

Determinants of gregariousness in the spectral tarsier (Prosimian: *Tarsius spectrum*)

Sharon Gursky

Department of Anthropology, Texas A&M University, TAMU 4352, College Station, TX 77843–4352, U.S.A.

(Accepted 19 March 2001)

Abstract

Interspecific comparisons of mammals and primates suggest that the major determinants of gregarious behaviour are the distribution of food resources in space and time, predation pressure and infanticide avoidance. This study of gregarious behaviour in the spectral tarsier *Tarsius spectrum* at Tangkoko Nature Reserve, Sulawesi Indonesia suggests that all three may be important in understanding the relatively gregarious nature of spectral tarsiers. To test whether predation pressure was the major determinant of sociality for this species, I mimicked predation pressure by using predator models and playback predator vocalizations. In response to increased predation pressure from rubber models of snakes, the family group was observed mobbing the 'predator'. On the other hand, when plastic bird of prey models were placed throughout the tarsier's territory the adult group members often increased their distance from one another. No significant response was made by the spectral tarsiers in response to playbacks of predator vocalizations. To test whether infanticide avoidance was the major determinant of sociality for this species, I compared the distance between adult males and females for three reproductive phases. When adult females were lactating, adult males were observed to decrease the distance between themselves and the adult female, while the female often attempted to increase the distance. However, groups containing either a pregnant female or a non-reproductive (cycling) female did not differ in their gregariousness. To explore whether the temporal distribution of resources was the major determinant of sociality in spectral tarsiers I collected insects hourly. The diet of spectral tarsiers is restricted to insects. Distance between group members closely followed hourly and monthly changes in insect abundance. During hours when abundance was high, distance between group members decreased and vice versa. Additional long-term and more fine-grained data need to be collected to ascertain the relative importance of resources, predators and infanticide in determining sociality in the spectral tarsier.

Key words: tarsier, *Tarsius spectrum*, sociality, predation, infanticide

INTRODUCTION

Interspecific comparisons of mammals and primates suggest that the major determinants of gregarious behaviour are: (1) the distribution of food resources in space and time (i.e. patch size, renewal rate); (2) predation pressure (van Schaik & van Hooff, 1983; Krebs & Davies, 1984; Terborgh & Janson, 1986; Janson, 1992; Kappeler & Ganzhorn, 1993; Isbell, 1994); (3) reproductive condition (Wrangham, 1980; Dunbar, 1988; Gursky, 1997; van Schaik & Kappeler, 1997). For example, many studies have demonstrated that sociality, and group size in particular, often reflects food patch size (Caraco & Wolf, 1975; Kruuk, 1975; Lamprecht, 1978; Robinson, 1981; Janson, 1992). Unfortunately,

while models relating the spatial distribution of food resources (i.e. patch size) and group size have been very successful for frugivores, these models have not been particularly successful for predicting group size or gregariousness in insectivorous mammals (Waser, 1981).

Waser (1981) found that while the spatial distribution of food resources did not adequately explain the presence/absence of sociality in insectivorous viverrids, temporal distribution of resources did account for much of the variation. Specifically, Waser noted that how fast prey return to their original frequency once an animal has foraged in the area had a major effect on sociality in carnivores. For species that relied on insect prey, which return to their original frequency rapidly, the cost of social tolerance is small. Waser calculated that a mon-goose excluding a single competitor from its foraging range will only gain a 1% increase in prey density, thus

the cost of excluding a group member would not be offset by the added gains. In contrast, in species that rely on prey, which return to their original frequency slowly, the cost of social tolerance is much greater. Thus, species that have prey which return to their original frequency slowly are more likely to be solitary foragers, whereas species that have prey which return to their original frequency quickly are much more likely to live in social groups.

Other researchers have also observed changes in sociality relative to temporal changes in resource abundance. For example, many primates have been observed reducing their group size or maximizing their dispersion during the dry season in order to minimize competition (Caldecott, 1986; Boinski, 1987; Doran, 1997). Caldecott (1986) observed that the paucity of fruit during the dry season forces pig-tailed macaque groups to disperse while foraging. Doran (1997) also found similar dispersion patterns in response to seasonality with chimpanzees at Tai Forest.

Infanticide avoidance has also been hypothesized to be an important determinant of gregariousness. For example, Kappeler (1997) has suggested that male-female dyads form in some prosimians as a form of protection against infanticidal attempts by strange or neighbouring males. This hypothesis is indirectly supported by a study of the greater dwarf lemur, *Cheirogaleus major*. Ganzhorn (cited in Kappeler, 1997) observed that the proportion of gregarious *C. major* was only 13% during the mating season (September–October). In contrast, during and after the birth season (December–January), the proportion of gregarious *C. major* increased to 46%. That is, *C. major* were more gregarious during and after the birth season when there was a dependent infant in the group. This pattern of increased gregariousness during and after the birth season has also been observed in *C. medius* and reflects the fact that *C. medius* males leave torpor before females (Muller, 1998, 1999).

Reichard & Sommer (1997) and others (Palombit, 1994) have also provided some indirect evidence that infanticide avoidance may be important in the formation of gibbon groups. They found that despite intensive mate guarding by gibbon males, Reichard & Sommer (1997) report that as many as 12% of all matings were extra-pair copulations. They argue that female extra-pair copulations may be a female counter strategy to limit infanticidal attempts by neighbouring males. This may be a very important counterstrategy since they also observed extensive overlap between neighbouring group territories as well as frequent intergroup encounters.

Avoiding predation has also been argued to have a profound impact on the evolution of sociality in primates (Alexander, 1974; van Schaik *et al.*, 1983; van Schaik & van Hooft, 1983; Janson, 1992; Isbell, 1994). Large group size in diurnal primates is one factor that has been argued to afford increased protection from predation. For example, van Schaik *et al.* (1983) demonstrated that in long-tailed macaques *Macaca fascicularis*, larger groups detected approaching predators at signifi-

cantly greater distances than did smaller groups. Yet despite studies demonstrating that larger groups aid predator detection, the evidence available for actual predation events on primates remains limited (Cheney & Wrangham, 1987; Isbell, 1994). Due to the swiftness with which predation typically occurs, the probability of observing a kill is extremely low (Terborgh & Janson, 1986; Cheney & Wrangham, 1987; Alvard, 1993; Isbell, 1994; Wright, 1997). Consequently, most scientists must rely on indirect indications of predation and not on observations of the actual predation event. To overcome this limitation, numerous biologists are beginning to study the predators (Goodman, O'Connor & Langrand, 1993) with the hope of increasing the opportunities for seeing actual predation events. In addition, primatologists also use predator models in the field (Cheney & Seyfarth, 1981; van Schaik & van Noordwijk, 1989; Macedonia & Young, 1991; Chapman & Chapman, 1996) in order to mimic high predation pressure.

Recent studies of a nocturnal primate, the spectral tarsier *Tarsius spectrum*, have demonstrated that this species exhibits substantial amounts of gregariousness, relative to its sister species (*T. bancanus* and *T. syrichta*) as well as relative to other nocturnal prosimian primates (Crompton & Andau, 1986, 1987; Dagosto & Gebo, 1998). For example, not only do spectral tarsiers sleep together in small family groups (MacKinnon & MacKinnon, 1980; Nietsch & Niemitz, 1992), whereas the sister species *T. bancanus* and *T. syrichta* sleep solitarily, but adult group members of this species have also been observed to spend approximately 11% of their night activity budget in physical contact with another adult group member. An additional 17% of their nightly activity budget was spent within a radius of less than 10 m from another adult group member. These observations of encounters with other group members are not the result of chance, given the home-range size, nightly path length and travel speed of this species. Given that the spectral tarsier is gregarious, the goal of this paper is to begin to elucidate the major determinant(s) of gregarious behaviour in the spectral tarsier, by testing predictions generated from the three hypotheses: (1) temporal distribution of resources; (2) infanticide avoidance; (3) predation pressure.

If the temporal distribution of food resources is the major determinant of gregariousness in spectral tarsiers, then it is predicted that: (1) seasonal (monthly) fluctuations in resource abundance will affect their gregariousness (that is, in months when insect abundance is low, spectral tarsiers will be less gregarious compared to months when insect abundance is high); (2) hourly fluctuations in resource abundance will also affect their gregariousness. During hours when nightly abundance is high, spectral tarsiers will be more gregarious than during hours when insect abundance is low.

If infanticide avoidance tactics determines gregariousness in spectral tarsiers, then it is predicted that: (1) when females are pregnant, groups will be less gregarious than during other reproductive phases – this is because the male does not need to guard the female from

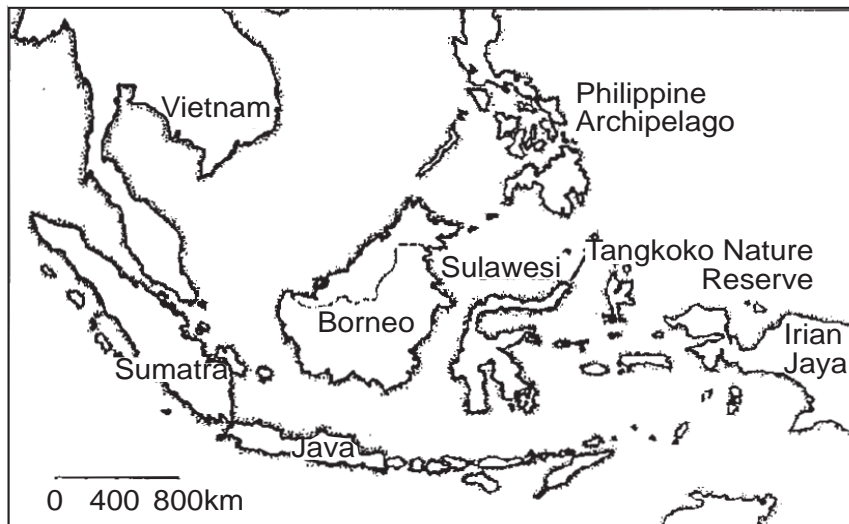


Fig. 1. Map of South-east Asia with Sulawesi and Tangkoko Nature Reserve identified.

mating with other males since she is already pregnant, nor does he need to guard the infant since it has not yet been born; (2) when females are lactating, groups will be more gregarious than during other reproductive phases since males will need to guard the parked infant from infanticidal individuals while the female forages.

If predator pressure is the critical factor in selecting for sociality in spectral tarsiers, then it is predicted that (1) on nights when the predator models are placed throughout the study group's territory, group members will be more gregarious compared to nights when the predator models are not distributed throughout the group's territory; (2) on nights when the predator vocalizations are played throughout the study group's territory, groups will be more gregarious compared to nights when the vocalizations are not distributed throughout the group's territory.

METHODS

Field site

Sulawesi (Fig. 1), formerly known as Celebes, is a four-armed island located to the east of Borneo and north-west of Australia–New Guinea (long. $125^{\circ} 14'$ east, lat. $1^{\circ} 34'$ north) (Audley-Charles, 1981). Sulawesi is the eleventh largest island in the world. It is also the largest and most central island of the biogeographical regions of Wallacea, where the Australian and Asian zoo-geographical regions meet. Sulawesi shows a blend of Asian and Australian elements in its fauna and flora, but also exhibits very high levels of local endemics. Throughout the island's protected areas, various species of the marsupial *Phalanger* live sympatrically with the primates *Macaca* and *Tarsius*. Of the 127 indigenous mammals, 79 (62%) are endemic including the spectral tarsier (Musser, 1986). Endemic species include: *Macaca nigra* (Celebes ape or black monkey); *Phalanger ursinus* (bear

cuscus); *Babyrousa babirussa* (babirusa). In comparison, the neighbouring island of Borneo, the largest Indonesian island, has only 36 endemic mammal species.

This study was conducted at Tangkoko Nature Reserve on the easternmost tip of the northern arm of the island. Based on a vegetation survey made by MacKinnon & MacKinnon (1980), the reserve exhibits a full range of floral communities from sea level coastal communities, to lowland forests, submontane forests to mossy cloud forests on the summits of Dua Saudara and the Tangkoko Crater (MacKinnon & MacKinnon, 1980; World Wildlife Fund, 1980; Gursky, 1997). Gursky (1997) quantitatively characterized the habitat within a 4 ha plot, from which 127 different tree species (all trees that were greater than 1 m in height), were identified. The most common tree species as measured by the Importance Value Index (Brower, Zar & von Ende, 1990) were: *Leea indica*, *Morinda citrifolia*, *Piper aduncum*, *Palaquium obvatum*, *Barringtonia acutangula* and *Vitex quinata* (Gursky, 1997). In the 4 ha plot, 3164 trees had a diameter at breast height (dbh) ≥ 5 cm, with a mean of 791 trees per ha. The total number of trees with a dbh ≥ 10 cm was 1727 trees, with a mean of 432 trees per ha (Gursky, 1997). The majority of the reserve has been disturbed by human influence of selective harvesting for fishing boat production and firewood. Annual rainfall at Tangkoko Nature Reserve averaged ≈ 2500 mm (Gursky, 1997).

Data collection

In this study, 3 groups (comprised of adult male/adult female pairs) were observed for a 5-month study period. One month prior to data collection I spent locating, trapping, radio-collaring and habituating groups. Groups were located from the early morning vocalizations each individual tarsier emits upon returning to its sleeping site each morning (MacKinnon

& MacKinnon, 1980; Niemitz, 1984; Nietsch & Niemitz, 1992; Gursky, 1997). These vocalizations were given for 3–5 min and were heard from 300–400 m. The age and sex of all group members sharing a sleeping site was recorded. Sex was determined, based on the sex-specific vocal calls given by all group members (MacKinnon & MacKinnon, 1980; Niemitz, 1984; Gursky, 1997). Age was determined, relatively, based on body size (Gursky, 1997). Mist nets were then set up at the sleeping site(s) of the study groups approximately 1 h before dusk and were continually monitored (Bibby, Southwood & Cairns, 1992). Upon capture, a radio transmitter weighing approximately 4 g was attached to the animal's neck. The groups were each identified according to the location of their sleeping tree within the trail system. The 3 groups were identified as M600, M300 and L250.

A radio received using 151 MHz frequency and a 3-element collapsible Yagi antenna were used to determine the location of each individual radio frequency. A field assistant and myself conducted behavioural focal follows. Initially, the assistant and I conducted focal follows together on a single individual until approximately 99% of the data recorded by both of us were the same. At this point, I felt comfortable enough with the consistency in data recording to permit the assistant to make independent focal follows. Thus, while I followed the adult male in each group, the assistant followed the adult female. Once each month thereafter, the assistant and I conducted an inter-observer reliability test to determine if we were still consistent in our data recording. Our data recording was at least 98% during each inter-observer reliability test.

Over the course of this project, 60 simultaneous full-night focal follows were conducted. This accounts for 619 h of simultaneous focal follow data or 1238 h of individual focal follow data. This amounts to 2476 15-min data points of simultaneous locational data; 1943 simultaneous behavioural data points were also collected at 15-min intervals. In addition, on 9 additional nights non-simultaneous data were obtained. Basically, data were only obtained on 1 individual for the full night and only part of the night for the other member of the male–female pair. Reasons for the non-simultaneous data collection involved numerous forms of equipment problems and failures. The non-simultaneous (part-night) data are not included in this paper.

Testing the predictions requires 4 types of data: behavioural, spatial, reproductive and environmental. Five methods of data collection (Altmann, 1974) were used to collect these data: (1) simultaneous focal follows; (2) combination of reflective flagging tape, tape measure and compass locational positions; (3) resource abundance collection (insects); (4) assessment of female reproductive phase; (5) predation experiments. Resource abundance collection and predation experiments were always conducted on separate nights to avoid potential confounding effects from the 2 types of data.

Focal follows

Simultaneous focal follows were used to record both focal individual's behaviours at 15-min intervals by the researcher with the aid of an ITT third generation nightscope, moonlight and red filtered flashlights. The following behaviours were recorded: resting, travelling, foraging, feeding, calling, allo- and auto-grooming, mobbing, marking, copulating, height in forest and locomotor style. Definitions of behaviours are presented in Gursky (1997).

Simultaneous spatial positions

Each individual's spatial position was determined at 5-min intervals using a combination of reflective flagging tape, tape measure and compass locations. During the focal follows, reflective flagging tapes noting the individual, the day and the time were attached to the substrate the focal individual was using during the scan. The following day, 2 field assistants located all flagging tapes from the previous night's focal follows and used the compass and tape measure to determine the location of each reflective flagging tape relative to the trail system in the reserve.

Resource abundance

As the diet of spectral tarsiers is restricted to insects (Gursky, 1997, 2000), 3 methods of insect sampling were used to record resource abundance: (1) sweep nets; (2) pitfall traps; (3) malaise traps (Janzen, 1973; Brower, *et al.* 1990; Muirhead-Thompson, 1991; Southwood, 1993). These 3 trapping techniques were chosen because spectral tarsiers are known to consume insects from the air and from vegetation, as well as from the ground (Gursky, 1997, 2000). On nights when hourly insect sampling was conducted, a local PHPA counterpart (Department of Forestry) and field assistant were responsible for sweeping the air and vegetation throughout the territory of each focal group with sweep nets 100 times (sweeps) each hour from dusk until dawn. Twenty pitfall traps were also placed in the ground and 2 malaise traps were distributed throughout the tarsier group's territory. The local PHPA counterpart and field assistant were responsible for collecting the insects from the pitfall and malaise traps each hour throughout the night. The contents from the sweep nets, malaise traps and pitfall traps were measured (insect length) and weighed to the nearest mg using an Ohaus digital scale. The assistants and I identified each insect to their taxonomic level of Order and then dried them to determine biomass for the sample period. Hourly insect sampling was conducted on 60 nights – 20 nights within the territory of each of the 3 focal groups. Data from the 3 sampling methods are lumped together in the analyses.

Predator models

Spectral tarsiers are small (110–130 g) and very susceptible to predation. Their main predators include: monitor lizards, snakes, civets and various birds of prey (Gursky, 1997). To test the effect of predation pressure on gregariousness in spectral tarsiers, 3 types of predator experiments were conducted during this study. Each experiment was conducted approx. every fourth night. On 15 nights, 12 rubber snakes (mimicking 4 red-tailed boa constrictors, 4 green tree snakes and 4 coral snakes) were randomly distributed throughout the home range of each group – 5 nights for each of the 3 focal groups. These snakes were relatively life-like in size and colour. The locations and positions of the predator models were changed nightly.

On 15 additional nights, plastic models of birds of prey were randomly distributed throughout the home range of each group – 5 nights for each of the 3 focal groups. The locations of the birds of prey were changed nightly. Two bird of prey models were used: owls and falcons. Although the latter is not a nocturnal bird, it does forage at dawn and dusk and is believed to be the cause of at least 1 spectral tarsier's death.

In addition, the vocalizations of nocturnal birds of prey were recorded using a Marantz tape player at a local zoo in Bitung that housed endemic birds of prey. This enabled the recording of the birds' calls without the background noise of the forest. The vocalizations of the birds of prey were played-back throughout the home range of each group – and 15-min intervals, for 5 nights for each of the 3 focal groups. The vocalizations were generally played about 10 m from either the focal female or focal male at periodic intervals throughout the night. The speakers were concealed behind a large palm leaf (*Livistonia rotundifolia*).

Physical measurements

Each animal was weighed on a digital Ohaus scale (± 0.01 g). Individuals were sexed, aged relatively (infant, juvenile subadult, adult) and reproductive status assessed (pregnant, lactating) visually and through palpation. The size of the testes was also measured using digital callipers. Females were aged relatively (nulliparous vs. primiparous) based on any distention of the mammae. In addition, numerous morphological measurements were taken to enable comparison of this population of tarsiers with measurements routinely collected on Malagasy prosimians and other tarsier species (Musser & Dagosto, 1987; Niemitz *et al.* 1991; Glander *et al.* 1992).

Two of the 3 adult females gave birth during the course of the study (late July). Therefore, samples of distance between adult males and adult females from before late July represent pregnant status for 2 females (M300 and L250). The other female was non-reproductive for the entire 5-month period (M600). The 2 months following parturition (late July through mid-

September) represented lactation for the adult females in M300 and L250. These females then became non-reproductive from late September through the end of October.

Data analyses

Behaviours sampled at short time intervals are often autocorrelated (Sokal & Rohlf, 1981; Janson, 1992). As a result, considering each sample as independent, exaggerates sample size and biases the statistical results. I performed a chi-square contingency table analysis to determine if the data collected in this study were autocorrelated (Sokal & Rohlf, 1981). Data collected at 15-min intervals were not found to be autocorrelated.

For the insect abundance analyses, hours when insect biomass was greater than the average nightly insect biomass ($x = 0.365$) were considered hours of high insect biomass. Conversely, hours when insect biomass was less than nightly average insect biomass were considered low insect biomass hours.

RESULTS

Temporal changes in resource availability

Figure 2 illustrates the mean rate of insect biomass each hour averaged for the 60 nights. The average number of insects captured was initially high during dusk (17:00 and 20:00), tapered off between 21:00 and 02:00, and then increased greatly between 03:00 and 05:00. By breaking down the night into periods of high and low insect biomass, I found that the mean distance between group members during hours when the insect abundance was high was 26.5 m (SD = 12.18, $n = 1357$ nights) whereas the mean distance between group members during hours when insect abundance was low was

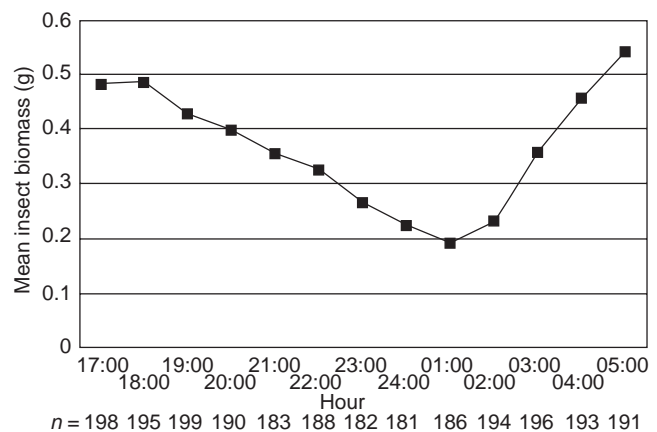


Fig. 2. The mean hourly insect biomass (g) obtained by combining the hourly insect biomass (g) from pitfall traps, malaise traps and sweep nets at Tangkoko Nature Reserve between June and October 1999.

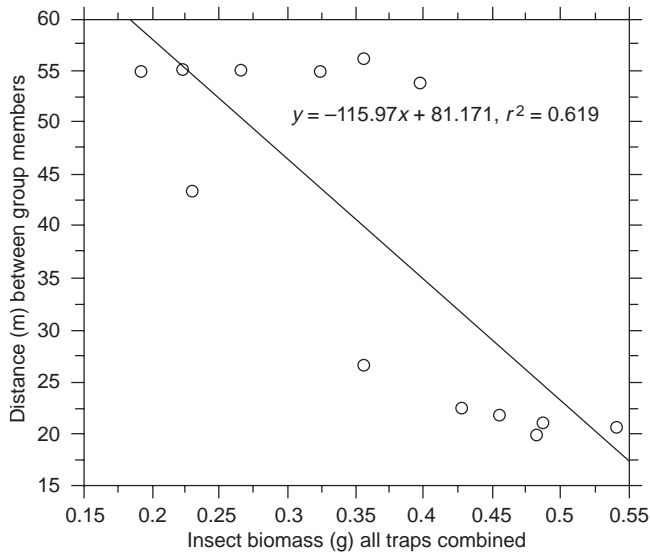


Fig. 3. Regression of the mean distance (m) between adult group members against the mean hourly insect biomass (g) obtained by combining the hourly insect biomass from pitfall traps, malaise traps and sweep nets.

Table 1. Monthly insect biomass collected at Tangkoko Nature Reserve June–October 2000

Month	Biomass (g)
June	3.15
July	3.35
August	6.18
September	6.46
October	6.58

53.218 m ($SD = 4.84$, $n = 1119$, $t = -5.008$, $P = 0.0004$, $df = 2474$). Distance between group members closely follows the hourly change in insect abundance (Fig. 3; $r^2 = 0.619$; $P = 0.0014$). That is, there was a strong negative relationship between hourly insect biomass and distance between adult group members. As hourly biomass increased, the distance between group members decreased. Similarly, as hourly biomass decreased, the distance between group members increased.

Table 1 lists the total insect biomass collected each month, demonstrating a period of high insect biomass and a period of low insect biomass. These periods correspond to the rainy and dry seasons, respectively. The mean distance between group members during months when the insect abundance was high was 28.3 m ($SD = 5.42$, $n = 1857$ scans, $n = 15$ nights) whereas the mean distance between group members during months when insect abundance was low was 54.5 m ($SD = 9.01$, $n = 619$ scans, $n = 45$ nights, $t = -4.2$, $P = 0.0246$, $df = 2474$). Figure 4 illustrates the mean distance between group members each month regressed against the mean insect biomass each month ($r^2 = 0.861$; $P = 0.0231$). There is a negative relationship between monthly insect biomass and the distance between group members.

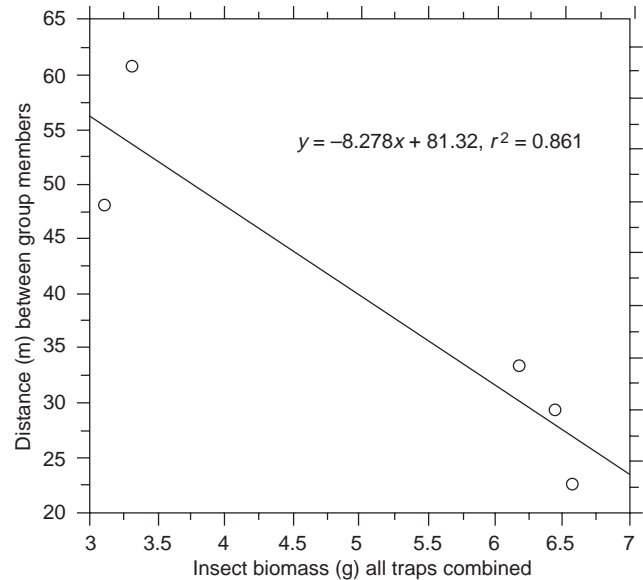


Fig. 4. Regression of the mean distance (m) between adult group members against the mean monthly insect biomass (g) obtained by combining the monthly insect biomass from pitfall traps, malaise traps and sweep nets.

Infanticide avoidance

The mean distance between the adult male and the adult female varied significantly based on female reproductive condition ($F = 21.586$; $P = 0.0001$; $df = 2474$). Females that were pregnant or non-reproductive were found at significantly greater distances from the group's adult male than the females that were lactating. The mean distance between adult group members when females were pregnant was 40.31 m ($SD = 34.67$, $n = 314$). The mean distance between the male–female pair when the female was non-reproductive (cycling) was 41.78 m ($SD = 35.86$, $n = 1266$). The mean distance between adult group members when females were lactating was 26.34 m ($SD = 18.14$, $n = 896$).

Predation pressure

The mean distance between adult group members for nights when predation pressure experiments were conducted (snake models, birds of prey models, or vocalizations of birds of prey were distributed or played back) in the focal group's territory was statistically different from the mean distance between adult group members for nights when no experiments were conducted ($F = 11.41$, $P = 0.0001$, $df = 3, 57$) (Fig. 5).

On nine of the 15 nights (60%) that the rubber snakes were placed in a group's territory, the spectral tarsiers were observed mobbing the rubber snake. Mobbing involved all group members travelling to the area of the individual who initially located the snake. Group members began vocalizing loudly, and then began

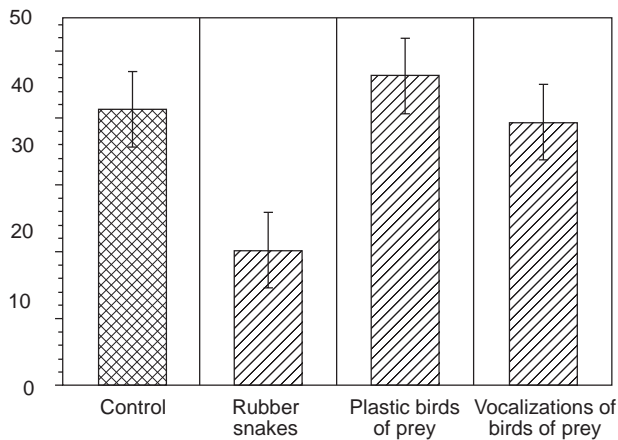


Fig. 5. Mean distance (m) between adult group members on nights when rubber snakes, plastic birds of prey, or vocalizations of birds of prey were distributed/played throughout the focal group's territory. The mean distance between adult group members when no experiments were conducted is represented by the control.

lunging and retreating at the snake. The adult females and their offspring occasionally lunged and retreated at the rubber snake (two out of nine instances, 22%), while the adult and subadult males always exhibited this behaviour (all nine instances). Individuals of all ages and sexes produced loud vocalizations. On three occasions, a spectral tarsier was observed literally biting the rubber snake! In each instance, it was the group's adult male. The spectral tarsiers did not exhibit this behaviour for rubber models of the green tree snake or the coral snake, only for the boa constrictor. The mean distance between group members on nights when no rubber snakes were present was 41.3 m ($SD = 12.98$, $n = 15$) whereas the mean distance between group members on nights when rubber snakes were distributed throughout the group's territory 20.3 m ($SD = 11.05$, $n = 15$, $t = -5.619$, $P = 0.0001$, $df = 28$). If the nine observations of mobbing are omitted from the analysis, the pattern of decreasing distance between adult group members when there are rubber snakes distributed throughout the group's territory was no longer as evident. The mean distance between group members when there were rubber snakes distributed throughout the group's territory, but no mobbing was 32.1 m ($SD = 7.04$, $n = 6$) whereas the mean distance between group members when there were no snakes distributed throughout the group's territory was 41.3 m ($SD = 14.69$, $n = 15$, $t = -1.146$, $P = 0.2659$, $df = 19$).

The spectral tarsiers also encountered three wild live snakes (all boa constrictors) while observations were taking place. On two occasions, the spectral tarsiers exhibited the same mobbing behaviour toward the live boa constrictors as that observed to the rubber boa constrictors. No noticeable change in behaviour was observed during the third live snake encounter.

When large plastic models of birds of prey were

randomly placed throughout a tarsier group's territory the response of the spectral tarsier upon encountering the model always involved giving a series of alarm calls (15 encounters out of 15 experiments). Group members did not move toward the group member giving the alarm call. Instead, they moved further away from the group member or remained where they were. The mean nightly distance between group members on nights the plastic birds of prey were distributed throughout the group's territory was 46.3 m ($SD = 15.54$, $n = 15$) whereas the mean nightly distance between group members on nights when there were no plastic bird of prey models was 32.6 m ($SD = 14.00$, $n = 45$, $t = -3.18$, $P = 0.0024$, $df = 58$).

The focal individual's response to the playback vocalizations of large nocturnal birds of prey involved alarm calling (12 out of 15 times) or increased crypsis (three out of 15 times). Increased crypsis involved moving into a darkened area, moving behind a leaf, or remaining completely still including arms or legs in mid-air in mid-stride. Once again, group members did not move toward the group member giving the alarm call. Rather, they moved further away from the group member and model birds or remained where they were. The mean distance between group members on nights when the birds of prey vocalizations were played was 39.3 m ($SD = 14.69$, $n = 15$) whereas the mean distance between group members on nights when birds of prey vocalizations were not played throughout the territory was 34.9 m ($SD = 15.71$, $n = 45$, $t = -0.934$, $P = 0.3541$, $df = 58$).

DISCUSSION

From this study to identify the determinants of sociality in the spectral tarsier, while the results are clear, the conclusions that can be drawn from them are not as clear-cut. Temporal changes in insect availability do affect, and perhaps determine, sociality in the spectral tarsiers. The distance between adult group members significantly decreased during the nightly hours when insect abundance was higher. This result suggests that there was an increase in gregariousness during hours when there were lots of insects. The spectral tarsiers are only solitary foragers when insect abundance is low and become gregarious foragers when insect abundance is high. This observation is further supported by previous analyses indicating that spectral tarsiers increase the time they allocate to foraging when only 10 m from another group member. In contrast, when group members are 50 or 100 m apart, they decrease the time allocated to foraging and increase time spent travelling.

The regression of mean distance between adult group members on insect biomass also seems to indicate that there may be some kind of threshold that insect biomass must be greater than (0.35 g/h) before the spectral tarsiers become gregarious. That is, when insect biomass was less than 0.35 g/h the average distance between adult group members was approximately 55 m.

However, when insect biomass increased over 0.35 g/h, suddenly there was a dramatic drop in the average distance between adult group members from 55 m to 20 m.

The infanticide avoidance hypothesis was also partly supported by this study. Females were located closer to the adult male during lactation compared to other reproductive phases (pregnancy and non-reproductive). Thus, they were more social when young infants were in the group than when there were no infants in the group. This raises the question concerning who was responsible for the change in distance between the male and the female? Observations suggest that the change in distance was not a co-ordinated effort by the male and female, at least initially. During the first few weeks of lactation, the female resides at a sleeping site of the group but not her normal sleeping site. This behavioural change begins several days before parturition. The male then actively tries to enter the female's new sleeping site emitting a series of vocalizations that state his intentions. The adult male is always chased away, as are all group members including previous offspring. Thus, the female is actively trying to increase distance between herself and the new baby and the rest of the group including the adult male, while the adult male and other group members are actively trying to decrease distance. Part of this may be the group member's initial curiosity about the new infant. However, there is more to this decreased distance than simple curiosity, because the curiosity and decreased distance do not end as soon as the group members become acquainted with the new infant but continue throughout the infant's entire dependency.

Although the temporal effects of the insect abundance hypothesis and the female reproductive condition hypothesis were both supported, this study was unable to untangle their confounding effects. This is because the period of time with low insect abundance was also the months when the females were pregnant. Both pregnancy and lower insect abundance were predicted and found to be in association with more distance between pairs. The best way to begin to untangle the confounding effects would be to observe the spectral tarsiers during November to January. This constitutes a time of high insect abundance (rainy season) but also represents a second birth peak in the population. Comparing groups with pregnant females during times of high insect abundance with groups with pregnant females during times of low insect abundance will help to separate out the effect of insects relative to infanticide pressure. Unfortunately, due to the short duration of this study, it did not permit data collection during this second birth peak.

The importance of predation pressure for the evolution of gregarious social systems was also observed during the study. In response to predator pressure, the spectral tarsiers spent more time together, often meeting up to try and scare away the predator. This was especially true for the male and subadult male. The females often gave alarm calls to scare away the predator but rarely lunged at the predator as did the males.

One interesting aspect of the rubber snake experiments was that the spectral tarsiers did not respond equally to all rubber snakes. Although they alarm called for all snake encounters, their mobbing response was restricted to the boa constrictors. Part of this response may be due to the much larger size of the boa constrictors compared to the green tree snake and the coral snake. The latter two snake models, although long in length (≈ 60 cm), were relatively small in diameter (≈ 7 cm). In contrast, the boa constrictor model was not only long in length (120 cm), but had a diameter > 17 cm. Thus, the boa constrictors may be more effective models due to their substantially larger size.

The spectral tarsiers response to large birds of prey was more substantial than their response to the played back vocalizations. While the spectral tarsiers did not modify their distance to other group members in response to birds of prey vocalizations, the presence of bird of prey models resulted in the spectral tarsiers increasing their crypsis and moving further away from the model and the individual who gave the initial alarm call.

The results of this study suggest that temporal changes in insects, infanticide avoidance and predation pressure are all important for the development of sociality in the spectral tarsier. However, the most obvious ecological factor affecting sociality was predation pressure by boa constrictors. Additional research using longer sample durations of changes in insect availability (> 5 months), model predators that are mobile and more detailed assessment of female reproductive condition by using hormonal assays from faecal samples will be extremely useful in determining the proportion of the variation in spectral tarsier sociality that can be accounted for by each of the proposed hypotheses.

CONCLUSIONS

Spectral tarsiers were observed to increase their gregariousness in response to temporal changes in resource availability, infanticide avoidance and increased predator pressure. Additional studies of longer duration and with larger sample sizes will help us to further understand the evolution of sociality in spectral tarsiers and in all nocturnal mammals.

Acknowledgements

Funding for this research was provided by: National Science Foundation 9817705, L.S.B. Leakey Foundation, Primate Conservation Inc., and PSC-CUNY. The author thanks the Indonesian Institute of Sciences (LIPI), the Directorate General for Nature Preservation and Forest Protection (PHPA) in Manado, Bitung, Tangkoko and Jakarta, SOSPOL, POLRI, and University of Indonesia and Jatna Supriatna for their sponsorship while in Indonesia and Tigor P.N. (UNas). The trapping and radio-tracking protocol was reviewed

and approved by Queens College IACUC. Special thanks go to my Indonesian field assistants for their help in collecting the data (Franz, Ben, Celsius). Thanks to Eric Delson (NYCEP) for his assistance in obtaining the nightscope.

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