

Lunar Philia in a Nocturnal Primate

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*The influence of moonlight on behavior has been well documented for many nocturnal mammals, including rodents, lagomorphs, badgers and bats. These studies have consistently shown that nocturnal mammals respond to bright moonlight by reducing their foraging activity, restricting their movement, and reducing their vocalizations. Lunar phobia among nocturnal mammals is generally believed to be a form of predator avoidance: numerous studies indicate that predation increases during moonlit nights. A study I conducted at Tangkoko Nature Reserve in Sulawesi, Indonesia, demonstrates that spectral tarsiers, (*Tarsius spectrum*), are not lunar phobic, but are lunar philic; they become more active during full moons. During full moons, spectral tarsiers increased foraging, decreased resting, increased travel (distance traveled per unit time, nightly path length, and home range size), increased the frequency of group travel and decreased the frequency of olfactory communication. I explore several potential hypotheses to account for the lack of lunar phobia and potential increased risk of predation resulting from this unusual behavior. Two hypotheses that may account for the behavior are that: 1) foraging efficiency increases during full moons and outweighs the increased risk of predation, and 2) predation risk is not greater during full moons. Instead, predation risk increases during new moons.*

KEY WORDS: lunar; nocturnal; primate; Indonesia; Sulawesi; *Tarsius spectrum*.

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INTRODUCTION

The influence of moonlight on behavior has been well documented for many nocturnal mammals, including rodents, lagomorphs, badgers and bats (Bowers, 1988, 1990; Butynski, 1984; Cresswell and Harris, 1988; Gilbert and Boutin, 1991; Jahoda, 1973; Kotler, 1984; Lockard and Owings, 1974; Morrison, 1978; Wolfe and Summerlin, 1989; Price *et al.* 1984), which respond to bright moonlight by reducing their use of open space, restricting their foraging activity, restricting their movement, reducing their vocalizations, reducing the duration of the activity period, or by switching their activity to darker periods of the night. For example, old field mice and snowshoe hares decrease the amount of time they spend in open areas during full moonlight (Gilbert and Boutin, 1991; Wolfe and Summerlin, 1989). Similarly, Allenby's gerbils, greater Egyptian sand gerbils, and Merriam's kangaroo rats decrease their total activity during full moons (Daly *et al.*, 1992; Kotler *et al.*, 1993). Exceptions to the lunar phobic behavioral response occur among less than a handful of bat and bird species, but do not involve lunar philia as much as lunar neutrality (Brigham and Barclay, 1992; Negraeff and Brigham, 1997).

It might be assumed that nocturnal primates, would also be lunar phobic. However, the majority of studies on the effect of moonlight on the behavior of nocturnal primates have shown that nocturnal primates are lunar philic. For example, night monkeys (*Aotus trivirgatus*) increased their activity levels during the full moon (Erkert, 1976, 1989; Erkert and Grober, 1986; Wright, 1981, 1985, 1989, 1997). The increase in activity levels during bright moonlight also occurred during artificial stimulation in captivity (Erkert, 1974, 1976; Erkert and Grober, 1986). Nash (1986) also reported that both *Otolemur crassicaudatus* and *Galago zanzibaricus* travel substantially more during full moons versus nights when moonlight is less available. *Galago zanzibaricus* also vocalized more during moonlight nights versus moonless nights.

Bearder *et al.* (2002) found similar behavioral responses to moonlight exhibited by two additional primates: *Galago moholi* and the Mysore slender loris (*Loris tardigradus*). They noted that slender lorises call more frequently when there is more moonlight (full moon) compared to moonless nights (new moon). Bearder *et al.* (2002) also noted that slender lorises increased foraging and traveled during the full moon and decreased their behavior during the new moon.

Bearder *et al.* (2002) and Martin (1980) reported that South African *Galago moholi* traveled more during moonlight. Interestingly, they only observed this pattern for adult males and not subadults or females. *Lepilemur mustelinus* calls more frequently during nights with bright moon relative

to nights with little or no moon (Charles Dominique and Hladik, 1971).

A similar behavioral pattern also occurs in a cathemeral prosimian primate. Colquhoun (1998) showed that when *Eulemur macaco* is nocturnal, they increase their activity during full moons relative to other moon phases. Specifically, black lemurs increased their calling, and the frequency of group progressions during full moons relative to nights with little or no moon.

My primary goal is to assess whether spectral tarsiers (*Tarsius spectrum*), exhibit the lunar phobic behavioral response observed in almost all other nocturnal mammals and a few nocturnal primates (slow loris, *Nycticebus coucang*; mouse lemur *Microcebus murinus* (Erkert, 1989; Trent *et al.*, 1977) or are lunar philic, increasing their activity levels during moon light. My secondary goal is to explore several hypotheses concerning why some nocturnal primates are not lunar phobic.

METHODS

Study Site

Sulawesi is a 4-armed island located to the east of Borneo and northwest of Australia-New Guinea (long. 125° 14' East, lat. 1° 34' North) (Audley-Charles, 1981). Sulawesi is the 11th 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 zoo-geographical regions meet. Sulawesi comprises 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 *Macaca* and *Tarsius*. Of the 127 indigenous mammals, 79 (62%) are endemic including, spectral tarsiers (Musser, 1986). Other endemic species include *Macaca nigra* (Celebes ape or black monkey), *Phalanger ursinus* (bear cuscus), and *Babyrousa babirussa* (babirusa). In comparison, the neighboring island of Borneo, the largest Indonesian island, has only 36 endemic mammalian species.

I conducted this study at Tangkoko Nature Reserve on the easternmost tip of the northern arm of the island. Based on a vegetation survey (MacKinnon and 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 (Gursky, 1997; MacKinnon and MacKinnon, 1980; World Wildlife Fund, 1980). Gursky (1997) quantitatively characterized the habitat within a 4-ha plot of lowland forest. I identified 127 different tree

species, which were >1 m in height). The most common tree species as measured by the Importance Value Index (Brower *et al.*, 1990) were: *Leea indica* (Leeaceae), *Morinda citrifolia* (Pubiaceae), *Piper aduncum* (Piperaceae), *Palaquium obvatum* (Sapotaceae), *Barringtonia acutangula* (Lecythidaceae), and *Vitex quinata* (Verbenaceae) (Gursky, 1997). In the 4-ha plot, the total number of trees with a diameter at breast height (dbh) ≥ 5 cm was 3,164 trees, with a mean of 791 trees per ha. The total number of trees with a dbh ≥ 10 cm was 1,727 trees, with a mean of 432 trees per ha (Gursky, 1997, 1998). The majority of the reserve has been disturbed by human influence due to selective harvesting for fishing, boat production and firewood (Gursky, 1998, 1999). Rainfall at Tangkoko Nature reserve averaged *ca.* 2300 mm (Gursky, 1997) per year and is very seasonal, with most rainfall occurring between November and April and the dry season from May through October. Some months <10 mm of rain fell. Because rainfall is so seasonal, the forest contains a large number of deciduous trees.

The main predators of spectral tarsiers include monitor lizards (*Varanus indicus*), snakes (*Python reticulatus*), Malaysian civets (*Viverra zibetha*), and various birds of prey, including falcons (*Falco sp.*) (Gursky, 1997). Although I did not conduct a quantitative survey of the abundance of predators, I noted (*ad libitum*) encounters with possible predators while conducting focal follows. For example, over the course of the study I had >15 encounters with civets. The tarsiers emitted a series of alarm calls in response to the presence of a civet. In most cases, this was how I first observed it. I observed only 1 predation event and inferred another event. The observation involved predation by a python (Gursky, 2002), and the inference involved predation by a falcon. I found a radio collar and part of the skeleton in a tree hole *ca.* 1 km away from the individual's territory and sleeping tree. The hole was visited regularly by a large bird of prey (*Falco sp.*), but it is difficult to say with certainty what animal killed the tarsier and brought it to the tree hole.

Data Collection

I observed 13 individuals from 6 groups from April 1994 until June 1995. I obtained *ca.* 605 h of observation on 8 adult females and 484 h of observation on 5 adult males. I spent 1 mo before data collection locating, trapping, radio-collaring and habituating individuals. I located subjects from the early morning vocalizations each tarsier emitted upon returning to its sleeping site each morning (Gursky, 1997; MacKinnon and MacKinnon, 1980; Niemitz, 1984; Nietsch and Niemitz, 1992). The vocalizations were given for 3–5 min and were audible from 300 to 400 m. I recorded the age and sex of all

group members sharing a sleeping site. I determined sex of subjects based on the sex-specific vocal calls given by each group member (Gursky, 1997; MacKinnon and MacKinnon, 1980; Niemitz, 1984). Relative age is based on body size (Gursky, 1997). I set up mist nets at the sleeping site(s) of the Subjects *ca.* 1 h before dusk and continually monitored them (Bibby *et al.*, 1992). I placed captives in a cloth bag and weighed them with a portable digital scale providing an accuracy of 1 g. I affixed an SM1 radio collar (AVM Instrument Co., Ltd., Livermore, CA, USA) weighing *ca.* 4 g to the Subject's neck. Capturing individuals did not require immobilization with drugs. I used a radio receiver with 151 MHz frequency and a 3 element collapsible Yagi antenna to determine the location of each individual. I observed them with the aid of an ITT 3rd generation nightscope.

An assistant and I conducted behavioral focal follows. Initially, we conducted them together on a single individual until *ca.* 99% of the data recorded were the same. At this point, we conducted independent focal follows, but once per month thereafter, I tested inter-observer reliability to determine if we were still consistent in our data recording. In these tests, our data recording was $\geq 98\%$ the same.

I recorded the focal individual's behavior at 5 min intervals (Altmann, 1974). The behaviors are recorded: foraging, resting, traveling, and socializing, *i.e.*, scent-marking, allogrooming, playing, and vocalizing, which are defined following Gursky (1997). In addition, I collected all occurrences of scent-marking, vocalizations, intra-group encounters, copulations and territorial disputes continuously and opportunistically.

I collected location data at 15-min intervals by marking them with flagging tape with the time, the individual and the date. On the following day, I plotted the flagged locations with the aid of a compass and tape measure with reference to the 50-m trail system in the study area. Based on these data, I calculated home range size via minimum convex polygons (Kenward, 1987; White and Garrott, 1987). To determine the distance individual tarsiers traveled per unit time, I used 15-min step distances (Kinnaird, 1992; Whitten, 1982). Accordingly, I calculated distance traveled as the straight line distance between successive 15-min locations. I calculated nightly path length as the total distance individuals traveled per night, a cumulative total of the 15-min step distances throughout the night.

I categorized moon phase into the following 5 phases: 1) new moon ($n = 90$) occurs when the moon's unilluminated side faces the Earth so that the moon is not visible; 2) in waxing crescent and waning crescent (herein referred to as crescent) ($n = 89$) the moon appears to be partly, but $> 50\%$, illuminated; 3) in first quarter and last quarter (herein referred to as quarter) ($n = 113$) one half of the moon appears to be illuminated; 4) in waxing gibbous and waning gibbous (herein referred to as gibbous) ($n = 119$) the

moon appears to be >50% but not fully illuminated; and 5) in full ($n = 31$) the moon's illuminated side faces Earth and the moon appears to be completely illuminated.

Data Analysis

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 auto-correlated; which they were. Therefore, I sub sampled data points until they were no longer autocorrelated at the .05 level of significance (Sokal and Rohlf, 1981; Janson, 1990). I began subsampling at the first data point and continued until statistical independence was achieved. All samples for the analysis are from 20-min intervals. I subsampled data until equal amounts of data were available for each night for each individual.

All my analyses use statistically independent samples. Previous analyses have shown that male and female spectral tarsiers exhibit different activity budgets (Gursky, 1997). Consequently, my analyses of activity patterns—% time spent foraging, home range, distance traveled and nightly path length—treat the behavior of males and females separately. I analyzed data via analyses of variance (ANOVA) for several variables—% time foraging, % time resting, number of loud calls, number of scent-marking episodes, number of territorial disputes, number of intragroup encounters, home range size, nightly path length, mean distance traveled—according to each phase of the moon.

RESULTS

The amount of time adult males and females spent foraging varied significantly according to moon phase. Males and females both increased the amount of time foraging during full moons, gibbous and quarter moons, while decreasing foraging during the other moon phases ($F = 68.348$, $P = .0001$, $df = 4, 298$, females; $F = 106.589$, $P = .0001$, $df = 4, 298$ males (Fig. 1). In contrast to the increase in foraging time, spectral tarsiers decreased the amount of time resting during full moons relative to new moons, crescent, quarter and gibbous moons ($F = 269.546$, $P = .0001$, $df = 4, 298$ females; $F = 296.626$, $P = .0001$, $df = 4, 133$ males (Fig. 2).

The ranging behavior of both the adult male and adult female spectral tarsiers also varied significantly according to moon phase. Overall, the mean distance traveled per 15-min interval are 29.2 m and 26.6 m for males and

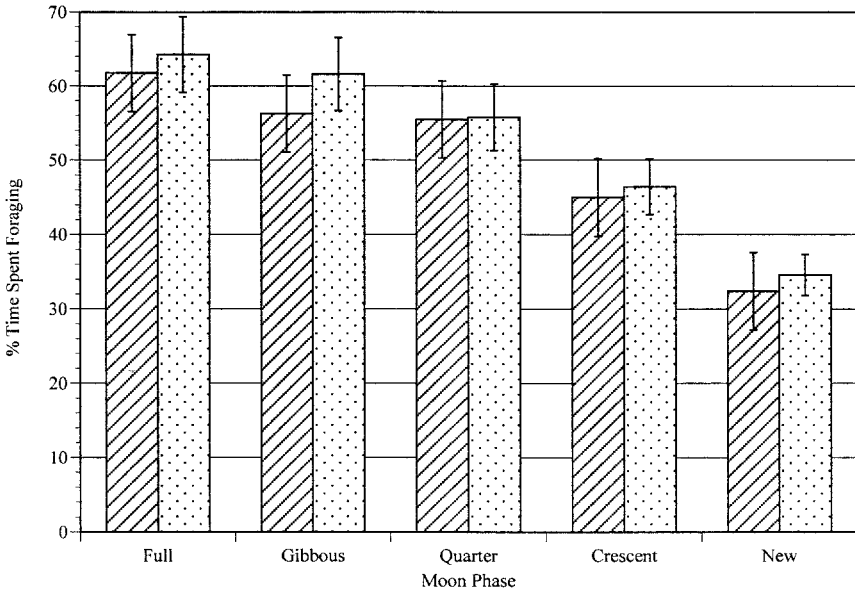


Fig. 1. The mean percent time male (diagonal lines) and female (dots) spectral tarsiers allocated to foraging during various phases of the lunar cycle.

females, respectively. During full moons, the mean distance traveled per 15-min interval by male and female spectral tarsiers was substantially greater than the mean distance traveled per 15-min interval during other moon phases (Fig. 3) ($F = 13.555, P = .0001, df = 137$ males; $F = 18.123, P = .0001, df = 303$ females).

The mean nightly path length is 790.6 m for males and 447.7 m for females. During full moons, the mean nightly path length was substantially greater than the mean nightly path length used by males and females during other moon phases (Fig. 4) ($F = 17.928, P = .0001, df = 137$ males; $F = 17.538, P = .0001, df = 303$ females).

Overall, the average home range size for males and females throughout the study is 2.32 ha for females and 3.07 ha for males. During full moons, the home range used by male and female spectral tarsiers was substantially greater than the home range used during other moon phases ($F = 29.318, P = .0001, df = 137$ males; $F = 43.762, P = .0001, df = 304$ females) (Fig. 5).

The frequency that spectral tarsiers gave loud calls also varied significantly according to moon phase ($F = 84.605, P = .0001, df = 441$). They emitted a total number of 286 loud calls over 442 nights. The mean number

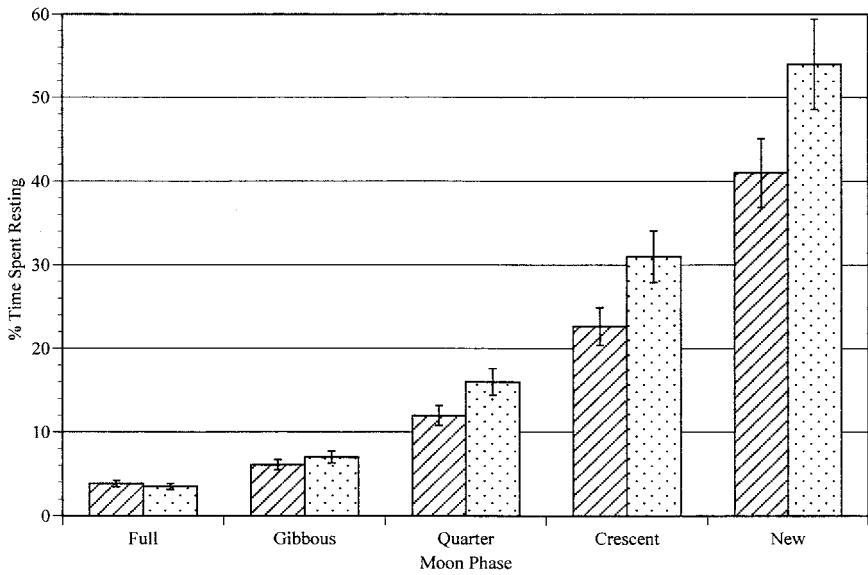


Fig. 2. The mean percent time male (diagonal lines) and female (dots) spectral tarsiers allocated to resting during various phases of the lunar cycle.

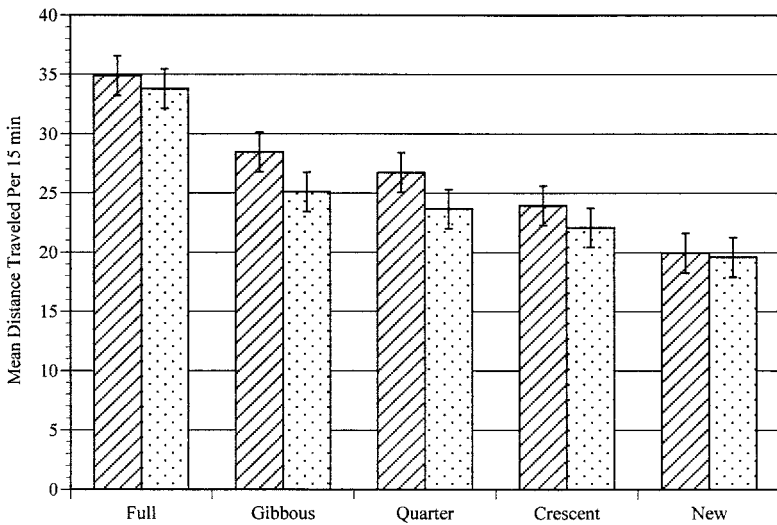


Fig. 3. The mean distance (m) traveled per 15-min interval for male (diagonal lines) and female (dots) spectral tarsiers during various phases of the lunar cycle.

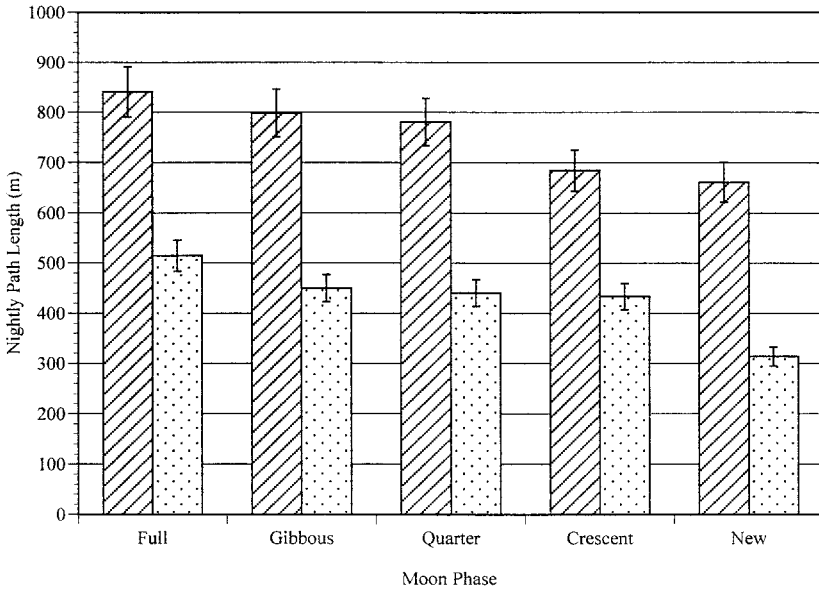


Fig. 4. The mean nightly path length (m) for male (diagonal lines) and female (dots) spectral tarsiers during various phases of the lunar cycle.

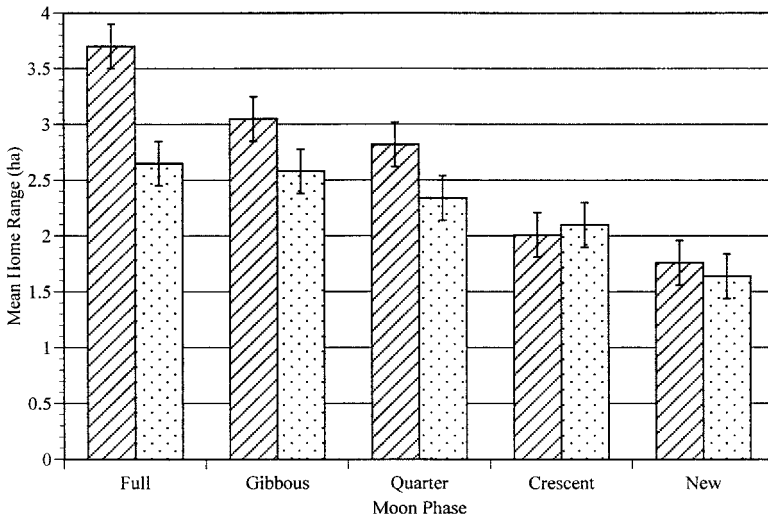


Fig. 5. The mean home range (ha) for male (diagonal lines) and female (dots) spectral tarsiers during various phases of the lunar cycle.

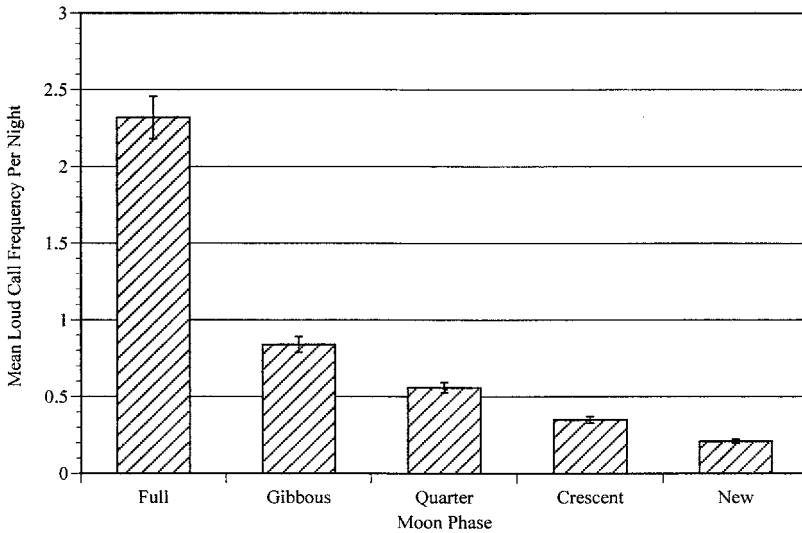


Fig. 6. The mean frequency spectral tarsiers emitted loud calls each night during various phases of the lunar cycle.

of loud calls is 0.65 loud calls per night (± 0.06). During nights when there was a full moon, the mean number of loud calls is 2.32, which is substantially greater than the mean number of loud calls given during other moon phases (Fig. 6).

Olfactory communication was also affected by moonphase ($F = 6.639$, $P = .0001$, $df = 441$). A total of 307 scent marks were made by spectral tarsiers during scan samples (excluding *ad libitum* data) over a period of 442 nights. The mean number of scent marks is 0.69 per night. During nights when there was a full moon, the mean number of scent marking episodes per night of observation is 0.32 (± 0.48), which is substantially less than the mean number of scent-marking episodes during other moon phases (Fig. 7).

I observed 243 territorial disputes. The mean number is 0.55 disputes per night. The frequency of territorial disputes varied significantly according to moon phase ($F = 12.136$, $P = .0001$, $df = 441$). During nights when there was a full moon, the mean number of territorial disputes per night is 0.89 ($\pm .32$), which is substantially greater than the mean number of territorial disputes per night during other moon phases (Fig. 8).

I observed 1072 intra-group encounters over a period of 442 nights. The mean number of intragroup encounters is 2.42 encounters per night. The frequency of encounters between group members during focal follows varied

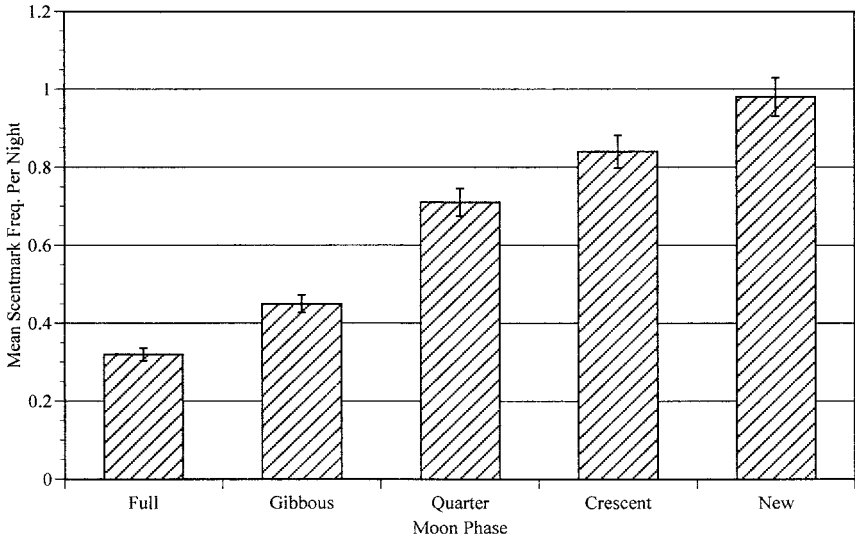


Fig. 7. The mean frequency spectral tarsiers scent-marked each night during various phases of the lunar cycle.

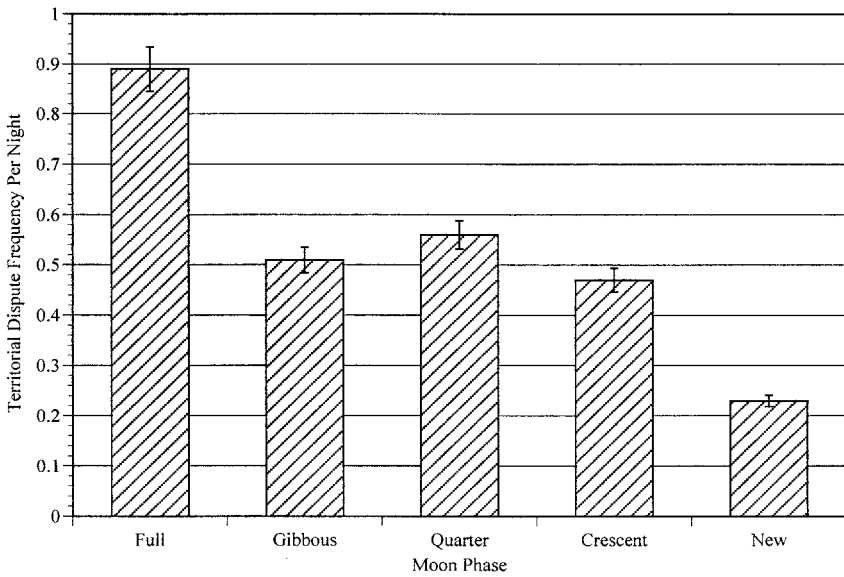


Fig. 8. The mean nightly frequency male spectral tarsiers engaged in territorial disputes during various phases of the lunar cycle.

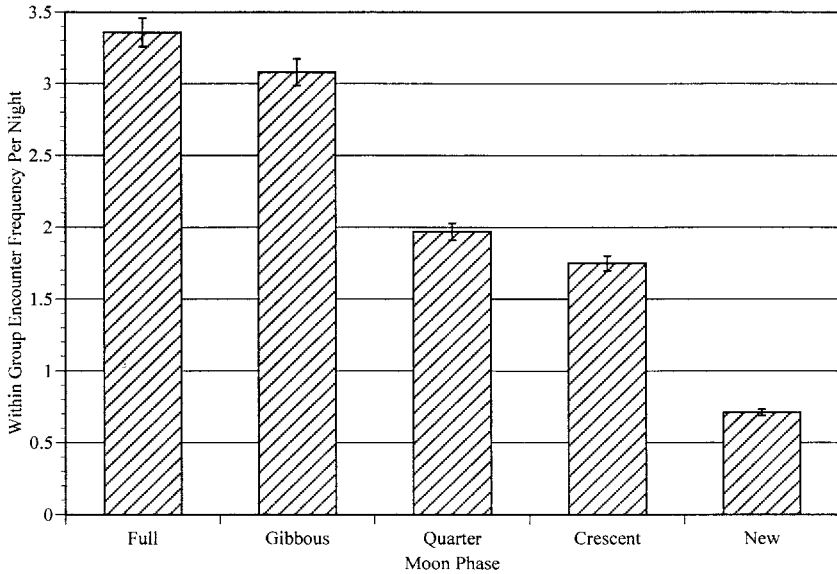


Fig. 9. The mean nightly frequency spectral tarsiers encountered another group member during various phases of the lunar cycle.

significantly according to moon phase ($F = 19.358$, $P = .0001$, $df = 441$). During full moon, the mean number of intragroup encounters per night is $3.36 (\pm 2.71)$, which is substantially greater than those during other moon phases (Fig. 9).

DISCUSSION

The spectral tarsiers substantially modified their behavior according to available moonlight. Specifically, they became more active during full moons compared to other moon phases (Erkert, 1974, 1989; Wright, 1981). This behavioral response is intriguing because the majority of nocturnal mammals are lunar phobic; they actively avoid any bright light and decrease their behavior during full moons. Lunar phobia is generally believed to be a form of predator avoidance (Bowers, 1990; Daly *et al.*, 1992; Fenton *et al.*, 1977; Kotler *et al.*, 1993; Kramer and Birney, 2001; Lockard and Owings, 1974; Morrison, 1978; Nelson, 1989; Watanuki, 1986). Specifically, it has been argued that during full moons, nocturnal animals are more easily seen and preyed upon by nocturnal and diurnal predators. For example, according to Watanuki (1986) Leach's storm-pestrels avoid moonlight to prevent being

preyed upon by slaty-backed gulls. His data indicate that the pestrels are primarily preyed upon during moonlit nights and not new moon nights. Similarly, Nelson (1989) demonstrated that for Cassin's auklet, predation risk is correlated with the lunar cycle. He found that the birds suffer heavier predation by western gulls (*Larus occidentalis*) on moonlit nights than on dark nights.

If the hypothesis is accurate, one might expect that tarsiers and other nocturnal primates increase their exposure to predators when they increase activity during full moons. The hypothesis raises two equally intriguing questions. First, are the benefits of foraging during the full moon high enough to outweigh the costs of increased predation pressure? Second, how do spectral tarsiers deal with increased predator pressure during full moons? As the goal of this study was only to determine the tarsier's response to moonlight, only limited data are available to address these questions.

In regard to the 1st question, a comparison of foraging efficiency (defined as the number of insects captured per unit time) during full moon relative to the other moon phases suggests that the benefits of foraging during the full moon are in fact tremendous. The tarsiers captured 286 insects during 90 full moon nights, which amounts to *ca.* 3.2 insects per night. Contrarily, they captured only 36 insects during 31 nights when there was no moonlight (a new moon). The numbers do not just reflect a bias in observation conditions because this pattern also occurred in terms of the numbers of insects captured in the malaise and pitfall traps and sweep nets during the different moon phases (Gursky, 1997, 2000). That is, the number of Orthopterans and Lepidopterans captured in the malaise traps during full moons was significantly greater than the number of Orthopterans and Lepidopterans captured during the other moon phases (Gursky, 1997). Thus, for spectral tarsiers the benefits of foraging during full moons are tremendous. Another possibility is that the tarsiers only increased their activity during full moons because their prey—Orthopterans and Lepidopterans—increase their activity on brightly lit nights.

Conversely, the increase in foraging efficiency during full moons may have to do with improved visual acuity. Although spectral tarsiers are presently nocturnal, historically they may have been diurnal. Unlike the majority of nocturnal mammals, including primate ones, tarsiers lack a tapetum lucidum, a reflective layer behind the eye that enhances all available light. The lack of a tapetum lucidum, in conjunction with the presence of a fovea, an anatomical feature found only in the eyes of diurnal mammals, supports this hypothesis (Castenholz, 1984; Hill, 1955; Woolard, 1925). If tarsiers are secondarily nocturnal, then the spectral tarsier's improved vision during full moon nights might account for the modified activity patterns and the tremendous improvement in foraging efficiency then.

In regards to the 2nd question, to deal with the increase in predation during full moon (when diurnal and nocturnal predators can take advantage of the additional light), spectral tarsiers modified other aspects of their behavioral repertoire. Most interestingly, they increased the frequency that group members traveled together. In particular, the frequency that any two group members were together increased substantially during full moons. The more individuals that are in a group to scan for predators, the less time each individual will have to spend in vigilance (Krebs and Davies, 1986). Living in a group can be costly in terms of intragroup foraging competition. Spectral tarsiers overcome this costly behavior by consuming insects that are abundant in moonlight.

Another possibility explanation for the lack of lunar phobia by spectral tarsiers is that full moons do not increase predation pressure for nocturnal primates. Nash (1986) suggested that the nocturnal primates are actually safer from predators during full moon than they are during new moons. Although the tarsiers and other nocturnal primates would be more easily seen during full moon, they would also be more likely to see their predators before an attack. The probability of a successful hunt is tremendously decreased if the prey becomes aware of the predator before the attack. A major distinction between primates and other mammals is their highly developed visual system (Fleagle, 1998; Martin, 1990). This emphasis on visual systems, even in primates that still rely on olfaction, makes increased moonlight attractive. Many nocturnal primates also do not use concealment to avoid predators, but instead rely on the visual sense to detect and then mob them, e.g., in some galago and tarsier species. Additional support for this paradoxical hypothesis comes from the observation of Bearder *et al.* (2002) that genets are more likely to capture *Galago moholi* when there is no moon than when there is full moon. The genets take advantage of darkness and the inability of galagos to see them during new moons, and thus, are more successful in capturing them. This hypothesis is much more parsimonious in accounting for the unusual behavior of nocturnal primates, including spectral tarsiers, during full moons.

In summary, spectral tarsiers did not exhibit lunar phobia. Instead, they increase their activity during full moon and decrease it during new moons. The increased activity during full moons may increase their exposure to predators. To counter the possible risk of predation, the spectral tarsiers increased the frequency of group travel. They also increased consumption of insects that are abundant during full moons to counter intra group competition for insects that may result from traveling in groups. It is also possible that the lack of lunar phobia in nocturnal primates may reflect the lack of correlation between lunar cycle and predation risk for these visually-oriented mammals.

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