysis of mean height in relation to hour showed a significant relationship between the two (Kruskal-Wallis nonparametric one-way ANOVA $\chi^2 = 89.009$, $P = 0.0000$) (Fig. 11). Duncan's multiple-range test ($P = 0.005$) distinguishes the high means from 1800 to 2100 hr from the low means between 0100 and 0500 hr, and the peak at midnight from both. The Tukey-HSD procedure also makes these major distinctions.

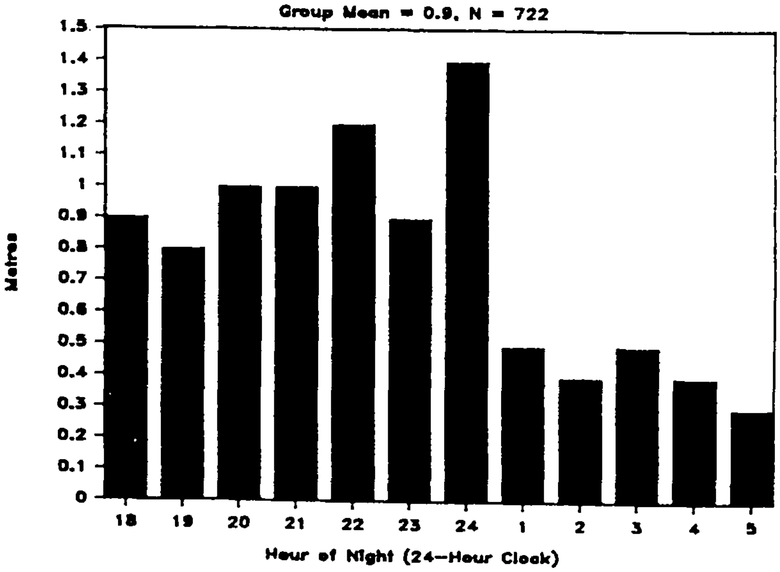

Fig. 11. Variation in mean height of observation by time of night.

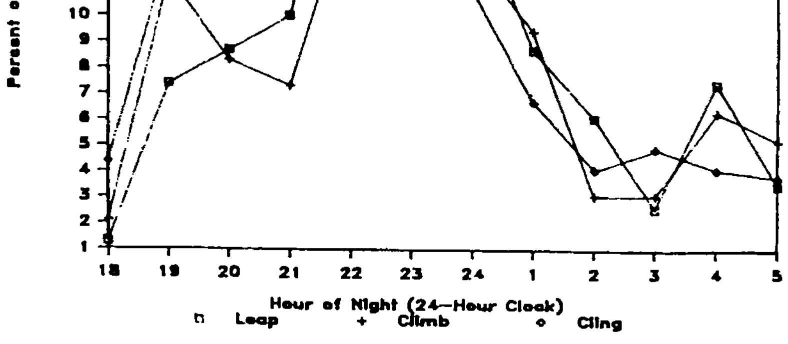

Fig. 12. Variation in frequencies of leaping, climbing, and clinging by time of night.

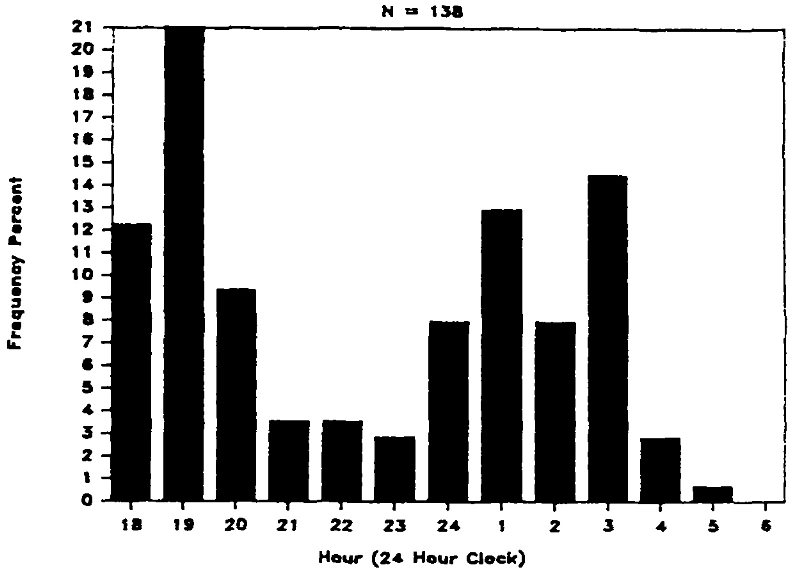

Fig. 13. Variation in frequency of calling by time of night.

We present for information purposes only a single plot of changes in locomotor and postural mode frequencies with time (Fig. 12). The three curves are not significantly different from each other, but each shows significant variation with time (nonparametric one-sample χ^2 test: *leap*, $x^2 = 73.03$ df $= 11$, $P = 0.000$; *climb*, $\chi^2 = 28.25$, df $= 11$, $P = 0.003$; *cling*, $\chi^2 = 27.51$, df $= 11$, $P = 0.000$). Plots of climbing and leaping show a broad similarity with Fig. 10, mean distance traveled per hour, as would be expected: it is of some interest, however, that the most common *postural* behavior, clinging, varies in a rather similar fashion to two *locomotor* modes.

Calling behavior (Fig. 13) has a different pattern, with (again) a peak in the second hour (which might be understood in terms of reestablishment of the relative spatial position of individuals within calling distance), followed by a sharp decline (while locomotor frequency is peaking), and a second peak during the time when locomotion and distance traveled decrease. As locomotor frequency and distance traveled rise to a peak in the second-to-last hour, calling diminishes correspondingly. There is no peak on returning to the sleeping site, in contrast to *T. spectrum* (MacKinnon and MacKinnon, 1980). The curve for mean height is different again.

DISCUSSION

Home-Range Size

The sizes we calculated for "minimum home range" (a_2) in *Tarsius bancanus*, at 4.5 to 11.25 ha, are 6 to 10 times larger than our estimates of "minimum sleeping area" or a_1 (0.3 to 1.9 ha). This contrasts markedly with Bearder and Martin's (1979) findings for *G. senegalensis*, where an individual's minimum sleeping area was more often than not 80% of the size of its minimum home range as determined by tracking results. Previous estimates of home range in *Tarsius bancanus* vary from Niemitz's estimate of 0.9 to 1.6 ha "per family group" to Fogden's estimate of 2.5 to 3 ha for adult males (both for Semongok Forest Reserve in Sarawak). Fogden's figure is based on trapping records of random sightings; Niemitz also used urine-deposition and epigastric gland making sites.

We have noted that tarsiers are often caught in nets close to their sleeping sites; and it is evident from Figs. 4 and 9 that communication (albeit calling, not marking) also concentrates near sleeping sites. Further, it is likely that random sightings made either in the early evening or near dawn, in the absence of all-night follows, will again concentrate near sleeping sites. We suggest, therefore, that Fogden's and Niemitz's figures represent a_1, minimum sleeping area, *not* a_2, minimum home range.

While Niemitz captured 34 individuals in an area of about 40 ha over 2 years, Fogden, although capturing 26 individuals over 2 years, found that only 12 animals formed 54 of 71 trapping and sighting records in a trapping area of 1 km^2. We know, too, from other studies (Bearder and Martin, 1979), that animals may occasionally make "prereproductive" or other forays outside their "regular" home range (as did male 2 in our study, which was trapped well outside its "normal" range). Thus, while about 12 animals may represent the regular population of the area (those animals with a substantial part of their range inside the trapping area), occasional migrants – "vagabond" (Bearder and Martin, 1979) males and animals with only a very small part of their range inside a trapping area – may occasionally be caught. Their inclusion will grossly overestimate the true population density of an area. (This, again, is a strong argument for basing population density estimates on systematic close following of individuals, not trapping records.) It is also possible, of course, that Semongok, Fogden's and Niemitz's study site has a higher carrying capacity than Sepilok: there might well be more fruit trees in their study area. But Sepilok is perhaps more typical of much of Bornean lowland dipterocarp rainforest.

We can no longer assume that the close similarity of a_1 and a_2 found in *G. senegalensis* will hold for any other species. Therefore we must argue that estimates of home range based on sleeping sites, random sightings, trapping records, and marking cannot be regarded as reliable sole measures of home-range size. MacKinnon and MacKinnon's (1980) 1-ha estimate of ranges of "family groups" of *Tarsius spectrum* must now be reviewed, since it was not derived from all-night follows.

The new, larger estimate for home-range size in *Tarsius bancanus*, together with the evidence of this study that *T. bancanus* individuals do not live in shared, family-group ranges, indicates that we must also adopt a much lower estimate of population densities. Using Niemitz's methods of calculation, we arrive at a figure of not about 80 animals per km^2 (Niemitz, 1979a, b, 1984d) but, perhaps, 14 to 20. This is not very different from figures for *Galago alleni* in Gabon of 15 to 20 (Charles-Dominique, 1977) or estimates of about 31 adult and subadult animals per km^2 for *G. senegalensis* (Bearder and Martin, 1979). Note that the figure for *G. senegalensis* derived by radiotracking is far lower than earlier estimates based on more traditional survey methods, at 87 to 500 per km^2 (Bearder and Doyle, 1974).

These lower estimates of population densities indicate that *Tarsius bancanus*' conservation status is poorer than had previously been thought. Moreover, larger home-range sizes and limited range overlap indicate that management plans must allow for much larger protected areas if local populations of *Tarsius bancanus* are to remain stable and genetically viable.

Range Utilization

Male *Tarsius bancanus* travel at least 2 km in an average night, and females travel about 1.4 km—rather more than the 1 to 1.5 km that Harcourt (1980) recorded for *G. senegalensis* and *G. crassicaudatus*, and much more than Pollock's (1979) figure of 0.7 km for *Indri*. But about half of the observations (time units) are concentrated in only 10% of the total home-range area. The degree of "clumping" of observations ($S^2/\bar{X}$) at an overall mean of 11.1 is similar to Harcourt's figure for *G. crassicaudatus* (1980) at 13.5 but much more "clumped" than *Indri*, where about 47% of the time is spent in 20% of the home range (Pollock, 1979). While Pollock (1979) found that home-range utilization in *Indri* is closely tied to food supply, we did not find major differences in food availability between the different forest types (as measured by arthropod damage to leaves) apart from the significantly lower arthropod activity demonstrated for regrowth over clear-cut forest. Nor does comparison of the distribution of forest types with plots of quadrat utilization reveal any clear concentrations of activity in certain forest types.

We find no evidence to support Fogden's (1974) suggestion that primary forest is a marginal habitat for tarsiers.

Indeed, if a female weighing 112g (i.e., female 2) can survive (and gain weight) on the food supply to be found in 4.5 ha, it is clear that a male of 119 g (male 2) does not need 11.25 ha simply to ensure a stable supply of food. Social factors must be involved in determining range size.

We cannot rule out the possibility of local concentrations of activity around fruiting trees (which would attract potential prey to fallen fruit) at this time but suggest that social factors may also be more significant in the *clustering* of observations. Comparison of the distribution of heavily used quadrats (Figs. 5 to 8) with that of sleeping sites (Fig. 4) reveals that a third of quadrats with over 6 observations, and a third of those with over 11 observations, lie in quadrats containing sleeping sites or adjacent to them. Excluding these, a further 18 and 20%, respectively, of frequently used quadrats lie at or adjacent to areas of range overlap or range borders between male 1 and female 1 and between female 1 and female 2. Further, comparison of the distribution of heavily used quadrats with the distribution of frequent and "concert" calling (Fig. 9) reveals further correlation between these factors.

In short, the available evidence suggests that concentrations of activity occur at or near to range boundaries or regions of overlap, and near sleeping sites (which are themselves often in overlap zones or near boundaries).

The evidence of our quadrat plots does not support the notion of a single, smaller "core area" within a larger "home range." Rather, there are, in each case two to four well-dispersed regions of concentrated activity in the home range of each animal, as indeed Harcourt (1980) found in *Galago*. The larger a home range, the more clumped is its utilization, and the relationship is such that the largest home ranges cannot, apparently, be completely "patrolled" in a night, despite the long paths followed, especially by males.

Communication

Calling, at present, appears to be the main medium of social interaction in *Tarsius bancanus* at Sepilok. We have observed that most observations involved only one or two animals calling at once. If the location of such calls is plotted (Fig. 9), obvious concentrations can be observed; one lies in the southern part of the range of female 2 (corresponding to a grouping of commonly used quadrats) near the capture site of an adult male (male 3), and another concentration lies in the overlap zone between the range of male 1 and that of female 1. Similarly, the "calling concerts" appear to be associated with range boundaries and range overlaps. One, involving female

1, lies near the boundary of her range and corresponds to an area of frequent activity. A second, involving female 2 and lasting 2 hr, is located near the capture site for an adult male tarsier, male 5. The most impressive and suggestive calling concert involved male 2 and lasted over 4 hr, from 2240 to 0440 hr. Its location corresponds to a major concentration of heavily used quadrats in the center of his home range. Its details are worth recording. Varying numbers of individuals—three, four, and sometimes possibly five—were calling simultaneously. The subject called back part of the time. It moved on a generally southwesterly bearing, traveling a linear distance of 70 m over 2 hr of continuous calling. The animals stopped calling briefly, and the subject traveled a further distance of 50 m in the same direction over 10 min, before retracing its route on a parallel path, when calling started again opposite the point where it had ceased. The calling continued in this region for the remaining time as the tarsier retraced its route. Calling was from all compass directions, with changing bearing, and moved with the subject animal. Charles-Dominique (1979) reports similar behavior in *Phaner*.

Since high frequencies attenuate very rapidly in the dense foliage of tropical forest and, also, attenuate sharply off-axis, we can be confident that these calls are directed at particular individuals within a small distance of the calling animal. Moreover, calls made in regions of range overlap or near boundaries are presumably intended to have an effect in that area.

Taken as a whole, the evidence strongly suggests an association of isolated calling with male/female relations near sleeping sites and in regions of range overlap and an association of calling concerts with boundary disputes. Little more can be said without more data.

Sociality

MacKinnon and MacKinnon (1980), in their field study of *Tarsius spectrum*, describe this tarsier as essentially monogamous, with bonded pairs as the usual social unit. Niemitz (1984d) argues that while not strictly monogamous, *Tarsius bancanus* also form male/female bonds and have the pair as the basic social unit, with entirely shared "family" home ranges of a small size. It is our belief that the evidence of the present study does not support this view. *Tarsius bancanus*, we found, forage alone and sleep alone (at least in our study period). Communication is common enough, but it is communication at a distance (with the obvious exception of mating) and is carried out by vocalization (and probably also urine-marking). It is very unlikely that, if pair-bonding existed, there would *not* be direct contact at or near the sleeping sites—and unlikely, too, that in 120 hr of following, we would not have seen tarsiers together. While Fogden (1974) reported eight sightings of more than one animal, he makes it clear that these were at accumulations of fallen fruit, which attract large numbers of potential prey. Only scattered and very limited fruit falls were observed in the study site at Sepilok.

Study of our plot of home ranges and capture sites (Fig. 4) reveals that female 1 at least had multiple associations with adult males. Her range was visited at least once by male 2 (119 g), as he was captured within her range. Male 5 (127 g) was also captured within her range. Male 1 (140 g), of course, had substantial range overlap with female 1 and sometimes slept within 50 m of her; and male 4 (135 g) was caught twice, and had at least two sleeping sites, within her range. Male/female relations in *Tarsius bancanus* thus appear to be multiple, although some relationships may be of particular strength. They are mediated at a distance by vocalization (and possibly marking), particularly in shared parts of the home range and at or near sleeping sites. Ranges overlap but are not entirely shared. Preliminary studies at Duke (P. C. Wright, personal communication) indicate that while male/female attachments certainly do form in caged specimens (Niemitz, 1979a, b, 1984d), the amount of contact is minimal compared to that observed for caged *Tarsius syrichta.* At present, while our prelimary data are inadequate to draw any firm conclusions, *Tarsius bancanus*' sociality seems to be closer to the generalized "noyau" pattern of many lorisines and galagines (Bearder and Martin, 1979) than to any form of monogamy or pair-bonding. But *Tarsius bancanus* remains distinguished by the extreme degree of its solitary habits and particularly by the apparent lack of sleeping huddles or any other physical contact at or near the sleeping site.

Activity Cycles

Our data clearly show distinct but complex cyclicity in the behavior of free-ranging *Tarsius bancanus.* Niemitz's (1984c) results based on two captive animals are an interesting comparison. Presaging our results, he found a peak in leaping activity at about 1900 hr and then a relative trough until a second peak between 0500 and 0600 hr. Moreover, just as we find a *drop* in the *mean height* of observation after midnight, so Niemitz found a clear *increase* in *ground use* in a corresponding period.

On the whole, there appears to be an overall similarity in behavior between the wild and the captive *Tarsius bancanus* but rather less complex variation in the captive specimens, as we might expect. It seems quite likely that gross activity levels are governed either by an internal clock (zeitgeber) or external cues of a simple nature—e.g., temperature, hunger, and ambient light levels (see especially Bearder and Martin, 1980). Crompton (1980) made some comparable observations in a field study of locomotion in *Galago senegalensis* and *Galago crassicaudatus,* on the basis of a much larger locomotor dataset, but not incorporating all-night follows. Significant relationships (χ^2 test, $P = 0.000$) existed in both species between time and locomotor frequencies. The peak occurs at the third hour of activity for *G. senegalensis* and the fourth for *G. crassicaudatus* (the difference may be an artifact of observability at the sleeping sites), and the frequency falls off in both species thereafter. Covert's results for captive *G. senegalensis* (personal communication to C. Niemitz) seem fairly similar. Biphasic activity rhythms, therefore, appear to be quite common in nocturnal prosimians. However, it should be observed that although several behaviors show distinct cyclicity in *Tarsius*, the cyclic pattern is not the same in all of them. For example, distance traveled and locomotor frequency show a peak in the second hour of observation (although the relative intensity of the peak for locomotor frequencies is less). There is a second peak at 2200 hr in both. Although locomotor frequency and distance traveled peak synchronously, the relative intensity is reversed, with a large peak for locomotor frequency. Again, there is a simultaneous peak for distance traveled and locomotor frequency at 0500 hr, but this time the "distance traveled" peak is larger. The results indicate that cyclicity, although present, is quite complex.

The high peaks in distance traveled in the second hour and in the second-to-last hour of observation might suggest that foraging behavior is carried out well away from sleeping sites. Thus the animal, on leaving the site, travels to a specific area before commencing foraging (or other) behavior.

SUMMARY

The present study reports preliminary results of a field study of *Tarsius bancanus*. Many more data are needed before a full analysis of ranging patterns and social organization can be presented. However, several points emerge.

(1) Home-range sizes, calculated on the basis of radiotracking, show ranges much larger than those calculated on the basis of sleeping-site locations. Sleeping site- or trapping-based estimates of range do not seem therefore to be reliable sole estimates of range size.

(2) Range sizes of between 4.5 and 11.25 ha imply population densities of 14 to 20 per km^2, not 80 as had previously been suggested. It follows that the conservation status of *Tarsius bancanus* is not as hopeful as appeared earlier, in terms both of crude numbers and of the area needed to maintain a minimal viable population.

(3) Range use is rather clustered compared to that of some diurnal prosimians but similar to that of some bushbabies; only 10% of the site home range is used in 45% of observations. Clustering of observations seems to

be associated more with social interactions than with any local variations in food availability.

(4) We have presented indirect evidence that arthropod densities may be lower in secondary regrowth in clear-cut areas and suggest that such areas may be a suboptimal habitat for tarsiers and other forest-floor insectivores. No evidence beyond this fact suggests any differences between primary and secondary forest or their variants. Nor does any evidence support Fogden's (1974) suggestion that primary forest is a marginal habitat for tarsiers.

(5) Vocal communication appears from this study to be the major mode of social interaction in *Tarsius bancanus*. It appears to be involved in male/female interactions and in the definition of territorial boundaries.

(6) *Tarsius bancanus* at Sepilok are solitary in their nocturnal activity and sleeping habits.

(7) Overall, evidence suggests that *Tarsius bancanus*' social organization is not pair-bonding or monogamy, but a variant of the typical "noyau" pattern seen in other nocturnal prosimians, with the emphasis on solitariness and communication at a distance by vocalization.

(8) Cyclicity of behavior like that observed in captive animals occurs in free-ranging *Tarsius bancanus*. It affects not only the gross activity levels, but also the type of activity and patterns of utilization of the habitat. Cyclicity, however, is likely to be more complex in free-ranging animals.

ACKNOWLEDGMENTS

This study represents a cooperation between the first author and the Wildlife Section, Forest Department, Sabah. It was sponsored by the World Wildlife Fund/Hong Kong and the World Wildlife Fund/Malaysia. We thank the State Economic Research Unit for permission to carry out the research. Invaluable field assistance was given by our research team: Steven, Sampladen, Bidi, James, and especially Simmon Ambi. Charles Phillipps and Alex Moad gave important advice on botany, and we thank all the Canadian and Australian volunteers at Sepilok for their support and encouragement. Karen Phillipps introduced R.H.C. to the study site and provided much direct and indirect help. R.H.C. also thanks his parents and wife for all kinds of help, support, encouragement, and advice.

NOTE ADDED IN PROOF

In Fig. 4, Sg. Sepilok kechil should read Sg. Sepilok besar. Also, Galago senegalensis and Galago crassicaudatus have recently been renamed Galago moholi and Galago garnettii, respectively.

REFERENCES

Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour* 49: 227-267.

AVM Instrument Co. (1979). *Radiotelemetry Equipment and Techniques Manual,* AVM Instrument Co., Champaign, Ill.

Bearder, S. K., and Doyle, G. A. (1974). Ecology of bushbabies *Galago senegalensis* and *Galago crassicaudatus,* with some notes on their behavior in the field. In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), *Prosimian Biology,* Pittsburgh University Press, Pittsburgh, pp. 109-130.

Bearder, S. K., and Martin, R. D. (1979). The social organization of a nocturnal primate revealed by radio-tracking. In MacDonald, D. W., and Amlaner, C. J. (eds.), *A Handbook on Biotelemetry and Radio Tracking,* Pergamon Press, Oxford, pp. 633-648.

Bearder, S. K., and Martin, R. D. (1980). Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). *Int. J. Primatol.* 1: 103-128.

Charles-Dominique, P. (1977). *Ecology and Behaviour of Nocturnal Prosimians,* Duckworth, London.

Charles-Dominique, P. (1979). Solitary and gregarious prosimians: evolution of social structure in primates. In Chivers, D. J., and Joysey, K. A. (eds.), *Recent Advances in Primatology. Vol. 3. Evolution,* Academic Press, London, pp. 139-149.

Chivers, D. J., and Joysey, K. A. (eds.) (1979). *Recent Advances in Primatology. Vol. 3. Evolution,* Academic Press, London.

Crompton, R. H. (1980). *Galago Locomotion,* Ph.D. dissertation, Harvard University, Cambridge, Mass.

Crompton, R. H. (1982). Age differences in locomotion of two subtropical Galaginae. *Primates* 24: 241-259.

Crompton, R. H. (1984). Foraging, habitat structure and locomotion in two species of *Galago.* In Rodman, P., and Cant, J. (eds.), *Adaptations for Foraging in Non-human Primates,* Columbia University Press, New York, pp. 73-111.

Crompton, R. H., and Andau, P. (1986). Locomotion and habitat utilization in free-ranging *Tarsius bancanus*: A preliminary report. *Primates* 27: 337-355.

Davis, D. D. (1962). Mammals of the lowland rain-fores of North Borneo. *Bull. Singapore Natl. Mus.* 31: 1-129.

Fogden, M. (1974). A preliminary study of the western tarsier, *Tarsius bancanus* Horsefield. In Martin, R. D., Doyle, G. A., and Walker, A. C. (eds.), *Prosimian Biology,* Pittsburgh University Press, Pittsburgh, pp. 151-165.

Fox, J. (1973). *A Handbook to Kabili-Sepilok Forest Reserve,* Borneo Literature Bureau, Kuching.

Greig-Smith, P. (1964). *Quantitative Plant Ecology,* Butterworth, London.

Harcourt, C. S. (1980). *Behavioural Adaptations in South African Galagos,* M.Sc. thesis, University of the Witwatersrand, Johannesburg.

Harcourt, C. S., and Nash, L. T. (1986). Species difference in substrate use and diet between sympatric galagos in two Kenyan coastal forests. *Primates* 27: 1-26.

Harrison, B. (1962). Gettin to know about *Tarsius. Malay Nat. J.* 16: 197-204.

Harrison, B. (1963). Trying to breed *Tarsius. Malay Nat. J.* 17: 218-231.

Layne, J. N. (1954). The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs) in central New York. *Ecol. Monogr.* 24: 227-267.

Le Gros Clark, W. E. (1924). Notes on the living tarsier (*Tarsius spectrum*). *Proc. zool. Soc. Lond.* 14: 216-223.

McKinnon, J., and McKinnon, K. (1980). The behavior of wild spectral tarsiers. *Int. J. Primatol.* 1: 361-379 .

Mohr, C. O. (1947). Table of equivalent populations of North American small mammals. *Am. Midland Nat.* 37: 223-249.

Niemitz, C. (1979a). Results of a field study on the western tarsier (*Tarsius bancanus borneanus* Horsfield, 1821) in Sarawak. *Sarawak Mus. J.* 48 (N.S.): 171-228.

Niemitz, C. (1979b). Outline of the behavior of *Tarsius bancanus*. In Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior,* Academic Press, New York, pp. 631-660.

Niemitz, C. (ed.), (1984a). *The Biology of Tarsiers,* Gustav Fischer, Stuttgart.

Niemitz, C. (1984b). Synecological relationships and feeding behaviour of the genus *Tarsius.* In Niemitz, C. (ed.), *The Biology of Tarsiers,* Gustav Fischer, Stuttgart, pp. 59-75.

Niemitz, C. (1984c). Activity rhythms and use of space in semi-wild Bornean tarsiers, with remarks on wild spectral tarsiers. In Niemitz, C. (ed.), *The Biology of Tarsiers,* Gustav Fischer, Stuttgart, pp. 85-115.

Niemitz, C. (1984d). An investigation and review of the territorial behaviour and social organization of the genus *Tarsius.* In Niemitz, C. (ed.), *The Biology of Tarsiers,* Gustav Fischer, Stuttgart, pp. 117-127.

Niemitz, C. (1984e). Vocal communication of two tarsier species (*Tarsius bancanus and Tarsius spectrum).* In Niemitz, C. (ed.), *Biology of Tarsiers,* Gustav Fischer, Stuttgart, pp. 130-141.

Niemitz, C. (1984f). Locomotion and posture of *Tarsius bancanus*. In Niemitz, C. (ed.), *The Biology of Tarsiers,* Gustav Fischer, Stuttgart, pp. 191-225.

Pollock, J. I. (1979). Spatial distribution and ranging behavior in lemurs. In Doyle, G. A., and Martin, R. D. (eds.), *The Study of Prosimian Behavior,* Academic Press, New York, pp. 359-409.

Poorman, P. A., Cartmill, M., MacPhee, R. D. E., and Moses, M. J. (1985). The G-banded karyotype of *Tarsius bancanus* and its implications for primate phylogeny. *Am. J. Phys. Anthrop.* 66: 215.

Proctor, J., Chai, P., and Vallack, H. W. (1983). Ecological studies in four contrasting rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment. *J. Ecol.* 71: 237-260.

Southern, H. N. (1955). Nocturnal animals. *Sci. Am.* 193 (4): 88-98.

Whitmore, T. C. (1984). *Tropical Rainforests of the Far East,* Oxford University Press, Oxford.

Wood, G. H. S. (1955). The dipterocarp flowering season in North Borneo, 1955. *Malay. Forest.* 18: 193-201.