RESEARCH ARTICLE

Social Lives of Adult Mysore Slender Lorises (Loris lydekkerianus lydekkerianus)

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Despite the persistent use of the word "solitary" to describe nocturnal primate social behavior, increasing numbers of studies are revealing sophisticated levels of social interactions among nocturnal primates. This study explores the relationships among 11 adult Mysore slender lorises (Loris lydekkerianus lydekkerianus) studied over 10_{1/2} months in Tamil Nadu, India. When all observations regarding dependent offspring are excluded, the animals spent on average 38% of their activity in various forms of neutral, affiliative, and agonistic behaviors. Affiliative behaviors were the most common type of social interaction, and males in general were more social than females. Low values for Cole's index (CI) of association emphasize that females rarely interacted with same-sex conspecifics, but commonly interacted with males. In turn, males also formed strong affiliative relationships with other adult males. This index also indicates that levels of affiliation are strongest among animals that share sleeping sites. The Hinde index (HI) suggests that males control proximity to females more than the reverse. A female's tolerance of multiple males in her home range and at a sleeping site may be related to high spatial variability of food resources. Such resources may constrain females with costly reproductive strategies (up to two sets of twins per annum) to a small home range. With their larger home ranges, males may be able to monopolize females by initiating social interactions. and also provide a benefit to females by contributing to parental care. Am. J. Primatol. 68:1171-1182, 2006. © 2006 Wiley-Liss, Inc.

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INTRODUCTION

Three factors must be considered to unravel the social organization of nocturnal primates: spacing system, mating system, and social behavior [Sterling, 1993]. Radiotracking and advances in genetic research have elucidated the first two components to a large degree in numerous taxa [e.g., Bearder & Martin, 1980; Fietz et al., 2000; Nash & Harcourt, 1986; Müller, 1999; Pimley et al., 2005a; Radespiel et al., 2001, 2002; Warren & Crompton, 1997, and it has become clear that nocturnal primates maintain spatial networks and mating systems that parallel the social organizations of diurnal primates [Müller & Thalmann, 2000]. Social behavior studies, on the other hand, have mainly concentrated on deferred olfactory and vocal communication [e.g., Ambrose, 2003; Clark, 1978, 1982; Masters, 1991; Zimmermann, 1995]. With the exception of a few excellent quantitative studies [Gursky, 2005; Pimley et al., 2005b; Schülke & Kappeler, 2003], the constraints of nocturnal field work have limited observations of social behavior. Accordingly, even though it is now accepted that nocturnal primates maintain spatial networks, many authors still view them as leading depauperate social lives [Gursky, 2005; Kappeler, 1997].

Lorises (Lorisinae) and pottos (Perodicticinae) [Groves, 2001] have been considered to be among the most solitary of the nocturnal primates, maintaining contact only during the mating season and between mother and offspring, with these interactions comprising only 2% of observations [Bearder, 1987; Charles-Dominique, 1974, 1977, 1978; Elliot & Eliot, 1967]. Recent radiotracking studies of Malay slow lorises (Nycticebus coucang coucang) and Milne-Edward's pottos (Perodicticus potto edwardsi) have undermined this perception, however, and revealed that these animals form regular social networks [Pimley et al., 2005a; Wiens & Zitzmann, 2003]. On the basis that lorises and pottos can communicate visually, via olfaction and via visual signaling at a distance of at least 20 m [Bearder et al., 2005], these studies scored interactions between individuals at 20 m as gregarious. Accordingly, adult slow lorises formed affiliations for 8% of their activity budgets, whereas pottos spent nearly 22% of observations within 20 m of a conspecific. In both taxa, animals allogroomed, played, and traveled together. Both taxa also formed sleeping associations of two (pottos) to three (lorises) adults and their dependent presumed offspring.

Slender lorises (*Loris tardigradus* and *L. lydekkerianus*) also do not fit the rule of a solitary lorisine. Field work in Sri Lanka revealed that *L. tardigradus* formed cohesive sleeping groups of up to four animals; when offspring are included, these lorises were seen together for 44% of nightly contact records [Nekaris & Bearder, 2006]. Sri Lankan *L. l. nordicus* slept in groups of up to six animals, were together for 50% of nightly activity, and once formed a group of nine animals, including infants [Nekaris, 2003b]. Observations in captivity support the notion that physical contact and grooming are essential to slender loris behavior [Rasmussen, 1986; Schulze & Meier, 1995].

In this paper I revaluate the social behavior of the Mysore slender loris (*L. l. lydekkerianus*) at Ayyalur Interface Forestry Division in India. Two studies have examined some aspects of the social behavior of this population, and both concur that lorises sleep socially in groups of up to seven animals comprised of one female, her dependent offspring, and one or more males [Nekaris, 2003a; Radhakrishna & Singh, 2001]. They both observed that females appeared to be at the core of a sleeping group's attention structure [Rasmussen, 1986], and that

females ended most grooming bouts. They also noted that males affiliated with more than one female, but neither study attempted to measure these relationships. These studies differed, however, in the quantification of social relationships. Radhakrishna and Singh [2001] narrowly defined social behavior as animals eventually coming into physical contact from a distance no greater than one tree length away, and concluded that lorises spent only 7% of observations in social behavior. About 60% of these data came from parked infants, which are parked alone most of the night and engage in limited social interactions [Radhakrishna & Singh, 2004]. I calculated activity budgets for Mysore slender lorises, defining social proximity at 5 m, but also allowed for neutral interactions whereby animals could pass near or stare at one another without physically coming into contact. I also included parked infants (comprising 34% of sample points) in the overall calculation, which indicated that animals were gregarious for 18% of their activity budget [Nekaris, 2001]. In both studies, including data from parked infants likely deflated the overall calculations of sociality.

Social behaviors related to parenting may be difficult to tease apart from those related to maintaining long-term affiliative bonds [Hinde & Atkinson, 1970; Rasmussen, 1986]. In K-selected primates, affiliation with offspring is vital and may occur over a long duration until the infant is independent of the mother [Trivers, 1985]. Dependent offspring are not chosen as social partners, and the nature of parent-offspring relationships will be mitigated chiefly by benefits in reproductive success [Trivers, 1972]. Studies of Milne-Edward's pottos [Pimley et al., 2005a], spectral tarsiers (Tarsius spectrum) [Gursky, 2005], and fork-marked lemurs (Phaner furcifer) [Schülke & Kappeler, 2003] have accounted for this by exclusively examining the social relationships of adults. This paper explores the social relationships among adult Mysore slender lorises. In particular, it seeks to address the degree and kind of social contacts that adult slender lorises maintain outside the 12 hr per day in which they sleep together. It also quantitatively explores the degree of contact and the regulation of social relationships between adults. It particularly addresses the peculiar presence of multiple adult males that were in regular contact with females.

MATERIALS AND METHODS

From 1997 to 1998 I conducted a socioecological study of the Mysore slender loris (*Loris lydekkerianus lydekkerianus*) over $10_{1/2}$ months in the Beerangi Karadu hill range of Ayyalur Interface Forestry Division, Dindigul District, Tamil Nadu, South India. I previously described this dry scrub forest in detail [Nekaris, 2001, 2003a].

Social behavior was recorded with both all-occurrences sampling and instantaneous point samples taken at 5-min intervals, yielding 7,591 sample points [Nekaris, 2001]. If more than one animal was present within 20 m of the focal animal, a scan was taken for each animal [Martin & Bateson, 1993]. The average follow time was $6.2\pm3.2\,\mathrm{hr}$, and the mode was $10.5\,\mathrm{hr}$ (n = 149 nights); 57% of all observation sessions were 7 or more hours long; and 38% of all sessions concluded with an animal being followed to its sleeping site [Nekaris, 2003a]. Social interactions were divided into three categories: neutral, affiliative, or agonistic [Clark, 1985] (Table I). Vocalizations [c.f., Schulze & Meier, 1995] were considered only if a focal animal uttered calls to a visible receiver. Olfactory

TABLE I. Definitions of Three Different Social Categories and Their Associated Behaviours Used to Describe Gregarious Behaviors Among Slender Lorises

Social category	Associated behavior
Neutral	Mutual proximity less than or equal to 20 m; pass by one another with or without brief pausing or glancing
Affiliative	Allogrooming, play wrestling, play face, facial contact, sniffing, licking, foraging or traveling together in the same or adjacent tree, appeasing vocalizations, copulation
Agonistic	Fighting, cuffing, aggressive whistling, submissive whistling, grappling, pushing another loris out of the tree, "female dominance" (female pushing male away during interactions or vocalizing)

behaviors were mostly deferred and were considered only if a loris scent-marked a conspecific.

The data were obtained only from identified animals that were no longer suckling. This included five adult females, one subadult female, six adult males, and one subadult male. The identification of animals and their age classes are described in detail elsewhere [Nekaris, 2001, 2003a]. Data were collected from the time when the animals awoke at dusk until dawn, just before they no longer were visibly moving.

The total social time for each individual was analyzed as the proportion of the total observed sample points in which animals were within 20 m of one another [Pimley et al., 2005; Schülke & Kappeler, 2003]. Superb visibility in the open scrub jungle meant it was usually possible to see animals beyond the 20-m cutoff. To take into account the various amounts of time spent observing different individuals, percentages were calculated for each individual loris and then averaged for all females, all males, and all animals [Martin & Bateson, 1993].

Bearder and Martin [1980] and Pimley et al. [2005] pointed out that in less socially active animals the degree of contact, even when the animals are in proximity but not overtly interacting, can be a measure of sociality or gregariousness. Following their studies, I estimated the degree of contact between individuals using Cole's index (CI) of association [Cole, 1949]. In the equation a = 2N/(n1+n2), N is the number of times animals were seen together within 20 m, and (n1+n2) signifies the number of times lorises 1 and 2 were observed during the study. A value of 1.0 indicates that animals were always together, with time together decreasing as this value approaches 0.

To explore the social relationships between pairs with a relatively high CI (≥ 0.05), I calculated the Hinde index (HI) from all-occurrences social behavior data, when animals came within one body length of one another and proceeded to touch each other. This index is useful for elucidating which member of a dyad controls the maintenance of mutual proximity between the members by measuring their relative roles in making and breaking proximity [Hinde & Atkinson, 1970]. I employed the equation $[U_A/(U_A+U_B)]-[S_A/(S_A+S_B)]$, where $U_A=$ number of occasions when the pair were united by A's movements; $U_B=$ number of occasions when the pair were united by B's movements; $S_A=$ number of occasions when the pair were separated by A's movements; and $S_B=$ number of occasions when the pair were separated by B's movements. When the animals were in a group of three or more, I analyzed the behavior of each dyad in the group separately. Descriptive statistics, including standard deviations (SDs),

and Mann-Whitney U-tests were generated with SPSS v11.0 or by hand, with significance set at 0.05.

RESULTS

Amount of Activity Budget Dedicated to Social Behavior

The proportion of sample points lorises spent in association with others in the three social categories is presented in Table II. When all 13 animals are considered, they were seen with one or more non-infant lorises 38% of the time. Lorises of both sexes engaged in all three types of social behavior, and the levels of neutral (Mann-Whitney U=23, P=0.451), affiliative (Mann-Whitney U=20, P>0.531), and agonistic (Mann-Whitney U=20, P=0.31) behaviors did not differ between the sexes. Although there was a trend for males (53%, n=7) to engage in social behavior more than females (28%, n=6), this was not significant (Mann-Whitney U=9, P=0.09). Affiliative behavior (61%, n=13) was the most commonly exhibited social behavior.

Types of Social Behavior

Social interactions between known adults were observed 981 times during all-occurrences sampling. The most common social activity (31%, n=300) involved members of a sleep group playing, grooming, huddling, and scrambling over one another before either going off to forage alone or in pairs or trios, or to sleep in a collective "sleeping ball." The other 69% (n=681) of interactions occurred throughout the night, and are detailed in Figs. 1, 2 (also Table I). Social

TABLE II. The Total Number of Sample Points Collected for Each Focal Animal, Followed by the Proportion of Its Activity Budget Spent Within $20\,\mathrm{m}$ of a Conspecific*

Loris	Total points	All social	Neutral	Affiliative	Agonistic
Females	4918				
Titania (Ti) ¹	2348	11% (n = 259)	18% (n = 46)	74% (n = 192)	8% (n = 21)
Morgaine (Mo) ²	1627	24% (n = 387)	18% (n = 68)	80% (n = 311)	2% (n = 8)
Ygraine (Yg) ³	413	37% (n = 152)	16% (n = 25)	82% (n = 124)	2% (n = 3)
Halva (Ha)	142	20% (n = 29)	7% (n = 2)	69% (n = 20)	24% (n = 7)
Fanny (Fa)	78	$42\% \ (n = 33)$	100% (n = 33)		
Ophelia (Op) ³	310	31% (n = 97)	19% (n = 18)	$78\% \ (n = 76)$	3% (n = 3)
Female average	n = 6	$28\pm11\%$	$30\pm35\%$	$64\pm32\%$	$7\pm 9\%$
Males	2673				
Donald (Do) ¹	781	35% (n = 274)	14% (n = 39)	75% (n = 206)	11% (n = 29)
Mickey (Mi)	140	21% (n = 30)		7% (n = 2)	93% (n = 28)
Billie (Bi) ^{1,2}	352	67% (n = 237)	7% (n = 17)	93% (n = 220)	
Sudden (Su) ³	343	31% (n = 107)	28% (n = 30)	$71\% \ (n = 76)$	1% (n = 1)
$Vladomir (VI)^2$	312	64% (n = 199)	21% (n = 42)	79% (n = 157)	
Arcadio (Ar)	17	100% (n = 17)	100% (n = 17)		
Scary $(Sc)^2$	728	50% (n = 363)	14% (n = 52)	85% (n = 310)	1% (n = 1)
Male average	n = 7	$53\pm27\%$	$26\pm34\%$	$59\pm38\%$	$15\pm35\%$
All loris average	n = 13	$38\pm25\%$	$28\pm33\%$	$61\pm34\%$	$11\pm26\%$

^{*}Superscripts indicate animals that formed one of three sleeping groups [Nekaris, 2003a]. The third through sixth columns break down social behaviors sample points into three categories. Social behavior could occur simultaneously with other activities, such as foraging, traveling, or resting.

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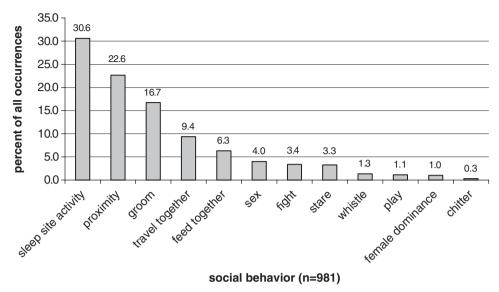


Fig. 1. This figure breaks down 981 social interactions between two to four adult Mysore slender lorises into specific types of social behavior.

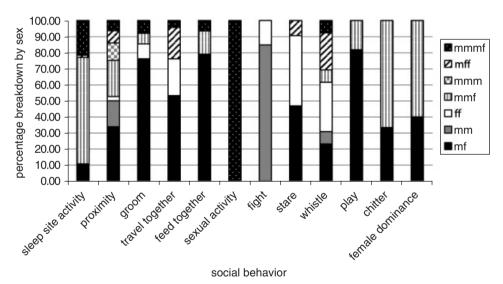


Fig. 2. This figure elucidates to what extent pairs, trios, or groups of four lorises participated in each type of social behavior. Males and females are represented by "m" and "f," respectively, in the key.

behaviors involved two to four adult animals, and often involved one to two infants [Nekaris, 2003b]. Pairs (50.2%, n=492) consisted of a single male and female (n=362), two males (n=65), and two females (n=65). Trios (35.6%, n=349) consisted of three males (n=24), two males and a female (n=280), and two females and a male (n=45). Three males and a female also formed groups (14.3%, n=140). The average number of non-infants involved in a social activity was 2.64 ± 0.72 .

CI of Association

Figure 3 is a sociogram based on the CI of association for every dyad with a CI>0.01. The average value was 0.075 ± 0.098 (n = 40 pairs), and values ranged from <0.001 to 0.34. Lorises with a CI <0.01 were infrequent social partners. Their associations consisted of fighting (e.g., Titania and Halva), grooming (e.g., Ophelia and Donald), and a female cuffing a male (e.g., Morgaine and Sudden). Animals with values >0.01 but <0.05 were in more frequent contact, but observations of the dyads were interrupted for various reasons (the female Ophelia migrated when she reached sexual maturity, the male Donald disappeared, and the female Halva also migrated). Animals with CI values >0.05 were in frequent contact throughout the night (Fig. 3). In general, animals with the highest CI were also members of the same sleeping groups (Table I) [Nekaris, 2003a], and engaged in social behavior throughout the night. It should be noted that data collection ceased when the animals were asleep, but social contact among these group members continued throughout the diurnal cycle.

HI

To explore the social relationships between pairs that were in more frequent contact (CI>0.05), I calculated the HI (Table III). Of the 981 social occurrences, only 141 observations were clear enough to ascertain who initiated and who ended an interaction. In all male/female dyads, the males were responsible for maintaining proximity. Males usually initiated social contact by sniffing the muzzle or anogenital region of the female. Females usually ended the social contact by moving away from the male or cuffing him. In the case of male dyads,

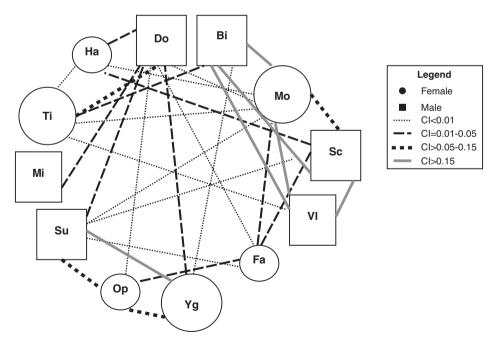


Fig. 3. Associations among lorises according to the CI. Larger circles represent the main study females that were at the core of the sleeping groups; smaller circles represent females that migrated. Stronger interactions are clearly present within sleeping groups.

	U_{A}	U_{B}	S_A	S_{B}	Hinde index
Sc(M):VI(M)	10	7	8	9	0.12
Sc(M):Bi(M)	9	5	9	5	0
VI(M):Bi(M)	6	3	1	8	0.55
Mo(F):Sc(M)	25	12	29	8	-0.11
Mo(F):Bi(M)	12	6	15	3	-0.17
Mo(F):VI(M)	10	4	12	2	-0.15
Ti(F):Bi(M)	3	8	7	4	-0.36
Yg(F):Su(M)	4	8	10	2	-0.50
Ti(F):Do(M)	1	8	7	2	-0.66

^{*}For each pair, the first animal in the pair is "A'" and the second is "B", "F" indicates females and "M" indicates males. An Index nearer to-1.0 indicates that B is responsible for maintaining proximity; an index nearer to +1.0 indicates that A is totally responsible; a value of 0 suggests that the partners are equally responsible for maintaining proximity [Martin & Bateson, 1993].

an equal or nearly equal relationship existed between Vladimir and Scary, and between Scary and Billie, in that contacts were initiated equally between individuals. Vladimir and Billie, who were seen to feed and travel together and who also regularly slept together and groomed at their sleeping site, showed the highest HI among the males.

DISCUSSION

It is clearly no longer appropriate to envision a strict dichotomy between nocturnal and diurnal primates as "solitary" vs. "gregarious" [Kappeler & van Schaik, 2002]. Studies of carnivore social organization reiterate that supposedly solitary species often display a different continuum of behavior compared to animals that are indeed usually alone, and those that interact at greater levels [Caro, 1994; Lee, 1994]. Uncovering the variables that influence this greater level of interaction may also help us understand the evolution of permanent gregarious social groups [Kays & Gittleman, 2001].

The Mysore slender lorises in this study interacted throughout the night and slept together in the daytime [Nekaris, 2001, 2003a]. Females, whose home ranges are almost exclusive of each other's [Nekaris, 2003a], engaged in few interactions; with the exception of mothers and subadult daughters, all interactions were neutral or agonistic. Although females interacted with several males, they showed the highest affiliation with males with which they shared a sleeping site.

Males, whose ranges are nearly twice the size of females' ranges [Nekaris, 2003a], behaved aggressively only toward males from outside their sleeping group. They showed high levels of positive interaction with males with which they shared a sleeping site. These males also interacted with infants at the sleeping site throughout the night [Nekaris, 2003b]. Because of their larger ranges, males were more difficult to follow than females in the absence of radio collars; thus, the higher rates of social behavior in part may reflect the greater detectability of males when they were with a partner. However, an ongoing radiotracking study of red slender lorises (*L. t. tardigradus*) in Sri Lanka is revealing similar patterns of male social behavior, providing support to the observations made here (Nekaris, personal observation).

Although all males engaged in gregarious behavior, some males (e.g., Billie and Donald) interacted more with adult females. It was noted during the study

that these males were superficially larger; however, the ages and relationships of the males could not be ascertained. Previous studies of other slender loris taxa (L. l. malabaricus and L. t. tardigradus) noted behavioral differentiation between dominant large-bodied alpha males and smaller beta or satellite males [Kar Gupta & Nash, 2005; Nekaris & Jaywardene, 2003]. The dominance relations among these males closely mirror those exhibited by some bushbabies [Bearder, 1987]. Should handling of animals be permitted in future studies of Mysore slender lorises, quantitative morphological data may further distinguish different "classes" of males.

Of the three sleeping groups observed, only one contained multiple males, whereas the others contained an adult male, adult female, and her offspring [Nekaris, 2003a]. Data from other sites indicate that multiple males sharing a sleeping site with a single female is a frequent occurrence, and thus appears to characterize slender loris social behavior [Kar Gupta & Nash, 2005; Nekaris & Jaywardene, 2003].

Affiliative male associations are not as rare among nocturnal mammals as previously thought. Studies of raccoons (*Procyon lotor*), kinkajous (*Potos flavus*), slender mongooses (*Herpestes sanguineus*), and cheetahs (*Acinonyx jubatus*) have uncovered relationships not unlike those exhibited by lorises [Caro, 1994; Gehrt & Fritzell, 1998; Kays & Gittleman, 2001; Waser et al., 1994]. Among primates, aye-ayes (*Daubentonia madagascariensis*) display a similar social organization, although group members maintain cohesion by vocalizations [Sterling & Richard, 1995].

Various hypotheses attempt to explain why some nocturnal mammals form larger groups, particularly by tolerating additional males. Both nocturnal and diurnal primates may include additional males in their groups as a response to predation pressure [Gursky, 2005; Hill & Dunbar, 1998; Janson & Goldsmith, 1995; van Schaik & Hörstermann, 1994]. Slender lorises, however, rarely show outward signs of alarm toward potential predators, which suggests that other mechanisms may provide better defense than increased group size [Bearder et al., 2002; Nekaris et al., in press].

A more tenable hypothesis might be the resource dispersion hypothesis, which asserts that a species must be able to defend a resource throughout the year, and that the resource must be distributed in patches over space and time [Bacon et al., 1991; Carr & Macdonald, 1986]. In this view, home-range size is determined by the spatial and temporal variability of a resource rather than the minimum home-range size. In this manner, an additional male may share a home range without negatively affecting a female's food availability. In fact, the cost to females of ousting males may be greater than that incurred by allowing them to share food resources [Kays & Gittleman, 2001]. This hypothesis has received support from studies of thick-tailed bushbabies (Otolemur crassicaudatus) and spectral tarsiers (Tarsius spectrum), which are relatively gregarious and rely on temporally available patchy resources [Clark, 1985; Gursky, 2000; Harcourt, 1986]. Conversely, when resources are rare or when within-group scramble competition might deplete resources, woolly lemurs (Avahi occidentalis) and forkmarked lemurs (*Phaner furcifer*) may be constrained to minimize their group size to pairs [Schülke, 2005; Schülke & Kappeler, 2003; Thalmann, 2001].

The slender lorises at Ayyalur are almost exclusively insectivorous, relying on insects that occur in renewable colonies, and occasionally consuming gum, a discrete renewable resource that is highly abundant at the study site [Nekaris & Rasmussen, 2003]. Although the animals usually foraged alone, they also foraged peacefully together during 6% of social observations. No disputes over food were

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observed, which suggests limited competition, and the wide dispersion of food resources suggests that they would be difficult to defend [Nekaris & Rasmussen, 2003]. Thus, in contrast to *Avahi* and *Phaner*, food availability appears to be an unlikely constraint on group size.

Despite food abundance, loris females face additional energetic constraints. Slender loris females may give birth to two sets of twins per annum [Izard & Rasmussen, 1985; Nekaris, 2003b]. The high costs of reproduction may constrain females, who defend a smaller home range than males. These small home ranges may allow more than one male to monopolize the entire range of one female, while still maintaining "checks" on females in neighboring ranges. This is particularly the case with males with the largest home ranges. Although such males formed the strongest relationships with the females with which they slept the most, they occasionally engaged in affiliative interactions with females in neighboring ranges [Nekaris, 2003a]. Such behavior has also been seen in a number of bushbaby and lemur taxa [Bearder, 1987; Nash, 2005], and has been particularly well studied in carnivores [Caro, 1994; Gehrt & Fritzell, 1998; Kays & Gittleman, 2001; Waser et al., 1994]. The unusual additional behavior of males "checking up" on and socializing with infants throughout the night may actually confer an advantage to females [Nekaris, 2003b].

This study shows that at this study site, Mysore slender lorises engage in regular social interactions more than either pottos or lesser slow lorises [Pimley et al., 2005; Wiens & Zitzmann, 2003]. Future studies of Mysore slender lorises would benefit from estimating the seasonal availability of food to different sleeping groups, and correlating that information with group size.

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