

Spacing System of the Mysore Slender Loris (*Loris lydekkerianus lydekkerianus*)

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ABSTRACT *Loris lydekkerianus lydekkerianus* has been shown to have a promiscuous copulatory pattern, to maintain social networks via frequent loud calls, to interact socially throughout the night with all age classes, and to sleep socially. Though these behaviors point towards a multimale social system, no study of their spacing system has yet been provided to support this view. From October 1997–August 1998, I conducted a study of the Mysore slender loris in Ayyalur, India. During 1,400 field hours, data were collected on range use of 3 adult females, 3 adult males, 1 subadult female, and 1 subadult male. Lorises slept in groups averaging 4 individuals, composed of an adult female, her offspring, and 1–2 adult and subadult males. Sleeping sites for three groups were lo-

cated within 1.9 ha in the center of the study area. The minimum convex polygon in hectares encompassing each animal's range was determined, as well as overlap among home ranges of individual lorises. Average home range sizes were: adult males, 3.6 ha \pm 0.09; subadult/smaller males, 1.17 ha \pm 0.26; and adult and subadult females, 1.59 ha \pm 0.24. Male ranges overlapped with at least 2–3 other adult males (0.72 ha \pm 0.23). Female ranges overlapped slightly with at least 2 other female ranges (0.22 ha \pm 0.25). Male ranges overlapped those of at least 3 females (0.82 ha \pm 0.51). Patterns of home range and sleeping site support previous suggestions of a multimale social system, similar to aye ayes and some galagos. *Am J Phys Anthropol* 121:86–96, 2003. © 2003 Wiley-Liss, Inc.

The slender loris (genus *Loris*) is a small nocturnal prosimian primate endemic to Sri Lanka and South India. Only recently have we begun to understand its behavior and ecology in the wild (Kar Gupta, 1995; Nekaris, 2000, 2001a,b, 2002; Radhakrishna, 2001; Nekaris and Jayewardene, 2002). The slender loris is a member of the subfamily Lorisinae (Anonymous, 2002), which includes four extant genera, *Perodicticus* and *Arctocebus* from Africa, and *Nycticebus* and *Loris* from Asia. These animals share a remarkable suite of morphological traits, related to a unique nonsaltatory locomotor pattern (Osman Hill, 1953; Walker, 1969; Sellers, 1996). This locomotor pattern is said to limit their ability to move over a relatively large area in a given night. It is also said to limit frequent encounters with conspecifics, as animals may be too slow to meet often in the night, or to return to a communal sleep area before dawn (Charles-Dominique, 1977, 1978; van Schaik and van Hoof, 1983). In association with other behaviors, such as emitting no loud calls, and interacting infrequently via physical social contact throughout the night, the lorises as a whole have been described as highly cryptic (Sussman, 1999).

Research conducted on the potto, angwantibo, and slow loris have until now supported this view. In both African lorises, sleeping congregations consisted of single animals, or mothers and their offspring. These species almost always slept alone,

though there is strong evidence that male and female potto pairs sleep more often in close proximity to each other than to other pairs (Pimley, 2003; Pimley and Bearder, in press). Potto sleeping sites consist of tangled branches rather than tree hollows, and are changed often. The sleeping sites of the smaller-bodied angwantibo (*A. calabarensis*) consisted of tangled vines and branches. Neither pottos nor angwantibos regularly (if ever) emit loud calls throughout the night, and rarely come together in social interactions (Jewell and Oates, 1969; Charles-Dominique, 1977; Pimley, 2003). A recent study of slow lorises found they almost always slept alone, with the most common dyad being a mother and

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infant. Sleeping sites were found in branch tangles rather than tree hollows. They also never made loud calls during the night (Wiens, 2002).

This view that lorises as cryptic and almost completely solitary has been contrasted to the fact that closely related, similarly sized bushbabies that do include leaping and obvious speed in their locomotor repertoire form cohesive sleeping groups of 2–7 animals and produce loud contact calls throughout the night. Some species (e.g., *Galago moholi*, *Galago zanzibaricus*) also spend up to 20% of their time in gregarious social activity, unlike the 2–4% of the majority of nocturnal prosimians (Bearder, 1987; Sussman, 1999).

The slender loris is different from other lorises in many respects. First, slender lorises have been seen to move quickly in many contexts, to engage in short jumps, and even to run (Nekaris, 2001a; Nekaris and Jayewardene, 2002). They do produce a loud call throughout the night, at a rate similar to that of bushbabies or even more frequent than them (Bearder et al., 2002). They also frequently engage in gregarious social behaviour, in contrast to other species of nocturnal primates. Slender lorises in India (*L. l. lydekkerianus*) were found to be social for more than 18% of their activity budget, with some animals seen in association with others for more than 50% of their activity budget. (Bearder et al., 2002; Nekaris, 2001a, 2002; Nekaris and Rasmussen, 2003). Slender lorises (*L. l. nordicus* and *L. tardigradus tardigradus*) in Sri Lanka were observed in contact with other animals for more than 40% of their activity budget (Nekaris and Jayewardene, 2002). These social interactions occurred between adult males and females, and between adults and youngsters, but rarely between adults of the same sex (Nekaris, 2001a,b, 2002; Nekaris and Jayewardene, 2002; Radhakrishna, 2001). Slender loris mating in the wild also is a highly social event, with up to 5 males pursuing a single female in estrous, followed by multiple prolonged intromissions between a single female and male (Nekaris, 2001b; Radhakrishna, 2001; Nekaris, 2002, 2004). Based on a similar copulation pattern in captivity, Dixon (1995, 1998) predicted that lorises might have a multimale mating system.

These marked differences from other lorises and similarities to the galagines might also be expected to be reflected in their ranging patterns and social system. It is now widely accepted that a diverse range of social systems are evident among nocturnal prosimians, and the description of this variability has been the topic of numerous recent papers (e.g., Bearder, 1987; Sterling and Richard, 1995; Mueller and Thalmann, 2000; Sterling and Radespiel, 2000). In order to outline the complexities of nocturnal primate social systems, these authors all emphasized the importance of the study of social behavior, including sleeping group composition, mating behavior, and both dispersed and nondispersed gregarious behavior. Perhaps more important is the pat-

tern of range overlap exhibited by these species, or spacing system. Because many nocturnal prosimian species are studied only with the aid of radio tracking, the intricate pattern of range overlap becomes central to understanding their social organization (Sterling et al., 2000).

Bearder (1987) used differences in spacing and range overlap to characterize five social categories based on 15 species of nocturnal prosimians. Patterns of range overlap included: type 1, females overlap with other usually related females, and one or two larger male home ranges overlap those of several females (e.g., *Galago moholi*); type 2, male ranges are larger than female ranges and may overlap more than one female range, though same sex ranges overlap very little if at all (e.g., *Perodicticus potto*); type 3, ranges of individual males and females coincide (e.g., *Tarsius bancanus*); type 4, animals are almost fully solitary, with only some overlap of male ranges with female ranges at range borders (e.g., *Mirza coquereli*); and type 5, males, females, and their offspring forage together as a cohesive group (e.g., *Eulemur mongoz*). A study of the aye-aye (*Daubentonia madagascariensis*) revealed an additional pattern (type 6) where males overlap with one another, and with many female ranges, though female ranges do not coincide (Sterling, 1993).

More recently, Mueller and Thalmann (2000) reduced these types to four patterns of relations, linking them to social system: 1) The home ranges of a male and just one female coincide (= monogamy). 2) The home range of a male overlaps several females, and vice versa (= multimale system). 3) The home range of a male overlaps those of several females exclusively (= harem). 4) The home range of a female overlaps those of several males (= polyandry). Through this standard classification system, it will be possible to compare and understand the variation in nocturnal primate social systems in a broader perspective.

The above categories are based mainly on behavioral studies of the Galaginae, Lemuriformes, and Tarsiiformes. However, very little is known about spacing patterns among any of the lorises. A long-term study of the potto (*Perodicticus potto*) showed that the home ranges of males overlapped those of at least two females (Bearder's type 2) (Charles-Dominique, 1974). Home-range size of females was about 7.5 ha, and of males, 9–40 ha. Little is known about range overlap of the angwantibo (Jewell and Oates, 1969; Charles-Dominique, 1977).

Some success has been achieved in assessing range overlap in the Asian slow loris (*Nycticebus coucang*). Using radiotelemetry, Barret (1984), after 4 days, found the range of a female to be 4.19 ha. Wiens (1995), in a 3-month study, estimated the area used by a female to be about 8.75 ha. Male ranges were seen to overlap with female ranges, females were observed together, and some evidence for range overlap between males was seen. Sleeping

sites were found in branch tangles rather than tree hollows. Animals almost never slept together, beyond mother-infant dyads (Wiens, 2002).

No systematic study has been made of ranging behavior on any populations of the slender loris. Two brief reports of home range use are available. Petter and Hladik (1970) suggested that *L. l. nordicus* moved no more than 20–30 m per night. These data were based on 9 nights, and 7 unmarked individuals that were assumed to be the same animals, partially based on the assumption that nonleaping lorises would not move very far. More recent studies showed that lack of movement does occur for hours at a time, but instead may be part of an intricate male courtship pattern (Nekaris, 2004). Johnson (1984) calculated the range of a male *L. l. malabaricus* to be oblong in shape and 0.9 ha, without reporting the duration over which observations were made.

Before any assessment can be made of the social system of *L. l. lydekkerianus*, it is necessary to have a basic understanding of ranging behavior. In the current study, 10½ months were spent observing Mysore slender lorises throughout the night in an open scrub forest, where identifying and following lorises could be done at close range over long periods. From these detailed follows, I present data on home range size and overlap of adult Mysore slender lorises, as well as data on sleeping site locations and group composition at these sites.

METHODS

Study site and study subject

This study was carried out from October 1997–August 1998 in a semiprotected acacia scrub forest, Ayyalur Interface Forestry Division (AIFD), in Dindigul District, Tamil Nadu, South India (77°54′–78°17′E and 10°4′–10°40′N). The potential of this study site for loris research was first identified by Singh et al. (1999) during preliminary surveys. The area currently is disturbed heavily by local villagers, but is now under consideration by the Indian government for receiving wildlife sanctuary status (Singh et al., 1999). The area received less than 1,000 mm of rainfall during the entire 10½-month duration of the study. The 1-km² study site was located in the foothills of the Eastern Ghats. Home range data presented in this paper come from a 28-ha core of the study area.

This study had the advantage of taking place at a site where visibility was superb. The study site contained patchily distributed acacia trees and cacti, and was bordered by croplands and fenced-in orchards. Most of the vegetation consisted of thorny bushes and short trees that were separated from one another by up to 15–20 m of open ground or scrubby undergrowth no more than 6 inches in height. Common tree species included: *Albizia amara*, *Acacia leucophloea*, *A. planifrons*, *A. ferruginea*, *Prosopis juliflora* (Mimosoideae); *Cassia siamea* (Caesalpin-

aceae); *Azadirachta indica* (Meliaceae); *Tamarindus indica* (Tamaricaceae); *Euphorbia trikali* (Euphorbiaceae); and *Opuntia elata* (Cactaceae). A detailed study of botanical sampling is currently underway (Alexander, personal communication). Studies of bushbabies (*Galago moholi*, Pullen et al., 2000) at Nylsvley Nature Reserve, South Africa, an acacia thornveld site similar in structure to AIFD, also yielded better visibility of behavior than those in rain forests (e.g., Charles-Dominique and Bearder, 1979).

During instantaneous point sampling at 5-min intervals (see below), observers most often followed lorises from a distance of 1–3 m, though animals were sometimes observed from a distance of up to 7 m. Animals were observed at an average height of 3.4 ± 1.4 m, though they often could be watched at eye level. Throughout the entire study, 61% of observations of lorises occurred at 3 m or lower, with 90% of observations below 5 m (see also Nekaris, 2001a; Nekaris and Rasmussen, 2003).

Focal animals were seldom out of view, as most of the bushes were no more than 2 m wide. With the exception of some dense clumped shrubs, it often was possible to walk 360° around most vegetation. Except when animals entered dense cacti or shrubs, visibility was excellent, allowing for fine resolution of the details of loris behavior.

The subspecies observed during this study was *L. l. lydekkerianus* (Osman Hill, 1933; Jenkins, 1987; Schulze and Meier, 1995a; Groves, 2000). Males (294 g) are slightly larger than females (260 g) (Singh et al., 1999; Nekaris, 2001a). This subspecies is characterized by numerous features that aid in distinguishing individuals, including pronounced circumocular patches, white interocular stripe, variation in dorsal stripe, and variation in color of the belly.

Because of the excellent visibility mentioned above, it was possible to identify each individual by failsafe features, including missing or mutilated fingers and toes, shape and size of the nose, distinct facial masks, notches in the ears, and elongated nipples of females (the most consistently encountered individuals, excluding infants, are listed and described in Table 1; see also Nekaris, 2001a; Nekaris and Rasmussen, 2003). With practice, the sex of an individual was easy to distinguish: the male scrotum is surrounded by an area of dark fur, and females exhibit elongated clitorises distinct from male penises. In addition to these features, each loris had a unique behavioral pattern which distinguished it from other animals. Age was determined by pelage color and body size, and in females, by elongated nipples or presence of infants (see also a published key to aging and sexing lorises by Fitch-Snyder and Schulze, 2000).

Home-range data presented in this paper come from 8 adult or subadult individuals: 3 adult females (Titania, Morgaine, and Ygraine), 1 subadult female (Ophelia), 3 adult males (Donald, Billie Blue, and

TABLE 1. Key to identification of individuals for which home range was determined¹

Individual	Distinct morphology or behaviour
AM: Sudden	Large ears, skinny rump, circumocular patches dark chestnut
AM: Billie	Fur appeared rough rather than smooth; largest of males; more grey in color
AM: Donald	Large pronounced nose; very dark testicular patches
JM: Scary	Smaller-bodied; circumocular patches dark; wide band of white preauricular hair making eyes appear larger
SM: Vladimir	Dorsal hair pale grey/brown except for dark patches on hips and knees of rear legs; snowy white belly and chin with large white preauricular patch; ears small; body "clean" and lithe
AF: Titania	Ear notches and mutilated finger on right hand; very long nipples and clitoris; only loris to engage regularly in auto play hang (Nekaris, 2001a)
AF: Morgaine	Coat color tending to russet rather than grey; smaller in body; appeared more sleek; nipples small
AF: Ophelia	Smaller and fluffier; coat color tending more towards yellowish with dorsal stripe dark; fluffier ears
AF: Ygraine	Elongated nipples; clitoris pronounced (shaped like cigarette butt); pale circumocular patches; "sad" eyes, delicate muzzle; face was more triangular

¹ A, adult; S, subadult; J, juvenile; M, male; F, female.

Sudden), and 1 subadult male (Vladimir). Preliminary data on home-range size also are presented for 1 juvenile male (Scary), 2 adult males (Mickey and Arcadio), and 1 adult female (Halva) (for additional details, see Nekaris, 2000, 2001a). Juveniles and infants moved wholly within the ranges of their parents, and are considered only briefly in this paper.

Animals were habituated to the presence of human observers remarkably easily, almost always within the first hour of observing them. Initial observations were made by standing still and quietly, maintaining an initial distance of about 15 m, and most importantly by using lights covered with a red filter or a night-vision scope. White lights almost always elicited in the lorises a fleeing or freezing response, accompanied by urine washing. Gradually an observer could approach less than 5 m from an animal, and then could maintain this distance throughout the observation period. Animals were considered habituated when they did not freeze in the presence of an observer, or constantly glance at the observer, and when they actually came within inches towards the observer. Continuation of behaviors at the moment of first contact, such as feeding or allogrooming a conspecific, also suggested that the animals were not nervous. This easy habituation probably was aided by the fact that lorises are in constant contact with sights and sounds of local villagers during both day and night. It is important to note that, though the animals were unaffected by human voices at a standard level of speaking, they were made nervous by louder noises, such as rocks being kicked. Therefore, observers walked as softly on the ground as possible. Lorises also appeared nervous when more than three observers were present at a single time. Therefore, most observations were made with one observer and one assistant. Finally, a key to loris observation was never to move quickly towards an animal; the animals were always more comfortable if the observer moved slowly and nonabruptly, even mimicking the movements of the lorises themselves. Moving with quick or erratic movements almost always resulted in a fleeing response. Minimal use of flash photography,

with its fear-eliciting white light, also was important.

Upon spotting a loris, it was followed for as long as possible. The mean follow time was 6.2 ± 3.2 hr, and the mode was 10.5 hr ($n = 149$ nights); 57% of all observation sessions were 7 or more hours long; 38% of all sessions concluded with following an animal to its sleeping site. The minimum follow time was 25 min, and the maximum was 11 hr (Nekaris and Rasmussen, 2003). Because of the duration of these follow times, even if an animal was not recognized instantly, it eventually moved to a level where identification could be made with certainty. In addition, the nonsaltatory locomotor pattern described above further facilitated viewing ease. In his study of pottos, Charles-Dominique (1977) likewise described how viewing pottos was easier than viewing bush-babies due to this locomotor difference.

Sampling methods

Radio tracking was not permitted during this study due to laws in India regarding the trapping of mammals. Without the facility of radio tracking, conclusions regarding range use necessarily come from direct observation. In order to determine home-range use, focal animals were observed throughout the night, using the focal animal instantaneous point sampling method, recorded at 5-min intervals ($n = 13,717$) (Crook and Aldrich-Blake, 1968). Behaviors recorded not related to ranging included feeding, general activity, positional behavior, social behavior, and calling patterns, and are described elsewhere (Nekaris, 2000, 2001a,b, 2002; Nekaris and Rasmussen, 2001, 2003; Bearder et al., 2002). Sex, time, location, distance from focal animal, and behavior were recorded, as well as the identification of the individual, if known.

In addition, location records were made of animals during regular patrols of the study area. When an animal was spotted and identified, its location in the study area and time of night were noted. Each tree used by a loris was marked with flagging tape, with a unique color for each individual animal. These markers aided in determining the range use and overlap of individuals.

The location data for home ranges come from animals that were either observed or spotted on at least 10 different nights at different times of the night. Of 20 individuals identified throughout the duration of this study (Nekaris, 2000, 2001a), only the 8 individuals mentioned above fit these criteria. The home-range sizes of animals observed during only one observation session or who were not observed during each hour of the night, as well as infants, are not included in this analysis.

Though all areas used by an individual were included in its home range, for comparison of range use by each individual, "location points" are reported. Each time an animal was observed at a different hour of the night, even if it was observed throughout the entire hour, that hour was scored as one "location point." Through this method, it can be demonstrated that home-range sizes are determined readily from observations throughout each hour of the night, even in the absence of radio tracking. Table 1 presents the number of "location points" during different hours of the night, as well as the total number of hours each individual was observed during instantaneous point sampling.

All location data were entered into a mapping program, AutoSketch, version 6.0 (AutoCad). From these data, home-range sizes and areas of overlap were determined, and maps were generated. Simple statistics, with the alpha level set at 0.05, were conducted either by hand or using SPSS 10.0 for Windows.

Home-range size

The home range of an animal is the area the animal covers during its normal daily activities (Blair, 1953). A home range may overlap with those of other animals, and may contain a territory that is defended against other individuals. In order to determine the size of slender loris home ranges, a map was constructed of the study site. Local villagers used the study area extensively and many trails were already cut, dissecting the study area. These trails were mapped using a compass and a pedometer. Frequently used trees, sleeping sites, and other geographic features that occurred along the trails also were recorded, and their orientation and distance from points on a trail were measured. In most cases, these landmarks were measured from different trails to assure accuracy of the reading.

The minimum convex polygon method was used to determine the minimum size in hectares of each animal's range, as well as the amount of overlap with other individuals (Hayne, 1949; Southwood, 1966; Bearder and Martin, 1980). In AutoSketch version 6.0, a polygon was drawn around all of an animal's known locations, and the area within the polygon was calculated. This method was used rather than the "minimum sleeping area" (an area encompassing all sleeping sites) used in some studies (Charles-Dominique and Bearder, 1979), because animals regularly used the same sleeping sites in

the center of their ranges (see below). Furthermore, this method increases comparability with other studies, though it may overestimate range size if points rarely used by animals are included (Harris et al., 1990).

Definition of "group"

Typically in discussions of diurnal primates, the term "group" is used to refer to a cohesive group of animals regularly seen together (Richard, 1985; Sussman, 1999). The term "dispersed social units or groups" has been proposed for nocturnal prosimians, which may form units of two or more animals at sleeping sites, but spend most of their active time alone (Charles-Dominique, 1978; Mueller, 1999b; Mueller and Thalmann, 2000). During this study, 3 focal females and their offspring regularly formed three distinct sleeping units, almost always with the same males (see below). Throughout this paper, the term "group" refers to a focal adult female and other lorises that regularly formed sleeping congregations with her (see also Radespiel, 2000).

RESULTS

Sleeping site use

Slender lorises began their nightly movements from a sleeping site that was centrally located in their home range. Sleeping trees used by identified lorises included: *Euphorbia trikali* (68%, $n = 38$), *Acacia leucophloea* (9%, $n = 5$), *Albizia amara* (5%, $n = 3$), *Acacia planifrons* (5%, $n = 3$), and three other species (*Tamarindus indica*, *Acacia ferruginea*, and *Prosopis juliflora*) (together making up 13%, $n = 8$). The average height of sleeping sites for all observations was 3.2 ± 1.3 m ($n = 57$).

Slender lorises did not use tree hollows or nests, but preferred to sleep in cacti or tangled branches in trees. Animals typically slept in a posture called the sleeping ball or *Schlafkuegel* (Subramonian, 1957; Schulze and Meier, 1995b). Animals sleeping together almost always formed a large sleeping ball congregation, with limbs tangled together, making an accurate count of individuals in the ball time-consuming.

Slender lorises slept alone or in groups. From regular congregations, three fairly consistent social groups were identified (FCG, CZG, and CAG). A single adult female (Titania, Ygraine, or Morgaine) formed the core of a sleeping group; additional members included infants, juveniles or subadults, and adult males (Table 2). Of 57 observations of known individuals at sleeping sites, I observed the following aggregations: alone (14%, $n = 8$); mother and infant (19%, $n = 11$); and a group of two or more lorises containing at least 2 adults (67%, $n = 38$). Mean group size was 3.9 ± 2.3 individuals, with a maximum of 7. Both females and males were observed sleeping alone. All individuals that were observed sleeping alone were observed on other occasions in sleeping aggregations. In observations of

TABLE 2. Sleeping group composition of three focal groups¹

Group	Name	Sex	Age	No. of observations
1: FCG (February–May 1998)	Morgaine	F	A	11
	Chakki	M	I	
	Chakku (disappears March)	U	I	
	Scary	M	J	
	Halva	F	A	
	Donald (disappears March)	M	A	
1: FCG (June–August 1998)	Billie Blue (sometimes) appears in March	M	A	23
	Morgaine	F	A	
	Chakki (disappears in July)	M	I	
	Scary	M	J	
	Billie Blue (sometimes)	M	A	
	Vladimir	M	A	
2: CZG (February–August 1998)	Ygraine	F	A	11
	Isadora	F	I	
	Ophelia (disappears in April)	F	S	
	Sudden	M	A	
	Titania	F	A	
3: CAG (February–August 1998)	Puck	F	I	9
	Bottom (disappears March)	U	I	
	Donald (sometimes)	M	A	
	Billie Blue (sometimes)	M	A	
	Others possible in orchard			

¹ F, female; M, male; U, unknown; A, adult; J, juvenile; S, subadult; I, infant.

unidentified animals at their sleeping sites, male-female pairs were observed four times, mothers with young were observed four times, and on one occasion, 5 animals of unknown sex were observed together.

Several animals disappeared during the course of the study, thus changing group composition. Radio tracking would have greatly aided in knowing whether these animals simply left the area, or were killed. Group composition changed for group I, FCG, due to the departure of the adult female, Halva, in March, the overtaking of Donald's territory by Billie Blue in March, and by the death of the infant Chakku in March and its twin, Chakki, in July. In group II, CZG, the subadult female Ophelia left the group in April. Group III, CAG, also was affected by Billie Blue's takeover of Donald's territory.

In the case of CAG, group composition may have been underestimated due to my limited access to part of their range. This group ranged across the road into a fenced-off orchard to which I had limited access. This fence was only about 50 m away from another regularly used sleeping tree. Titania and her group clearly had a sleeping tree or trees over the fence, and group composition is not known.

Though the three focal groups of lorises used 28 ha of the study area for all activities, trees used by all three groups for sleeping were concentrated in an area of 1.9 ha (Fig. 1). The distances among sleeping sites of different groups from nearest edge to nearest edge were as follows: FCG to CZG, 155 m, and to CAG, 49 m; CAG to CZG, 97 m (Fig. 3). Though individuals were observed outside of regular sleeping trees, FCG was seen to use only three sleeping sites, CAG was seen to use three sleeping sites, and CZG was seen to use two different sleeping sites.

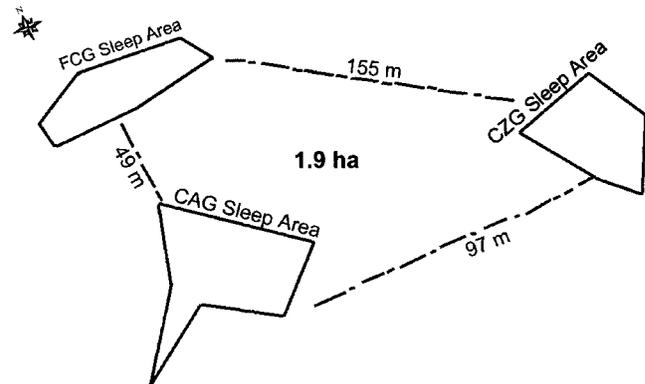


Fig. 1. Sleeping areas of three different groups of lorises in relation to one another; area encompassed by sleeping sites measured 1.9 ha.

Behavior at sleeping sites was very gregarious, and is described in detail elsewhere, but a general description is included here (Bearder et al., 2002; Nekaris, 2004). Slender lorises spent the entire day huddled closely together. At dusk, they awoke and groomed one another. Grooming occurred between all age and sex classes, and consisted of multiple animal allogrooming whenever three or more animals were present. Animals dispersed, sometimes foraging or traveling together for up to 1 hr within 20–30 m of the sleep site before moving off into other areas of their home ranges. Foraging pairs included adult males and adult females, adult males and juvenile males, and juvenile males and adult females. Foraging trios also were seen consisting of an adult male and female with a juvenile male (see also Nekaris and Rasmussen, 2003). Young infants were left parked in the sleeping tree.

TABLE 3. Home range size in hectares (ha) categorized by individual, age and sex, total hours observed during instantaneous point sampling, and total number of location points¹

Individual	Minimum home range	Total hours	Number of contact points			
			18:00–21:59	22:00–00:59	01:00–03:59	04:00–06:00
AM: Sudden	3.75 ha	28.6	22	20	6	4
AM: Billie	3.48 ha	29.3	7	7	8	23
AM: Donald	3.6 ha	65.1	24	37	19	6
Mean adult male	3.6 ha \pm 0.09					
JM: Scary	0.91 ha	60.7	16	23	16	32
SM: Vladimir	1.44 ha	26.0	10	14	4	11
Mean subadult/juvenile male	1.17 ha \pm 0.26					
AF: Titania	1.95 ha	195.7	59	73	57	18
AF: Morgaine	1.71 ha	135.6	43	45	40	43
SF: Ophelia	1.4 ha	25.8	4	16	8	3
AF: Ygraine	1.31 ha	34.4	21	19	6	8
Mean adult female	1.59 \pm 0.29					

¹ AM, adult male; JM, juvenile male; SM, subadult male; AF, adult female. Number of contact points used to determine range size are divided into four time intervals: 18:00–21:59 (after dusk), 22:00–00:59 (late evening), 1:00–3:59 (early morning), and 4:00–6:00 (before dawn).

Near dawn, animals returned to the sleeping site, either alone or in pairs. This movement was not signified by any audible communication, unless an infant was left in the tree and called to its mother. They came from separate directions, converging at one point 10–20 m from the tree, and then entered the tree in a single-file line. They moved in close linear formation; they were so close together that one loris' nose touched the next loris' rump, described by other authors as "follow the leader" (Subramonian, 1957; Schulze and Meier, 1995b). They moved in this fashion through several trees before entering the sleeping tree, often falling over each other. This line was always led by the adult female (Titania, Morgaine, or Ygraine). Once in the tree, grooming and play wrestling again occurred for up to 45 min, before the group reassembled into a huddled ball.

Home-range size

The average size of an adult male's home range was 3.6 ha \pm 0.09 ($n = 3$). The average size of an adult and subadult male's home range was 3.07 \pm 1.09 ($n = 4$). The average range size of smaller-bodied males (one juvenile and one subadult) was 1.17 ha \pm 0.26 ($n = 2$). Adult females had an average home range size of 1.66 \pm 0.32 ($n = 3$). When the subadult female is included, the average is 1.59 ha \pm 0.29 ($n = 4$). Not enough home-range sizes were calculated to allow for statistical comparison, although male ranges were more than twice the size of female home ranges (Table 3). Including both adults and subadults in the analysis, using a *t*-test for independent samples, males were found to have a significantly larger home range than females ($t = -2.612$, $df = 6$, $P = 0.04$). However, these results should only be treated as a trend towards significance, as sample size is small.

Home-range overlap: males

Males shared a portion of their ranges with at least 2–3 other adult males (Fig. 2). The mean over-

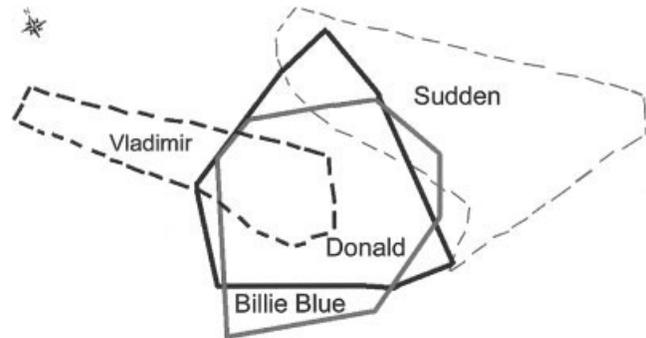


Fig. 2. Home-range overlap among adult and subadult male slender lorises: Billie Blue (grey line), Donald (black line), Vladimir (dashed black line), and Sudden (dashed grey line). Figures 2–4 are in scale to an area representing 850 \times 450 m (1 cm = 70 m).

lap of male ranges was 0.72 ha \pm 0.23 ($n = 4$). Donald's home range overlapped with those of both Sudden (0.85 ha) and Mickey (see below). Donald's range appears to overlap strikingly with those of Billie Blue and Vladimir; actually, he had disappeared when these two animals entered the study area, and Billie Blue took over Donald's range almost completely. Billie Blue's home range overlapped with that of Vladimir (0.93 ha) and that of Sudden (0.37 ha), and with the home range of another large unknown male who was occasionally seen on the southern fringe of his range. Besides overlap with Billie Blue, Sudden overlapped with two males (Mickey and Arcadio) who were seen on only five occasions (see below). Sudden's home range was in the northeastern-most part of the study area; I rarely entered this area, so little can be assessed about his relationship with these two males.

Two other males (Mickey and Arcadio) were observed, though not often enough to determine their ranges. The known ranging behavior of these males is nonetheless worth considering, because their ranges did overlap other focal males. Arcadio was observed for 1 hr within 20 m of Vladimir, and both animals ignored one another. Mickey was observed

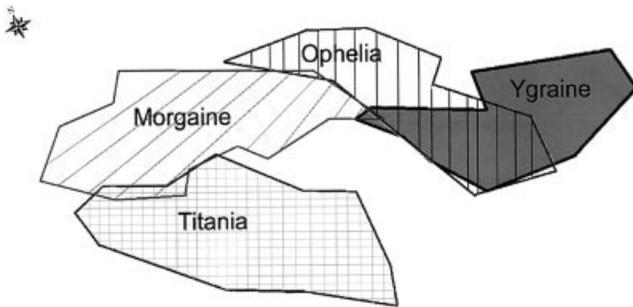


Fig. 3. Home-range overlap among adult and subadult female slender lorises: Titania (square hatching), Morgaine (diagonal hatching), Ophelia (vertical hatching), and Ygraine (grey-scaled).

within Donald's range on three occasions, which on one occasion resulted in an agonistic interaction. The observed movements of Mickey constituted a range overlap with Donald of 0.39 ha and with Sudden of 0.72 ha. Arcadio was also seen in Sudden's range on one occasion.

Home-range overlap: females

The mean home-range overlap among female home ranges was $0.22 \text{ ha} \pm 0.25$ ($n = 4$) (Fig. 3), just 30% of the mean home-range overlap observed among males. Female home ranges overlapped with those of at least two other females. Titania's range overlapped slightly with Morgaine's home range (0.06 ha). The home ranges of Morgaine and Ophelia also overlapped slightly (0.01 ha). Morgaine's home range also overlapped with the range of another adult female, Halva, who was not in the study area long enough to determine her range. The home ranges of Ophelia and Ygraine overlapped almost 40% (0.6 ha). However, Ophelia was fluffy and smaller-sized when first identified; as she grew larger, she spent increasingly less time in Ygraine's range, and eventually disappeared altogether. It is possible she was Ygraine's daughter, who later transferred to another territory (for further details, see Radhakrishna, 2001).

Home-range overlap: males and females

The average overlap of an adult male's home range (excluding the smaller-bodied Vladimir) over a female's range was $0.9 \text{ ha} \pm 0.53$ ($n = 3$). The average overlap of all male ranges (including Vladimir) over female ranges was $0.82 \text{ ha} \pm 0.51$ ($n = 4$) (Fig. 4).

Male home ranges overlapped the home ranges of several females, though males visited some females more frequently than others (Fig. 4). Donald's range overlapped at least three female home ranges: Titania (0.8 ha), Morgaine (1.67 ha), and Ophelia (0.07 ha). Billie Blue, who later overtook Donald's range, showed similar overlap with Titania (1.26 ha), Morgaine (1.48 ha), and Ygraine (0.06 ha). Sudden's home range overlapped the ranges of three females: Ygraine (1.31 ha), Ophelia (1.18 ha), and Morgaine (0.26 ha). The small male Vladimir's home range

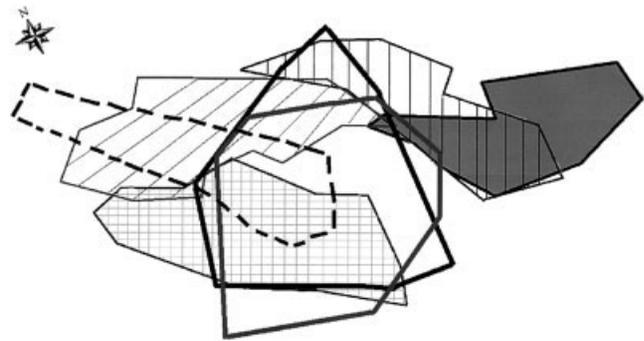


Fig. 4. Home-range overlap among all adult and subadult male and female slender lorises. Symbols follow those described for Figures 2 and 3.

overlapped the ranges of two females: Morgaine (0.86 ha) and Titania (0.11 ha). The ranges of Vladimir and Donald also definitely overlapped with Halva's home range, though not enough data on her ranging were collected to determine overlap. Mickey overlapped with the home ranges of Ygraine, Morgaine, and Ophelia.

DISCUSSION

Among diurnal primates, a variety of distinct social systems defined by group size, social interactions, and mating system are recognized (e.g., Crook and Gartlan, 1966; Eisenberg et al., 1972; Clutton-Brock and Harvey, 1977). Similarly, Sterling and Richard (1995) proposed that spacing systems, along with mating systems and social behavior, are the main components that define social organization in nocturnal primates. Numerous recent studies have added to our depth of knowledge of lemur and African lorid social organization (e.g., Sterling, 1993; Bearder, 1999; Fietz, 1999; Mueller, 1999b; c; Pullen et al., 2000; Radespiel, 2000; Pimley, 2003). This study provides an important contribution in being the first detailed information on the spacing system of a species of slender loris in its natural habitat.

Adult male home ranges (3.6 ha) were more than two times the size of adult female home ranges (1.67 ha). These range estimates are larger than the range of 0.9 ha reported for *L. t. malabaricus*. This discrepancy is not surprising, as observations were not systematic, and involved only locating a single loris at daytime sleeping sites (Johnson, 1984). Male home ranges overlapped those of several females as well as the home ranges of other males, but females' home ranges only overlapped with each other minimally. In particular, females rarely met in the areas of overlap.

The amount of overlap between male home ranges was three times greater than that between females. In both sexes, agonistic interactions were rare; however, male encounters were generally more neutral or positive than female encounters, particularly at the sleeping site of group FCG. Interactions between males and females occurred almost nightly, and both males and females interacted with more than

one member of the opposite sex (Nekaris, 2001, 2002; Bearder et al., 2002). Such visits were made by males, who entered each other's home ranges frequently; given the low frequency of male encounters, and the larger degree of range overlap between males than between females, it is possible that males were practicing mutual avoidance in areas of range overlap.

Slender lorises regularly emitted a high-pitched whistle throughout the night (Bearder et al., 2002). Schulz and Meier (1995b) interpreted this whistle to have a territorial function in their captive colony of *L. l. nordicus*. A recent study of the bioacoustic structure of this whistle revealed that it occurs in at least five distinct forms (Coults, 2002). The whistle was never heard before assembly at the sleeping site in the morning, but was often heard as a call with one or more responses from animals more than 200 m apart (Nekaris, 2004). One function of this whistle may be a spacing device, similar to the long call of orangutans, who use this call for mutual avoidance (Galdikas, 1983; Mitani, 1985). Sex differences in calling, and the exact function of each of the five types of whistles, are areas worthy of further research.

Adult females and their offspring never used the sleeping sites of other groups, and group-range overlap was also minimal. This consistent pattern of home-range size and sleeping-site use may be related to diet. The diet of Mysore slender lorises consists almost exclusively of insects (Nekaris and Rasmussen, 2003). In particular, they specialize in ants that were hyperabundant at AIFD. It is possible that the lack of competition for this readily available resource played a role in the consistent home-range sizes of males and females, in that they did not need to defend their food resources.

Home-range sizes within each sex are very similar, despite the fact that two females (Titania and Morgaine) were observed for longer periods than Ygraine, and Donald was observed two times longer than either Sudden or Billie Blue (Nekaris, 2001a). As noted above, most observations come from follows of approximately 6 hr. These results are probably fair indicators of home-range size. It is still possible that home ranges would increase in size if radio tracking was incorporated. This is particularly true for the subadult male Vladimir; data on this male were being accumulated only toward the end of the study, and it was clear from his entry into new areas on each follow that he was likely to have a larger range.

Petter and Hladik (1970) estimated that isolated animals in *L. l. nordicus* were spaced more than 100 m apart. Although in the present study, animals often were found 100 m apart, they certainly shared a core area from which they would move in and out. The density of animals within the study site is evidenced by the arrangement of sleeping trees of all three groups containing at least 14 animals found within an area of only of 1.92 ha near the center of

the 28-ha study site. These data are not an indicator of population density for the Ayyalur Interface Forestry Division; rather, the data suggest that lorises space themselves nearer to one another than previously thought.

Slender lorises differed from *Perodicticus potto*, *Arctocebus calabarensis*, and *Nycticebus coucang* in that the home ranges among animals of the same sex overlapped (Charles-Dominique, 1977; Barret, 1984; Wiens, 1995). This overlap may have profound influences on social organization, since slender lorises were able to come together more often in friendly interactions between all ages and sexes. Also, unlike pottos and angwantibos, slender lorises slept communally in sleeping sites that were used regularly. Slender lorises were similar to other lorises in their use of tangled vines and cacti rather than the construction of nests for sleeping sites. Social interactions were common in the night, and were not prevented by "slow" locomotion (Nekaris, 2001a, 2002).

The range use of slender lorises most closely approximates that of *Galago moholi* (type 1 system of Bearder, 1987), but also shows similarities to ranging in the aye-aye, *Daubentonia madagascariensis* (type 6) (Bearder, 1987; Sterling, 1993). Like *G. moholi*, lorises use few sleeping sites, male ranges are larger than those of females, small and large male ranges overlap, and range overlap exists between members of both sexes. Bushbabies in a similar habitat, however, made use of tree holes and nests as sleeping sites, and home-range overlap between related females was clearly delineated. In this regard, slender lorises were more similar to aye-ayes, where male ranges overlap with each other more than with females, while female home ranges overlap only marginally.

Slender loris male home ranges overlapped the ranges of at least three other males, and were twice the size of female ranges. Female ranges overlapped minimally with each other. This corresponds to the type 2 system of Mueller (1999a,b), or a multimale social system. This conclusion also supports predictions by Dixson (1995, 1998) who, on the basis of slender loris multiple sexual intromission patterns, predicted that lorises would have a multimale, multifemale mating system. Further evidence for this type of mating system comes from the fact that males visited and groomed several females and their infants, and females affiliated with at least two adult males (Nekaris, 2004; Radhakrishna, 2001). The mating system of slender lorises can only be clarified by paternity testing.

Several areas require further research. In this study, I did not use a grid system to mark the distribution of animals within the home range but, rather, key features of the study site. Methodology is available to calculate asymmetrical overlap between sexes based on time spent in different grids (Smith and Dobson, 1994). Such analyses might further

elucidate patterns of range overlap between males and females.

Vegetation at the study site was sparse. Slender lorises in more lush deciduous or tropical forests might make more use of vertical strata, making fewer horizontal movements, and thus may have smaller home-range sizes (though preliminary studies suggest that this is not the case; Nekaris and Jayewardene, 2002). Furthermore, very few other mammals and large reptiles were found at AIFD, making interspecific competition limited (Nekaris, 2001a; Bearder et al., 2002). Studying slender lorises in another environment where more potential competitors are found also may influence home-range size, in that animals may need to move further to forage, and may need to space themselves further apart. Studies of slender lorises in many different habitats are definitely warranted. Finally, a study of loris ranging with radio tracking will be essential to solidify knowledge of the ranging behavior of this species.

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