

Associations Between Adult Spectral Tarsiers

Sharon Gursky*

Department of Anthropology, Texas A&M University, College Station, Texas 77843-4352

KEY WORDS social behavior; *Tarsius*; prosimian; Sulawesi; Indonesia

ABSTRACT While anecdotal observations of gregarious behavior in nocturnal prosimian primates are common, most anthropologists continue to refer to them as solitary, perhaps based on the assumption that the occasional social interactions observed via ad libitum methods represent random chance encounters and not patterned social interactions. In this paper, I test the null hypothesis that nocturnal encounters between spectral tarsier (*Tarsius spectrum*) group members, outside of the sleeping tree, are the result of chance. Three male-female pairs were radio-collared and observed over a 4-month period, using continuous focal animal sampling at the Tangkoko Nature Reserve (Sulawesi, Indonesia). Using Waser's random gas model, I found that spectral tarsiers spent more time in proximity to other group members than expected by chance, given the size of their home range and nightly path length. Adult group members spent 11% of the night

in physical contact and an additional 17% of the night within a 10-m radius of one another. Spectral tarsiers were also observed to significantly increase the amount of time spent foraging when located less than 10 m from another group member. Individuals foraging in proximity to another adult group member had lower insect capture rates compared to individuals who were not foraging in proximity to another adult group member. If living in a group is costly to these tarsiers' foraging efficiency, then why don't they actively avoid one another when foraging? One situation in which it might benefit tarsiers to be gregarious is high predation pressure. Preliminary results suggest that predation pressure by snakes may be the most likely factor selecting for the tarsiers to forage in proximity. *Am J Phys Anthropol* 128:74–83, 2005.

© 2005 Wiley-Liss, Inc.

Over the last several decades, it has become clear that there is a tremendous amount of variation within the social systems of nocturnal primates. Increasingly detailed studies show that many nocturnal prosimian primate species reside in large groups at their sleeping sites (Bearder, 1987; Harcourt and Nash, 1986; Harcourt, 1980; Clark, 1985; MacKinnon and MacKinnon, 1980; Bearder and Martin, 1979; Charles-Dominique, 1977; Martin, 1972; Warren, 1994; Nietsch and Niemitz, 1992). For example, large groups of female galagos were observed sleeping together in the same nest (Bearder, 1987). This pattern was observed for Demidoff's bush baby (*Galagoides demidoff*) and Allen's bush baby (*Galago alleni*) (Charles-Dominique, 1977; Bearder, 1987). Martin (1972) also reported a similar pattern of sleeping-site associations in the gray mouse lemur (*Microcebus murinus*). Likewise, Warren (1994) also noted that Milne Edward's sportive lemurs (*Lepilemur edwardsi*) sleep in groups of 3–5 individuals.

These observations of nocturnal prosimians residing in social groups at their sleeping sites resulted in a rephrasing or reclassification of the nocturnal prosimians as solitary foragers (Bearder, 1987; Harcourt and Nash, 1986; Rowe, 1996; Janson, 1992). In other words, although they are gregarious animals at their sleeping sites, and in terms of their varied vocal and olfactory communication repertoire, they spend much of their nocturnal activity period forag-

ing alone (Bearder, 1987; Harcourt and Nash, 1986; Janson, 1992; Rowe 1996).

However, the classification of all nocturnal prosimians as solitary foragers is dubious, given that many of these species have also been observed in small groups during nightly foraging. For example, during the synecological study by Charles-Dominique (1977) of several African nocturnal prosimians, groups of 2–5 individuals of *Galagoides demidoff* were observed during 25% of his observations ($n = 263$). Mother infant pairs accounted for only 1% of these observations. Similarly, observations by Charles-Dominique (1977) of *Galago alleni* ($n = 97$) and *Euoticus elegantulus* ($n = 103$) indicate that these taxa likewise do not remain solitary throughout the night, being observed in groups of two or more during 14% and 24% of all nightly observa-

Grant sponsor: National Science Foundation; Grant sponsor: L.S.B. Leakey Foundation; Grant sponsor: Primate Conservation, Inc.; Grant sponsor: PSC-CUNY.

*Correspondence to: Dr. Sharon Gursky, Department of Anthropology, Texas A&M University, TAMU 4352, College Station TX 77843-4352. E-mail: gursky@tamu.edu

Received 9 April 2003; accepted 20 August 2003.

DOI 10.1002/ajpa.20104
Published online 10 March 2005 in Wiley InterScience
(www.interscience.wiley.com).

tions, respectively. Once again, only 2–4% of these observations are accounted for by mother-infant pairs. Clark (1985) also observed a high frequency of social interactions (e.g., grooming, play, sex, and agonism) during nightly forays by *Otolemur crassicaudatus*. She observed 2–3 social interactions per hour, or 865 social interactions, during 350 hr of observation. Clark (1985) wrote that *Otolemur* was not just tolerating conspecifics but actively seeking affiliative interactions. Sterling and Richard (1995) observed that encounter rates at feeding trees were higher than expected by chance for the aye-aye, *Daubentonia madagascarensis*. Similarly, Ganzhorn (cited in Kappeler, 1997) found that 2–5 greater dwarf lemurs, *Cheirogaleus major*, were frequently observed within 10 m of one another. Warren (1994) observed that among Milne-Edward's sportive lemur (*Lepilemur edwardsi*), 2–5 animals regularly travel together throughout the night as well as feed without aggression in the same tree. Together, these observations provide extensive anecdotal support for the idea that these nocturnal prosimians are not solitary foragers, but spend a significant portion of their nightly activity period travelling and foraging together, analogous to the social organization of the only nocturnal monkey, *Aotus* (Wright, 1985).

Unfortunately, while anecdotal observations of gregarious behavior in nocturnal prosimian primates are common, no study to date has tested the hypothesis that any of the nocturnal prosimians are gregarious foragers and that the nightly encounters between group members are not merely the result of chance. The lack of data on gregarious behavior in nocturnal prosimians results in part from a methodological shortcoming of previous studies. Studies of nocturnal prosimians often used radio telemetry to record the movements of a single individual during each night (e.g., Bearder and Martin, 1979). Further, different individuals were followed on different nights, and their individual ranges were recorded. The degree of overlap, or distinctness, of the individual home ranges of males and females is then used as one of the major traits for classifying the type of social system exhibited by the species (types 1–5; Bearder, 1987). Given the small size and cryptic nature of many nocturnal prosimians, researchers using these methods are rarely able to observe individuals other than the focal animal, except by *ad libitum* sampling. It is therefore possible that the nonfocal individuals are just not seen or heard by the researcher. Primatologists using these *ad libitum* methods are therefore unable to determine whether or not the association between group members during the night is a random, chance encounter (Waser, 1976; Jolly et al., 1993; Holenweg et al., 1996).

The spectral tarsier, *Tarsius spectrum*, is one of the most difficult nocturnal prosimians to observe in its natural habitat because of its rapid mode of locomotion and its lack of a *tapetum lucidum* in its

eyes (Fleagle, 1998). The first field observations of the spectral tarsier were conducted by MacKinnon and MacKinnon (1980) in Sulawesi, Indonesia. Their brief observations suggest that spectral tarsiers sleep together in family groups during the day inside strangler fig trees, and during nightly forays they maintain frequent auditory and olfactory contact via scent-marking (MacKinnon and MacKinnon, 1980). In addition, their anecdotal observations also suggest that spectral tarsiers encounter one another at intervals throughout the night. However, most anthropologists continue to refer to the spectral tarsier, and other nocturnal primates species, as solitary (e.g., Rodman, 1999; Falk, 2000; Rowe, 1996).

The goal of this paper is to test the hypothesis that spectral tarsiers are gregarious outside of the sleeping tree, or whether nocturnal encounters between group members are the result of chance. If spectral tarsiers are gregarious outside of their sleeping tree, it is predicted that: 1) individuals will not encounter one another at random intervals throughout the night, but will encounter each other at regular intervals throughout the night, when proximity is defined as less than 10 m; and 2) individuals will travel and forage together throughout the night, in addition to time spent socializing and resting in proximity/contact.

METHODS

Research design

If group members' movements are random and independent (i.e., solitary foraging), then following Waser (1976), Holenweg et al. (1996), and Jolly et al. (1993), their territory can be considered a two-dimensional gas of tarsier individuals. Collision (encounter) frequency, Z , or the frequency of approach to within the specified distance, d , is dependent on the mean distance traveled per day (night) in kilometers, v , and home range size in hectares, p , where: $Z = [8(p)(v)(d)]/3.14$. This model is based on two dimensions, even for arboreal primates who live in a three-dimensional habitat (Holenweg et al., 1996; Waser, 1976; Jolly et al., 1993), because the mathematics are not very tractable in three dimensions. In this paper, expected values of Z were calculated for a range of interindividual distances (0–150 m). Observed interindividual distance data were then tallied and divided by the number of nights both the male and female were simultaneously followed. Attraction between tarsiers will result in encounter frequency greater than expected by chance alone. Similarly, avoidance between group members will result in encounter frequency significantly less than expected by chance alone.

Study site

Sulawesi is a four-armed island located to the east of Borneo and northwest of Australia-New Guinea (longitude 125° 14' East, latitude 1° 34' North)

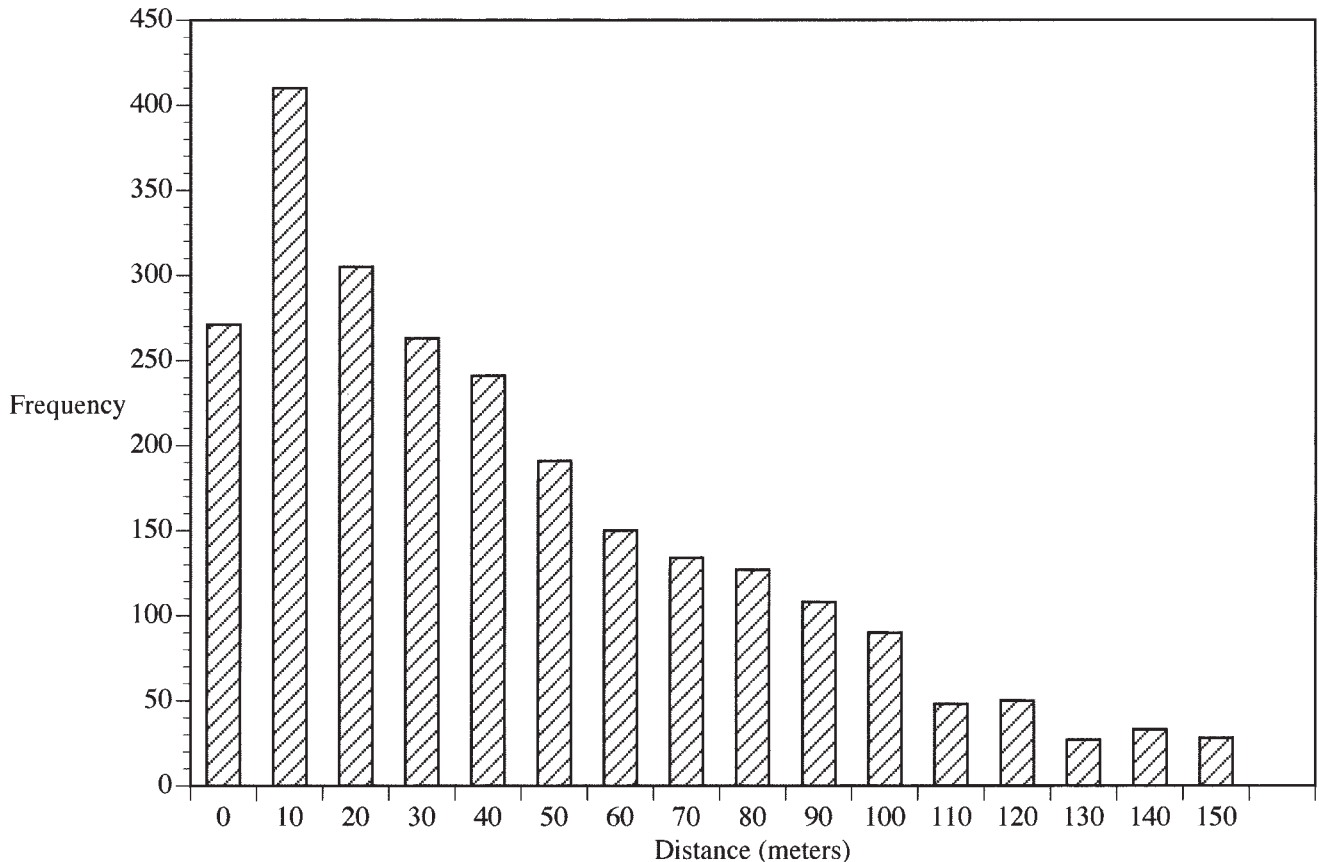


Fig. 1. Frequency distribution of observed distance between male-female pair for each simultaneous data point. $N = 2,476$ simultaneous data points for all three spectral tarsier groups. All distance values are less than or equal to value on X-axis, but greater than preceding value on X-axis.

(Audley-Charles, 1981). Sulawesi is the eleventh largest island in the world. It is also the largest and most central island of the biogeographical region of Wallacea, where the Australian and Asian zoogeographical regions meet. Sulawesi exhibits a blend of Asian and Australian elements in its fauna and flora, in addition to exhibiting very high numbers of endemics (Whitten et al., 1987; Musser, 1986).

This study was conducted at Tangkoko Nature Reserve on the easternmost tip of the northern arm of the island. The reserve, which is approximately 3,000 ha, exhibits a full range of forest types, including beach formation forests, lowland forests, submontane forests, and mossy cloud forests on the summits of the Tangkoko Crater (MacKinnon and MacKinnon, 1980; Whitten et al., 1987; Gursky, 1997). The reserve is far from pristine due to heavy selective logging and encroaching gardens along its borders. The forest canopy is very discontinuous and contains a high proportion of *Ficus* trees (Gursky, 1997, 1998). Rainfall averages approximately 2,300 mm annually (World Wildlife Fund, 1980; Gursky, 1997). Additional details concerning the habitat types at Tangkoko Nature Reserve can be found in Gursky (1997).

Study species

The spectral tarsier is a small nocturnal primate found exclusively on the island of Sulawesi, Indonesia. Although most groups exhibit a monogamous social system, a few exhibit a polygynous social system (Gursky, 1994, 1995). They are highly insectivorous, eating a wide variety of insects (Gursky, 2000). Spectral tarsiers have a 191-day gestation period that is followed by a 78-day period of lactation. The mean interbirth interval is 12.7 months. Births are seasonal, with most occurring in April–May and a few in November–December. Infants are not continuously transported by the mother or other group members following birth. Rather, they adopt a cache-and-carry infant caretaking strategy. Spectral tarsier infants are transported in the mother's mouth and then parked on branches while the mother forages nearby (Gursky, 1997). Spectral tarsiers at Tangkoko Nature Reserve utilized primarily strangling *Ficus* trees for their sleeping sites (MacKinnon and MacKinnon, 1980; Gursky, 1997). Most ranges contained 1–3 sleeping sites, but one site was used preferentially.

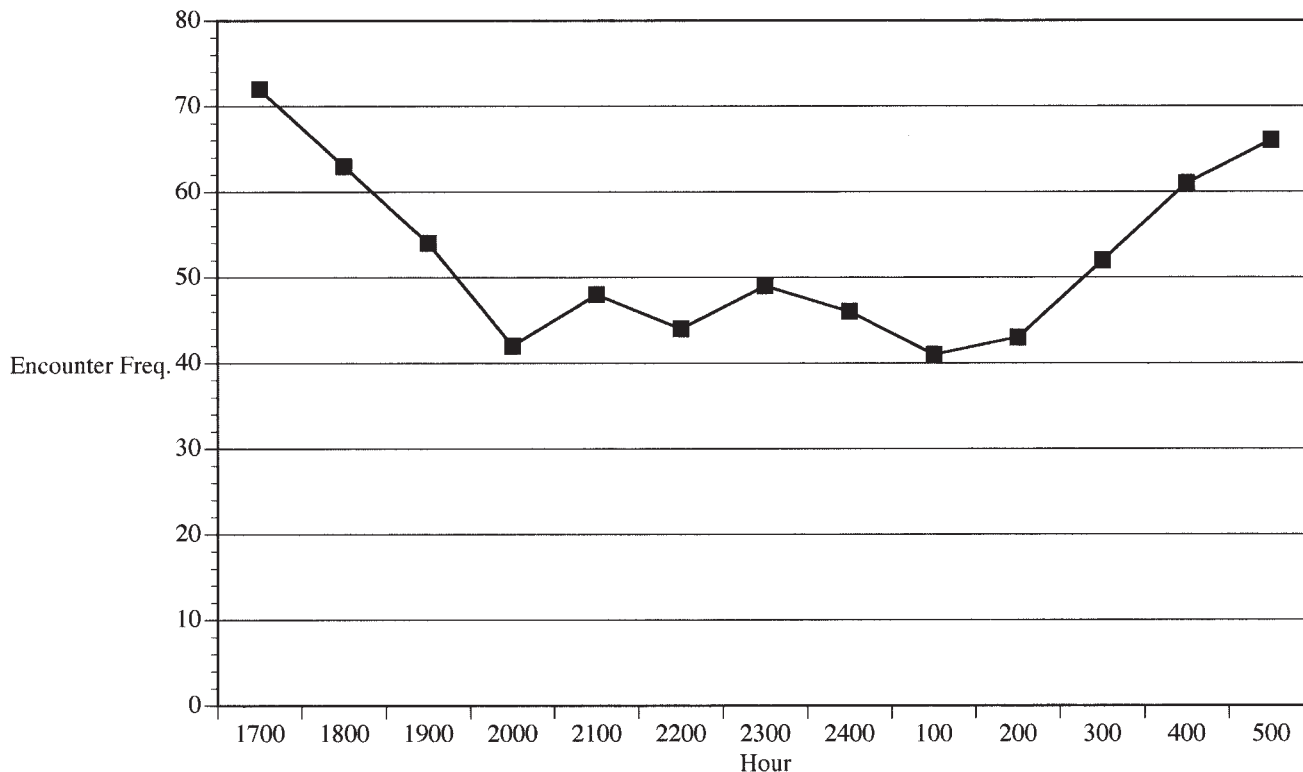


Fig. 2. Total frequency at which two adult group members encountered one another during each hour of night. Encounter is defined as less than or equal to 10 m. Equal number of observations were made during each hour of night ($n = 240$) over a total of 60 nights.

Data collection

In this study, three groups (comprised of adult male-adult female pairs with immature offspring) were observed during a 6-month study period during 1999. Prior to data collection, I spent 1 month locating, trapping, radio-collaring, and habituating these groups. Groups were initially located by the early morning vocalizations each individual tarsier emits upon returning to its sleeping site each morning (Gursky, 1997; Niemitz, 1984; MacKinnon and MacKinnon, 1980; Nietsch and Niemitz, 1992). These vocalizations are emitted for 3–5 min and can be heard from 300–400 m away. The age and sex of all group members sharing a sleeping site were recorded. Sex was determined based on the sex-specific vocal calls given by all group members (MacKinnon and MacKinnon, 1980; Niemitz, 1984; Gursky, 1997). Relative age was determined based on body size (Gursky, 1997). Mist nets were then set up at the sleeping site(s) of the study groups approximately 1 hr before dusk and were continually monitored (Bibby et al., 1992). Upon capture, individuals were placed in a cloth bag and weighed with a portable scale providing an accuracy of ± 1 g. Female reproductive condition was assessed visually and by palpating the abdomen. An SM1 radio collar (AVM Instrument Co.) weighing 4.0 g with a groove-loop was attached to the tarsier's neck by simply folding the thermoplastic band. Groups were identified ac-

ording to the location of their sleeping tree within the trail system. The three groups were thus identified as M600, M300, and L250. The radio collars were removed at the end of the study.

A radio receiver using a 151-MHz frequency and a three-element collapsible Yagi antenna were used to determine the location of each individual radio frequency. An Indonesian student assistant and I conducted instantaneous scan-sampling (Altmann, 1974). Initially, we conducted focal sampling together on a single individual until approximately 99% of the data recorded by both of us was identical. Subsequently, I collected data on the adult male in each group, while the Indonesian student assistant collected data on the adult female. Once each month thereafter, the student and I conducted an interobserver reliability test to determine if we were still consistent in our data recording. I found that our data recording was at least 98% consistent during each interobserver reliability test.

Over the course of this project, a total of 60 simultaneous focal animal sampling sessions was conducted. This yields 619 hr of simultaneous focal animal data (2,476 15-min simultaneous locational data points). A total of 1,943 simultaneous behavioral data points was also collected at 15-min intervals on each focal animal. The following behaviors were recorded: foraging, feeding, resting, traveling, and socializing (i.e., scent-marking, allogrooming,

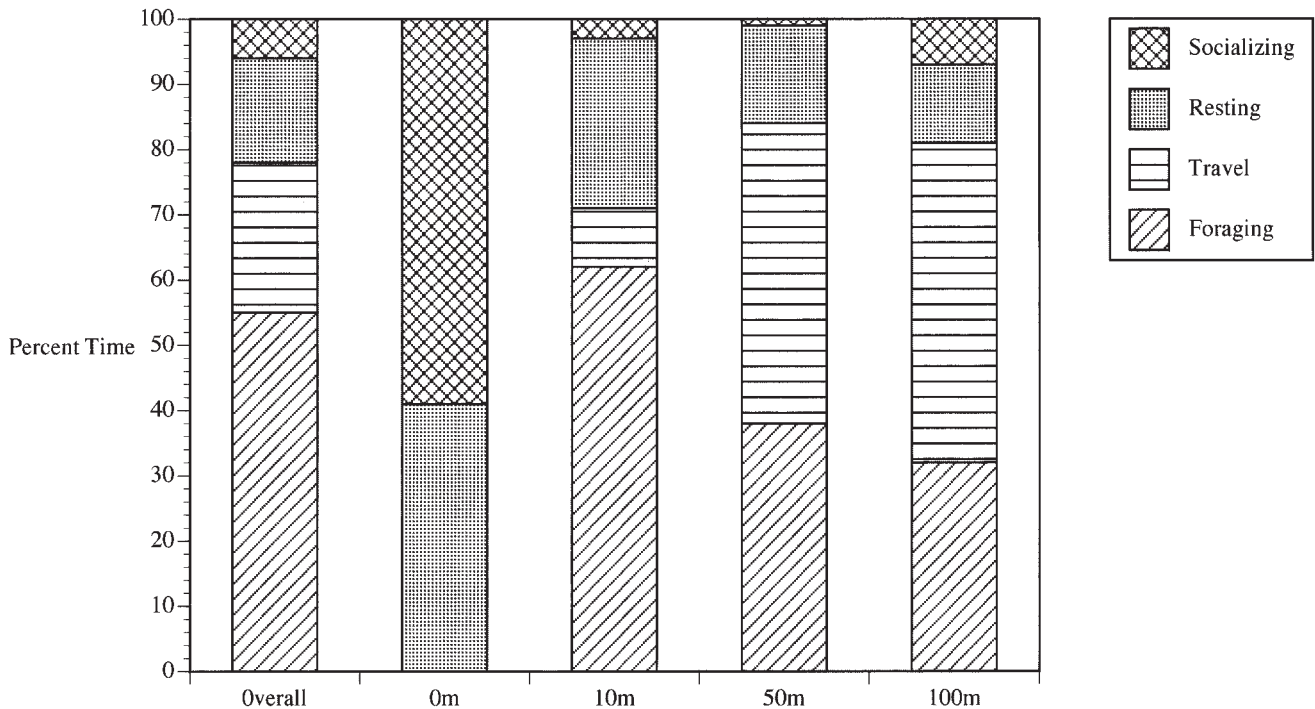


Fig. 3. Activity budget of spectral tarsiers for all distances lumped together compared with spectral tarsier's activity budget at 0 m, 10 m, 50 m, and 100 m.

playing, and vocalizing). Definitions of all behaviors recorded are presented in Gursky (1997, 1998).

Spatial locational data were also collected at 15-min intervals. The focal animal's location was marked with flagging tape, which noted the time, the individual, and the date. The next day, all flagging tapes were relocated. The actual location was measured with the aid of a compass and tape measure with reference to the 50-m trail system in the study area. Based on these locational data points, actual home range size was calculated using minimum convex polygons (Kenward, 1987; White and Garrott, 1987; Sterling et al., 2000). To determine the distance each tarsier individual traveled per unit time, I used 15-min step distances (Whitten, 1982; Altmann and Samuels, 1992; Kinnaird, 1992). Thus, distance traveled was calculated as the straight-line distance between successive 15-min locations. Nightly path length was calculated as the sum of all 15-min step distances each night.

Data analyses

Behaviors sampled at short time intervals are often autocorrelated (Janson, 1990). Thus, assuming each 5-min sample is independent would exaggerate sample size and bias the statistical analysis. I used chi-square contingency table analysis to determine if the activity budget data were autocorrelated, which they were. Therefore, data points were subsampled until they were no longer autocorrelated at the 0.05 level of significance (Sokal and Rohlf, 1981; Janson, 1990). Subsampling began at the first data

point and was continued until statistical independence was achieved. All samples for this analysis used 20-min intervals.

RESULTS

Figure 1 illustrates the frequency distribution of the observed distance between adults for each simultaneous locational data point. Approximately 28% of their nightly forays outside the sleeping tree were spent at distances from one another of less than or equal to 10 m. Almost 40% of their night was spent at less than 20 m from one another, and that includes 11% of their time which was spent in actual physical contact.

The mean number of intragroup encounters per night during this study was 11.3 (SD, 5.85; $n = 681$), where encounter is defined as distances less than or equal to 10 m. Nightly encounter frequency ranged from one encounter to more than 24 within group encounters per night. The mean duration of each intragroup encounter was approximately 13 min (SD, = 18.88, $n = 681$). There was substantial variation in the duration of intragroup encounters, ranging from less than 1 min to more than 73 min.

There was also considerable variation in encounter frequency according to hour of the night (Fig. 2). Most encounters occurred in the early hours of the night as well as during the later hours of the early morning. Encounter frequency ranged from approximately 16–25% of all observations according to the month. In June, July, and August there were 113, 124, and 131 encounters, respectively, while in

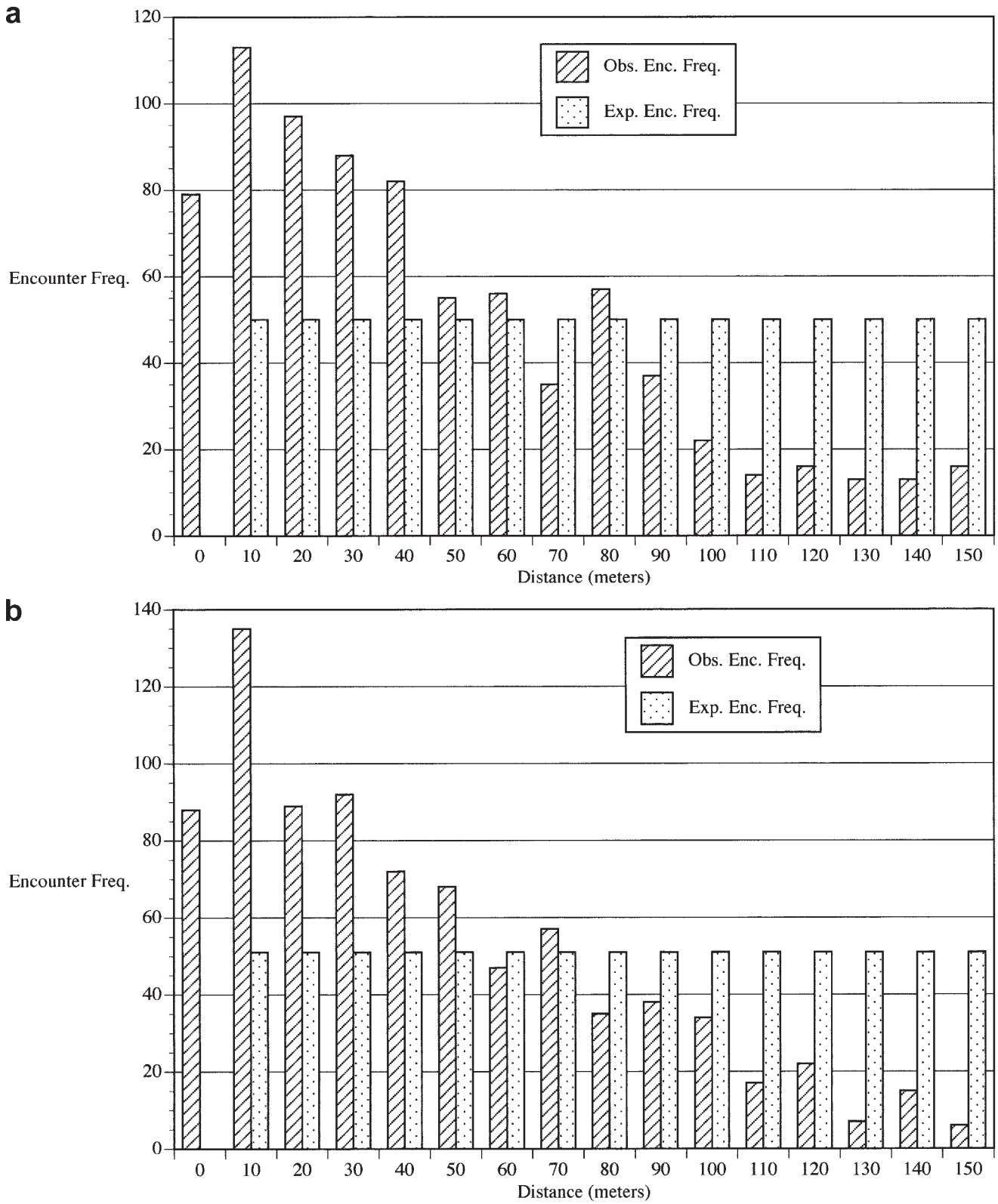


Fig. 4.

September and October there was a slight increase in encounter frequency with 146 and 167 encounters, respectively.

Overall, spectral tarsiers spent 55% of their time foraging, 23% traveling, 16% resting, and 6% socializing. However, their activity budget varied sub-

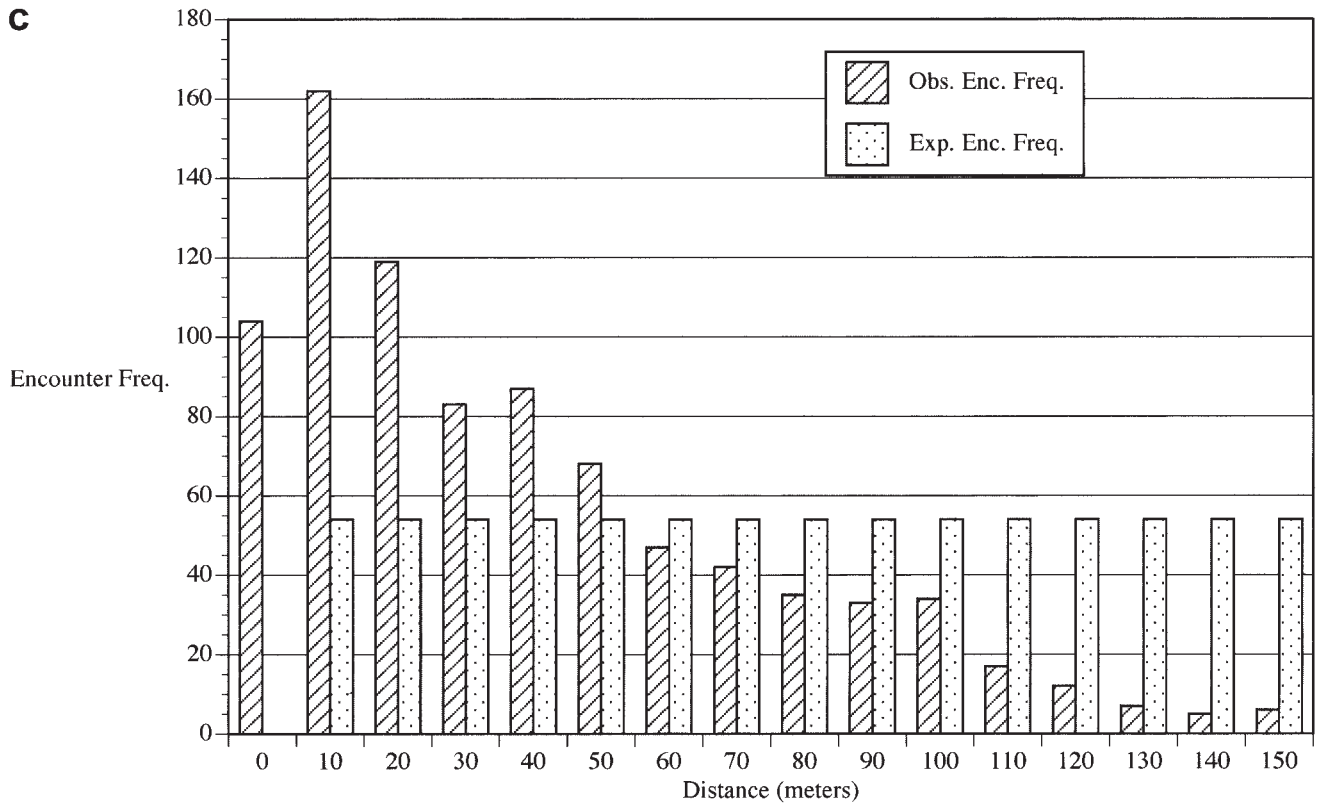


Fig. 4. a: Comparison of observed (Obs. Enc. Freq.) vs. expected encounter frequencies (Exp. Enc. Freq.) for specified distances in spectral tarsier group L250. Expected encounter frequencies were calculated using formula for Waser's random gas model and values presented in Table 1. **b:** Comparison of observed vs. expected encounter frequencies for specified distances in spectral tarsier group M300. Expected encounter frequencies were calculated using formula for Waser's random gas model and values presented in Table 1. **c:** Comparison of observed vs. expected encounter frequencies for specified distances in spectral tarsier group M600. Expected encounter frequencies were calculated using formula for Waser's random gas model and values presented in Table 1.

stantially with distance from the other adult group members (Fig. 3; $\chi^2 = 737.11$; $P = 0.0001$; $df = 9$). For example, while at 0 m the spectral tarsiers did not exhibit foraging or traveling, but spent all of their time resting and socializing. While at a distance of less than of equal to 10 m, there was a substantial increase in the amount of time allocated to foraging. Lastly, while at the furthest distances (50 and 100 m), there was an increase in the amount of time spent traveling. At the furthest distances, there was also an increase in time spent socializing.

During this study, a total of 882 insects was captured and consumed. There was a statistically significant difference in prey capture rates between males and females ($t = -19.375$; $P = 0.0001$; $df = 119$). Adult males captured 421 insects during 60 nights for a mean capture rate of 0.68 insects per hour of observation (SD, 1.56). Adult females captured 461 insects during 60 nights for a mean capture rate of 0.74 insects per hour of observation (SD, 1.67).

During approximately 277 hr while the spectral tarsiers were foraging solitary (more than 10 m from another adult group member), the adult female captured 405 insects, while the adult male captured 377 insects. Thus the mean insect capture rate while

foraging solitary was 1.46 insects per hour for the female (SD, 1.21) and 1.31 insects per hour for the male (SD, 1.32). In contrast, during the 64 hr during which spectral tarsiers were foraging gregariously (less than 10 m from another adult group member), the adult female captured 56 insects, while the adult male captured 44 insects. Thus, the mean insect capture rate while foraging gregariously was 0.875 insects per hour for the female (SD, 1.06) and 0.91 insects per hour for the adult male (SD, 0.73). Adult females while foraging solitary had a statistically significantly greater mean insect capture rate than adult females foraging gregariously ($t = 3.588$, $df = 399$, $P = 0.0040$). Adult males foraging solitary also had a statistically greater mean insect capture rate than adult males foraging gregariously ($t = 2.365$, $df = 339$, $P = 0.0186$).

The home range, p, in hectares (ha), based on a convex polygon for the male and female in group M300, was 3.48 ha and 2.23 ha, respectively. For the analysis, an average home range for this group, 2.86 ha, was calculated. The home range of the male and female in group M600 was 3.81 ha and 2.86 ha, respectively. For the analysis, an average home range for the group, 3.34 ha, was calculated. The home range of the male and female in group L250

TABLE 1. Values used in Waser's gas model

Group	p, home range size (ha)	v, mean nightly path length (km)	N, sample size
L250	3.16	0.659	40
M300	2.86	0.547	40
M600	3.34	0.747	40

was 3.61 ha and 2.71 ha, respectively. For the analysis, an average home range for the group, 3.16 ha, was calculated.

The mean nightly path length, *v*, in kilometers for the male and female in group M300 was 0.61 km and 0.48 km, respectively. For the analysis, an average nightly path length for the group of 0.545 km was calculated. The nightly path length of the male and female in group M600 was 0.81 km and 0.68 km, respectively. For the analysis, an average nightly path length for the group of 0.745 km was calculated. The nightly path length of the male and female in group L250 was 0.79 km and 0.53 km, respectively. For the analysis, an average nightly path length for the group of 0.655 km was calculated.

The expected encounter rates, if group members' movements were random and independent, *Z*, were compared with the observed encounter rates for each interindividual distance (Fig. 4). For all distances less than 50 m, spectral tarsiers encountered one another more frequently than expected by chance alone. The increase in encounter frequency is especially true at closer distances. Conversely, for distances greater than 100 m, the tarsiers encountered one another less frequently than expected by chance alone. This pattern held for each individual group, as well as when all the data overall were tested. These differences are statistically significant for each group and for the whole data set ($\chi^2 = 648.18$, $P = 0.0001$, $df = 15$).

DISCUSSION

For anthropoid primates, and more recently diurnal lemurs, sociality is often examined in terms of ecological variables such as patch size, crown size, and diameter at breast height (dbh) (Richards, 1985; Dunbar, 1988; Strier, 1999; Falk, 2000; Kappeler and Ganzhorn, 1993). When trying to understand sociality in nocturnal prosimian primates, or rather what is perceived as the lack of sociality in these prosimians, most authors have argued that the non-gregarious nature of these primates is due to their small body size and the random distribution of their resources, i.e., insects. For example, Bearder (1987) wrote that insect-eating demands a solitary foraging technique in primates. This argument is based on the idea that each individual insect is a food patch that is distributed in the forest in an erratic way. Thus, if group members foraged together, they would be in direct competition for the same resources. On the other hand, if they foraged indepen-

dently of one another, they would not be creating intragroup competition of resources.

At present there have been no observations in the literature, or during this study, of spectral tarsiers consuming fruits, leaves, or gum (Gursky, 2000; MacKinnon and MacKinnon, 1980; Niemitz, 1984). Thus, based on the above argument, i.e., the dietary strategy of this species (100% insectivory), one would predict that individual spectral tarsiers do not forage together, but rather forage solitarily. Despite this prediction, the results of this study suggest that the most predatory insectivore in the order Primates is found in proximity more frequently than expected by chance. According to Waser's random gas model, spectral tarsiers spent more time in proximity to other group members than predicted by chance, given the size of their home range and their nightly path length. This result, while demonstrating quantitatively that spectral tarsiers are not "solitary" outside of their sleeping site, does not clarify whether or not spectral tarsiers are solitary foragers.

However, additional analyses do address this issue. Firstly, the tarsiers were observed to increase the amount of time they allocated to foraging when located at less than or equal to 10 m from another adult. Secondly, individuals who were foraging in proximity to another adult had lower insect capture rates compared to individuals who were not (i.e., foraging solitarily). The decrease in foraging efficiency may be why these tarsiers increase the time they allocate to foraging when in proximity to other adults.

This result naturally begs the question: if the tarsiers are experiencing substantial intragroup competition over food resources when foraging in close proximity to another adult, then why do they continue to forage in proximity? Group living is predicted to occur only when the benefits of living in a group outweigh the costs incurred (Krebs and Davies, 1984; Kappeler and Ganzhorn, 1993; Dunbar, 1988). So, if living in a group is costly to tarsiers, then why don't they actively avoid one another while traveling throughout their territory? One possibility is that they are only foraging in proximity when the benefits of being in proximity outweigh the costs of intraspecific food competition (in the form of lower insect capture rates).

A few situations under which it might benefit them to be gregarious are: 1) when predation pressure is high; 2) when prospects of encountering potentially infanticidal males are high; and 3) when females are sexually receptive. Analyses published elsewhere (Gursky, 2002a) suggest that predation pressure by snakes may be the most likely factor selecting for tarsiers to forage in proximity to another group member. However, additional analyses are needed to understand more fully whether these tarsiers are benefiting from sociality by a reduction in predation pressure.

CONCLUSIONS

In summary, there were three intriguing results obtained during this study. First, the data suggest that spectral tarsiers are not completely solitary; they spent substantial parts of the night in association with another individual. The finding of higher rates of encounter at close distances than expected by chance, given the home range and nightly path length of this species, shows that spectral tarsiers do not behave as random gas molecules but rather as social animals, actively seeking each other out. Second, when in association with other adults, the tarsiers modified their activity patterns. Specifically, they were observed increasing the amount of foraging time when located at less than or equal to 10 m from another adult group member. The third result was that spectral tarsier individuals who were foraging in proximity to another adult had lower insect capture rates in comparison to individuals who were not (foraging solitarily). The benefits of gregariousness for the spectral tarsier may lie in reducing predation pressure, reducing the frequency of infant-icidal attempts, or increasing future mating opportunities. Additional research will help clarify which of these factors is important.

ACKNOWLEDGMENTS

The author thanks the Indonesian Institute of Sciences, the Directorate General for Nature Preservation and Forest Protection in Manado, Bitung, Tangkoko and Jakarta, SOSPOL, POLRI, the University of Indonesia, and Jatna Supriatna for their sponsorship while in Indonesia and Tigor P.N. Special thanks go to my field assistants for their help in collecting the data (Franz, Ben, Celsius, and Lende). The trapping and radio-tracking protocol was reviewed and approved by Queens College IACUC.

LITERATURE CITED

- Altmann J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227–267.
- Altmann J, Samuels A. 1992. Costs of maternal care: infant carrying in baboons. *Behav Ecol Sociobiol* 29:391–398.
- Audley-Charles M. 1981. Geological history of the region of Wallace's Line. In: Whitmore TC, editor. *Wallace's Line and plate tectonics*. Oxford: Clarendon Press.
- Bearder SK. 1999. Physical and social diversity among nocturnal primates: a new view based on long term research. *Primateology* 40:267–282.
- Bearder SK. 1987. Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts B, Cheney D, Seyfarth R, Wrangham R, Struhsaker T, editors. *Primate societies*. Chicago: University of Chicago Press. p 11–24.
- Bearder S, Martin RD. 1979. The social organization of a nocturnal primate revealed by radio-tracking. In: Amlaner D, editor. *A handbook on biotelemetry and radiotracking*. Oxford: Pergamon Press. p 140–159.
- Bibby R, Southwood T, Cairns P. 1992. *Techniques for estimating population density in birds*. New York: Academic Press.
- Charles-Dominique P. 1977. *Ecology and behavior of nocturnal primates*. New York: Columbia University Press.
- Clark A. 1985. Sociality in a nocturnal "solitary" prosimian: *Galago crassicaudatus*. *Int J Primatol* 6:581–600.
- Dunbar R. 1988. *Primate social systems*. Ithaca: Cornell University Press.
- Falk D. 2000. *Primate diversity*. New York: W.W. Norton.
- Fleagle J. 1998. *Primate adaptation and evolution*. New York: Academic Press.
- Gursky S. 1994. Infant care in the spectral tarsier, *Tarsius spectrum*: a preliminary analysis. *Int J Primatol* 15:843–853.
- Gursky SL. 1995. Group size and composition in the spectral tarsier, *Tarsius spectrum*: implications for social structure. *Trop Biodivers* 3:57–62.
- Gursky S. 1997. Modeling maternal time budgets: the impact of lactation and gestation on the behavior of the spectral tarsier, *Tarsius spectrum*. Ph.D. dissertation, SUNY-Stony Brook.
- Gursky S. 1998. The conservation status of the spectral tarsier, *Tarsius spectrum*, in Sulawesi Indonesia. *Folia Primatol (Basel)* 69:191–203.
- Gursky S. 2000. The effects of seasonality on the behavior of an insectivorous primate. *Int J Primatol* 21:477–495.
- Gursky S. 2002a. Determinants of gregariousness in the spectral tarsier (Prosimian: *Tarsius spectrum*). *J Zool* 256:401–410.
- Harcourt C. 1980. Behavioral adaptations of South African galagos. University of Witwatersrand, Johannesburg. M.Sc. thesis.
- Harcourt C, Nash L. 1986. Social organization of galagos in Kenyan coastal forests. *Galago zanzibaricus*. *Am J Primatol* 10:339–355.
- Holenweg A, Noe R, Schabel M. 1996. Waser's gas model applied to associations between Diana monkeys and colobus monkeys in Tai National Park, Ivory Coast. *Folia Primatol (Basel)* 67:125–136.
- Janson C. 1990. Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Anim Behav* 40:910–921.
- Janson C. 1992. Evolutionary ecology of primate social structure. In: Alden-Smith E, Winterhalder B, editors. *Evolutionary ecology and human behavior*. New York: Aldine. p 95–130.
- Jolly A, Rasamimanana H, Kinnaird M, O'Brien T, Crowley H, Harcourt C, Gardner S, Davidson J. 1993. Territoriality in *Lemur catta* groups during the birth season at Berenty, Madagascar. In: Kappeler P, Ganzhorn J, editors. *Lemur social systems and their ecological basis*. New York: Plenum Press. p 85–110.
- Kappeler P. 1997. Determinants of primate social organization: comparative evidence and new insights from Malagasy lemurs. *Biol Rev* 72:111–151.
- Kappeler P, Ganzhorn J. 1993. *Lemur social systems and their ecological basis*. New York: Plenum Press.
- Kenward R. 1987. *Wildlife radio tagging*. New York: Academic Press.
- Kinnaird M. 1992. Variable resource defense by the Tana River crested mangabey. *Behav Ecol Sociobiol* 31:115–122.
- Krebs J, Davies N. 1984. *Behavioral ecology*. Oxford: Blackwell Scientific.
- MacKinnon J, MacKinnon K. 1980. The behavior of wild spectral tarsiers. *Int J Primatol* 1:361–379.
- Martin RD. 1972. A preliminary field study of the lesser mouse lemur, *Microcebus murinus*. *Adv Ethol* 9:43–89.
- Mueller A. 1999. Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): inferences from body weights and trapping data. *Am J Primatol* 49:265–280.
- Musser G. 1986. The mammals of Sulawesi. In: Whitmore TC, editor. *Biogeographical evolution of the Malay Archipelago*. Oxford: Clarendon Press. p 29–41.
- Niemitz C. 1984. *The biology of tarsiers*. Stuttgart: Gustav Fischer.
- Nietsch A, Niemitz C. 1992. Indication for facultative polygamy in free ranging *Tarsius spectrum*, supported by morphometric data. *Int Primatol Soc Abstr* 1992:318.
- Richards A. 1985. *Primates in nature*. New York: Freeman.
- Rodman P. 1999. Whither primatology? The place of primates in contemporary anthropology. *Annu Rev Anthropol* 28:311–339.
- Rowe N. 1996. *A pictorial guide to the living primates*. New York: Pogonias Press.
- Sokal R, Rohlf J. 1981. *Biometry*. New York: Freeman and Co.
- Sterling E, Richard A. 1995. Social organization in the aye-ayes and the perceived distinctness of nocturnal primates. In: Alter-

- man L, Doyle G, Izard K, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Academic Press. p 439–452.
- Sterling E, Nguyen N, Fashing P. 2000. Spatial patterning in nocturnal prosimians: a review of methods and relevance to studies of sociality. *Am J Primatol* 51:3–20.
- Strier K. 1999. *Primate behavioral ecology*. New York: Allyn & Bacon.
- Warren R. 1994. *Lazy leapers: a study of the locomotor ecology of two species of a saltatory nocturnal lemur in sympatry at Ampijoroa, Madagascar*. Ph.D. thesis, University of Liverpool.
- Waser P. 1976. *Cercocebus albigena*: site attachment, avoidance and intergroup spacing. *Am Nat* 110:911–921.
- White G, Garrott R. 1987. *Analysis of wildlife radiotracking data*. New York: Academic Press.
- Whitten P. 1982. *Female reproductive strategies among vervets*. Ph.D. dissertation, Harvard University.
- Whitten T, Mustafa M, Henderson G. 1987. *The ecology of Sulawesi*. Yogyakarta: Gadjadara University Press.
- World Wildlife Fund. 1980. *Cagar Alam Gunung Tangkoko Dua Saudara Nature Reserve Sulawesi Utara management plan 1981–1986*. Bogor, Indonesia: World Wildlife Fund.
- Wright P. 1985. *Costs and benefits of nocturnality to the night monkey (Aotus)*. Ph.D. dissertation. Cuny, New York.