

Nature Watch

Sociality in a Solitary Primate: How Gregarious is the Slender Loris?

Sindhu Radhakrishna

Sindhu Radhakrishna is associated with the National Institute of Advanced Studies, Bangalore. Her research interests are in the fields of primate behaviour and communication, and she is currently involved in studying the sociobiology of the two strepsirrhine species of India, the slender loris and the slow loris.

Of the 20 or more extant mammalian orders, the order Primates is surely the most fascinating for us humans, as we too belong to this order; and the evolution of primate morphology and behaviour has important bearings on the development of our own society and culture. Most of us are familiar with the group-living sociality of the commensal monkeys and some of the bigger apes like the chimpanzees and the gorillas. However, another group of primates, the nocturnal strepsirrhines, which are equally fascinating in their behaviour and ecology, remain virtually unknown due to their small size and nocturnal habits. In this article I discuss the social behaviour of the slender loris, a nocturnal strepsirrhine found in India.

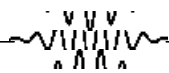
Before examining the behaviour of the slender loris, I first present a broad overview of primate taxonomy, and of the closest relatives of the slender loris, because that would give a better perspective into the sociobiology of this unusual primate. Cladistically, i.e. based on shared-derived anatomical traits, the order Primates is divided into two suborders - Strepsirrhini, the 'wet-nosed' primates, and Haplorrhini, the 'dry-nosed' primates (*Box 1*). Strepsirrhines include the lemurs, lorises and bushbabies, and are considered to be primitive in comparison to the haplorrhines, which comprise the tarsiers, monkeys, apes and humans. Some of the more distinctive anatomical differences between strepsirrhines and haplorrhines are explained in *Box 2*. An alternative classification is the gradistic one that is based on overall similarities of life histories and general appearance. According to this classification, tarsiers are placed along with the lemurs, lorises and bushbabies in the suborder Prosimii, and monkeys, apes and humans in the suborder Anthroidea. A

Keywords

Primates, strepsirrhines, social organisation, slender loris.



Box 1. Primate Taxonomy					
Order	Suborder	Infraorder	Family	Genus	
Primates	Strepsirrhini	Lemuriformes	Cheirogaleidae	<i>Cheirogaleus, Microcebus, Mirza, Phaner, Allocebus</i>	
			Lemuridae	<i>Eulemur, Hapalemur, Lemur, Prolemur, Varecia</i>	
			Megaladapidae	<i>Lepilemur</i>	
			Indridae	<i>Avahi, Indri, Propithecus</i>	
		Chiromyiformes	Daubentoniidae	<i>Daubentonia</i>	
		Loriformes	Loridae	<i>Arctocebus, Loris, Nycticebus, Perodicticus, Pseudopotto</i>	
	Galagonidae Otolemur		<i>Euoticus, Galago</i>		
	Haplorrhini	Simiiformes	Tarsiiformes	Tarsiidae	<i>Tarsius</i>
			Cebidae	<i>Callimico, Callithrix, Leontopithecus, Saguinus, Cebus, Saimiri</i>	
			Aotidae	<i>Aotus</i>	
Pitheciidae			<i>Pithecia, Chiropotes, Cacajao, Callicebus</i>		
Atelidae			<i>Alouatta, Ateles, Brachyteles, Lagothrix</i>		
Cercopithecidae			<i>Allenopithecus, Miopithecus, Erythrocebus, Chlorocebus, Cercopithecus, Macaca, Lophocebus, Papio, Theropithecus, Cercocebus, Mandrillus, Colobus, Piliocolobus, Procolobus, Semnopithecus, Trachypithecus, Presbytis, Pygathrix, Rhinopithecus, Nasalis, Simias,</i>		
Hylobatidae	<i>Hylobates</i>				
		Hominidae	<i>Pongo, Gorilla, Pan, Homo</i>		



Box 2. Differences Between Haplorrhines and Strepsirrhines

Typically strepsirrhines possess a moist rhinarium (the moist, hairless pad at the end of the nose seen in most mammalian species), toothcomb (a dental modification in which the incisor teeth form a comb-like structure), grooming or toilet claws (elongated claws on the second digits of the hind feet, used for grooming), tapetum lucidum (reflective layer of the retina), epitheliochorial placenta (in which six tissue layers separate the foetal and maternal blood supply and the chorionic villi rests in pockets in the endometrium), unfused mandibular symphysis (separate left and right mandibles i.e. lower jaw) and post-orbital bar (bony ring surrounding the lateral side of the eye socket). In contrast, the haplorrhines are distinguished by absence of rhinarium, toothcomb and grooming claws, and presence of retinal fovea, hemochorial placenta (here the chorionic villi are in direct contact with the maternal blood supply), fused mandibular symphysis (single mandible) and post-orbital closure (a posterior bony wall to the eye socket, so that it forms a cup-shaped structure).

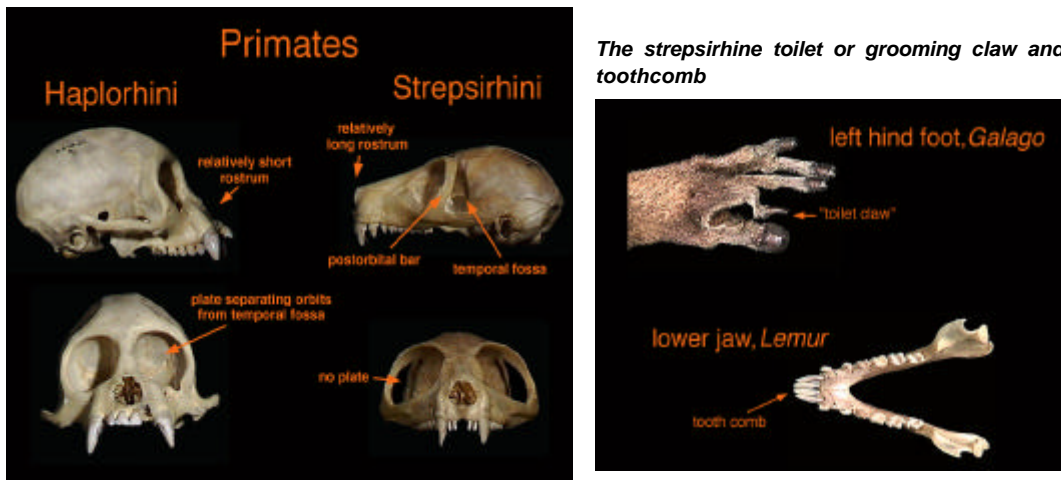
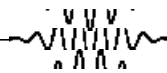


Photo credits: Phil Myers (<http://animaldiversity.ummz.umich.edu/chordata/mammalia/primates.html>)

cladistic classification is generally acknowledged to be more accurate as it is thought to be a more faithful representation of the phylogenetic relationships between species.

Haplorrhini

Members of this group are divided into two infraorders: Tarsiiformes (tarsiers) and Simiiformes (monkeys and apes). Found on the islands of south-east Asia, tarsiers (*Box 3*) possess morphological characteristics that are common to prosimians and anthropoids. Hence the different positions for this group in the gradistic and cladistic taxonomic classifications. Simiiformes



Box 3. Tarsiers

Tarsiers include five species. Weighing 80-150 g, they feed almost exclusively on animal prey, including insects, small birds, lizards, and snakes. Some of their 'prosimian' characteristics are nocturnality, small body size, unfused mandible and grooming claw, while their 'anthropoidean' features are the dry nose, retinal fovea, enclosed bony eye sockets and lack of toothcomb. Some unique tarsian characteristics are the size of their eyes (larger than the brain!), and the elongated hindlimbs (caused by the lengthening of the tarsal, or ankle, bones rather than the metatarsals).



Photo credits: www.primates.com

include the two main groups, Platyrrhini and Catarrhini. Platyrrhini means 'flat-nosed' and platyrrhines are so called because their nostrils have a wide septum and face outwards. They are also referred to as New World monkeys (*Box 4*) because of their geographic distribution in the tropical areas of Central and South America. Catarrhines derive their name from their

Box 4. New World Monkeys



Red uakari



Owl monkey

New World monkeys include the hapalines (tamarins, lion tamarins, marmosets, pygmy marmoset and Goeldi's marmoset), cebines (capuchins), chrysotrichines (squirrel monkey), aotines (owl monkey), pitheciines (sakis, bearded sakis and uakaris), callicebines (titis) and atelines (howlers, woolly, spider and woolly spider monkeys). They are small-to medium-sized primates with the hapalines being less than 1 kg, and some of the atelines weighing almost 10 kg.

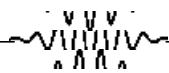


Cotton-top tamarin



Pygmy marmoset

Photo credits: www.primates.com



Box 5. Old World Monkeys

Old World monkeys are divided into two groups: the leaf-eating colobines and the cheek-pouched cercopithecines. Colobines include the colobus monkeys, the langurs and the odd-nosed monkeys, while the cercopithecines include the macaques, mangabeys, baboons, and guenons. The differences between the colobines and cercopithecines are mainly



Mandrill

related to their different dietary adaptations – the primarily folivorous colobines have a complex stomach, which is divided into four chambers, whereas the more omnivorous cercopithecines have a simple stomach, but possess cheek pouches which are used to store food temporarily.

Japanese macaque



Hamadryas baboon



Photo credits: www.primates.com

narrow septum and hook-like, forward-facing nostrils. They are found in Asia, Africa and Europe, and include the cercopithecoids or the Old World monkeys (*Box 5*), and the hominoids – lesser and the great apes, including humans (*Box 6*).

Box 6. Apes

Of the apes, the gibbons or lesser apes, and the orangutan, one of the great apes, are found in south-east Asia, while the other great apes – the chimpanzee, bonobo and the gorilla – are found in the tropical forests of Africa. *Homo sapiens*, needless to say, enjoys a geographic distribution that is unrivalled in its scope by any of the other primates.



Lars gibbon



Orangutan

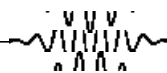


Chimpanzee



Mountain gorilla

Photo credits: www.primates.com



Box 7. Strepsirrhines



1



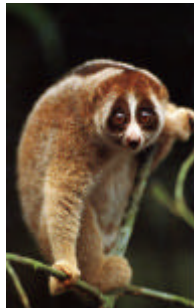
2



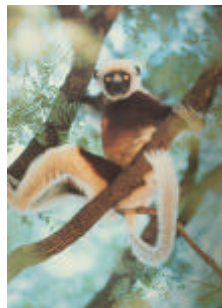
3



4



5



6

- 1. Mouse lemur
- 2. Black lemur
- 3. Lesser bushbaby
- 4. Aye-aye
- 5. Slow loris
- 6. Verreaux's sifaka

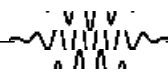
Photo credits: www.primates.com

Strepsirrhini

Extant strepsirrhines include five families – cheirogaleids, lemurids, megaladapids, indriids, and daubentoniids – that are found on the island of Madagascar, and two families (lorids and galagonids) that inhabit Asia and mainland Africa (Box 7). Living strepsirrhines retain several primitive morphological and behavioural characteristics. For example, they possess toilet claws and toothcomb, place greater reliance on olfaction rather than vision, are solitary in lifestyle, and tend to have shorter lifespan than other primates. Hence, they are of particular interest to evolutionary biologists and primatologists, for their socioecology is an important key to understanding the evolution of primate sociality and communication.

Social Organisation in the Strepsirrhines

The nocturnal strepsirrhines are usually labeled 'solitary', referring to the fact that individual members of these species are most often found alone and not in groups, as is more common with the



Solitary strepsirrhines are social, but the social network of relationships between conspecifics is organised along relatively subtle lines.

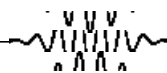
diurnal monkeys and apes. However, the use of this term has given rise to a number of misconceptions about the social organisation of these species. In 1978, Charles-Dominique called attention to the fact that the term 'solitary' denoted the opposite of 'gregarious', not of 'social'. Solitary strepsirrhines are social, but here the social network of relationships between conspecifics is organised along relatively subtle lines. Intra-specific communication is usually displaced in time and space, and species make use of chemical signals like urine and scent markings to message conspecifics. In 1987, Bearder introduced the term 'solitary forager' to distinguish between a solitary foraging state and a gregarious sleeping stage in most of these species. Since then, an increasing body of work on the socioecology of nocturnal strepsirrhines has shown that social organisation in these species is not uniformly similar. Instead, the species exhibit varying social structures, with differing degrees of gregariousness.

Social organisation in a primate species involves three main elements – social system, mating system and spacing system.

Social organisation in a primate species involves three main elements – social system, mating system and spacing system. Social system constitutes behaviour and relationships within a group. In the nocturnal strepsirrhines, direct social interactions between individuals seldom occur and communication is also displaced in time and space. Hence, assumptions about their social systems are made based on associations at sleeping sites (sites in trees where individuals may meet and sleep together). Mating system refers to reproductive interactions between individuals, whereas spacing system refers to the spatio-temporal distribution of these individuals. Every individual moves about in a specific area during the night and this is its home range. The size and quality of a home range represents extent of access to food and mates. Hence, the degree of range overlap between individuals is a critical pointer to inter-individual social relationships.

Divergent Social Organisations

Comparisons of behaviours among related species, based on



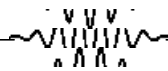
Box 8. Primates of India

A total of fifteen primate species are found in India, inhabiting a variety of habitats from the trans-Himalayan zone in the north to the dry scrub forests of the Eastern Ghats in the southern peninsular region. Twelve of these species are cercopithecoids, with 7 species of macaques (the bonnet macaque *Macaca radiata*, rhesus macaque *Macaca mulatta*, lion-tailed macaque *Macaca silenus*, stump-tailed macaque *Macaca arctoides*, Assamese macaque *Macaca assamensis*, pig-tailed macaque *Macaca nemestrina*, and crab-eating macaque *Macaca fascicularis*) and 5 species of langurs (golden langur *Trachypithecus geei*, Phayre's langur *Trachypithecus phayrie*, Nilgiri langur *Trachypithecus johnii*, capped langur *Trachypithecus pileatus*, and Hanuman langur *Seminopithecus entellus*). Two strepsirrhine species (the slender loris *Loris lydekkerianus* and the slow loris *Nycticebus coucang*), and one lesser ape, the Hoolock gibbon *Hylobates hoolock* make up the rest of the count.

Nine of these are classified as Schedule I species – endangered and threatened species that are legally protected from hunting, poaching and trade – while the remaining 6 are listed as Schedule II species under the Indian Wildlife Act 1991. Ironically, the biggest threat to the continued existence of these species is forest fragmentation and increasing pressure on wild ecosystems brought about by human populations.

differences in social organisation, morphological qualities and habitat variations, are often helpful in understanding the evolution of behavioural patterns currently displayed by a species. Strepsirrhines display diverse social organisations, ranging from solitary foraging, through dispersed pair-living, to large gregarious groups that share a common home range. A brief look at the various social organisations exhibited by strepsirrhine species follows.

Cheirogaleidae: Among the cheirogaleid species, the gray mouse lemurs are nocturnal, solitary foragers who form sleeping associations of up to 15 members. Males may join these groups of females and offspring, or sleep alone. The female sleeping associations are stable, though it is uncertain if the females are related. Males and females have highly overlapping home ranges and both sexes have spatial access to several potential mates. The fat-tailed dwarf lemur sleeps in family groups that are made up of an adult pair and their offspring, and the range of the adult male coincides with that of the adult female. Pygmy mouse lemurs, on the other hand, sleep alone and do not form sleeping aggregations. In the Coquerel's dwarf lemur, adults sleep alone



Most lemurs are diurnal and live in groups of 3-10 individuals. However some species like the black lemur, Sanford's lemur, the white-fronted lemur, the crowned lemur, and the red-bellied lemur are also occasionally active at night.

or in groups of up to 5 individuals. Male home ranges typically overlap several female ranges, and several sleeping nests can be found clustered in the same area. The fork-marked lemur is described to exhibit 'social monogamy' i.e. an adult male-female pair and their offspring associate together and share a home range. However the cohesiveness of pair partners is rather low and the social organisation is more accurately described as comprising of 'dispersed pairs'.

Lemuridae: Most lemurs are diurnal and live in groups of 3-10 individuals. However some species like the black lemur, Sanford's lemur, the white-fronted lemur, the crowned lemur, and the red-bellied lemur are also occasionally active at night. A prominent feature of lemur social organisation is marked female dominance. In the majority of the species, females are socially dominant (i.e. they win in all aggressive fights with males) and/or have female feeding priority. It has been hypothesized that the primary reason for this lies in the highly seasonal environment of Madagascar, where these primates live. Successful reproduction and survival of offspring require that females have first access to food.

Ring-tailed lemurs live in groups of 3-25 individuals that share a common home range. Home ranges are defended, mainly by females, but overlap with those of neighbouring groups. Black lemurs are reported to usually live in social groups of between 7 and 10 individuals, although group sizes of between 2 and 15 have also been observed. Group sex ratio is often biased in favour of males. Black lemur groups maintain separate home ranges during the day, but several groups may congregate at night. Similarly, large groups of individuals that gather together to sleep at night, but break up during the day into smaller foraging sub-units, also occur in the white-fronted lemur, and the crowned lemur. The mongoose lemur lives in small family groups of an adult pair and their offspring. These groups typically occupy small home ranges that overlap with the home ranges of neighbouring groups.



The bamboo lemurs typically live in groups of 2-6 individuals, though in the Alaotran gentle lemur, larger gatherings can be seen at the end of the wet season. The black-and-white ruffed lemurs are usually found in family units of 2-5 individuals. Larger associations of 8-10 animals occur when several pairs join together in highly degraded forest zones.

Megaladapidae: Lepilemurids or sportive lemurs are nocturnal and solitary in their lifestyle. Adults sleep alone or together. Males have larger home ranges than the females and both sexes have overlapping ranges. Members of the same sex strongly defend territories against one another, using vocalizations, chases, and even fighting to drive trespassers out.

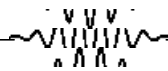
Indridae: Avahis or woolly lemurs are the only nocturnal species in this family. The basic group is composed of an adult male-female pair and their offspring. In the Western woolly lemur, home ranges of groups overlap considerably, whereas in the Eastern woolly lemur group ranges do not overlap. Predictably, there is also a great deal of inter-group aggression in the latter species, with much calling and chasing at group home range boundaries. Pair partners in the Eastern woolly lemur do not forage or travel together, but keep in contact during the night with 'distant communication' calls.

Named after the sound of their alarm calls, sifakas are relatively large-bodied diurnal strepsirrhines. Group size differs with the species, though generally they fall within the range of 2-9 individuals. Quality of habitat also affects group size, with larger groups forming in more degraded forest zones. In Verreaux's sifaka, females are socially dominant, and male dispersion occurs. Group size is usually limited to 3 animals, and it is common to find more males than females in a group. Coquerel's sifaka live in groups of 3-10 individuals, and age and sex composition of the groups vary widely. Here too, females are socially dominant to males.

Indris are diurnal and largest in size among extant strepsirrhines. The basic group here is composed of an adult male-female pair

Named after the sound of their alarm calls, sifakas are relatively large-bodied diurnal strepsirrhines.

Group size differs with the species, though generally they fall within the range of 2-9 individuals.



The aye-aye was considered a rodent rather a primate when it was first discovered. It has some specialized characteristics (for e.g. continuously growing large incisors, and a mobile third finger that can be twisted in any direction including backwards) unseen in other primates.

and their offspring. Larger groups of 7-8 individuals are rare, and tend to occur in disturbed forest areas. Females are socially dominant over males and have priority access to food resources. Females also lead group progressions on a regular basis. Groups are highly territorial, and there is minimal overlap with the home ranges of adjacent groups. Individuals from neighbouring groups use the common overlap area to engage in 'song' vocalisation battles to defend their home ranges.

Daubentoniidae: It is not surprising that the aye-aye was considered a rodent rather a primate when it was first discovered. For one, it looks completely bizarre, and for another, it has some specialized characteristics (for e.g. continuously growing large incisors, and a mobile third finger that can be twisted in any direction including backwards) unseen in other primates. Aye-ayes are nocturnal and solitary foragers who spend the major part of the night traveling and feeding. Adults sleep alone, and there is little contact between females. Male ranges overlap extensively, but female ranges do not overlap. Between the sexes, male home ranges overlap those of several females. The mating system is multimale-multifemale, with strong inter-male competition for a female in estrus. Females interact rarely and are usually highly aggressive. Following the birth of an infant, males and females remain in close proximity, with the male even sharing food with the infant.

Galagonidae: Bushbabies or galagos are nocturnal, solitary foragers that form daytime sleeping associations. The size of such sleeping groups is usually in the range of 2-8 members, though in some species it may be larger. The general pattern is a matriarchal system, wherein related females associate in groups and sleep together with their offspring. Males may sleep with the females or they may sleep alone. Males and females have overlapping ranges and the home range of a single male overlaps those of one or more female groups. Territoriality is year-round, and territory boundaries are signalled by scent marks and vocalizations. Females of one group are usually aggressive towards females of other groups. Males exclude conspecific males of



similar age and weight from their ranges, but tolerate the presence of younger and lighter males. The degree of this kind of tolerance varies between species, reaching a maximum in the brown greater galago. The Zanzibar bushbaby varies from the general bushbaby spacing system; here the range of an adult male coincides with the ranges of one or two females. Though they do not forage together, the adults of a group maintain contact during the night through vocalizations.

Loridae: In comparison to the galagos, the lorids are more solitary. Adults sleep alone or together, and though mother-offspring sleeping pairs occur, no matriarchal grouping has been reported in any of the species. Sleeping associations of more than 3 individuals has been reported only for the slender loris. Male home ranges are larger than female home ranges, and the general spacing pattern is characterised by male home ranges overlapping two or more female home ranges. Female home ranges overlap only minimally in the potto and the slender loris, whereas in the slow loris, female ranges overlap more than those of the males.

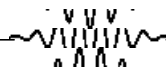
Against this background, it is interesting to examine the social behaviour of a nocturnal Indian strepsirrhine, the slender loris, and evaluate some of the more singular features of its social system.

Slender Loris

Physically, the slender loris has a ludicrous banana-shaped body perched on stilt-like legs, no tail, and huge eyes encircled by lighter markings (Box 9). The average weight is around 265 g, and the fur colour varies from dark grey to reddish brown. It is endemic to the Indian subcontinent, being found only in the dry and wet forests of Sri Lanka and southern India, and currently two species of slender loris are recognised: *Loris lydekkerianus* in India and Sri Lanka, and *Loris tardigradus* in south-western Sri Lanka.

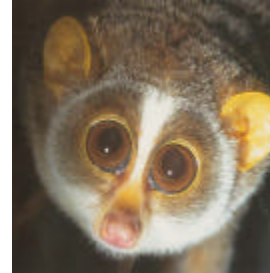
Slender lorises are nocturnal in their activity pattern. They

The slender loris is endemic to the Indian subcontinent, being found only in the dry and wet forests of Sri Lanka and southern India, and currently two species of slender loris are recognised.



Box 9. The Slender Loris: The Baby of the Forest

The slender loris is called *kadupapa* in Kannada, which quite literally translates as ‘forest baby’. In Tamil, it is called *thevangu*, and it is common for a Tamil speaker to liken a thin person to a *thevangu*. Unfortunately, however, this seeming empathy for the slender loris does not extend beyond its name. According to popular folklore, various body parts of the slender loris, most particularly its eyes, impart strength to the consumer, and potions made out of boiling its flesh and organs are recommended to cure illnesses.



Hunted for use in folk medicine, killed due to superstitious beliefs about the ill-luck it brings, trapped for laboratory dissections, and driven out of its natural habitat by forest fragmentation, the slender loris is being driven towards gradual extinction. Only pocket populations of the species survive today in scrubland, forest patches and orchards in some parts of peninsular India. Tragically ironic, when you consider the aeons that went into the evolution of the amazingly inconspicuous sociality of the slender loris.

Photo credits: www.primates.com

actively forage and explore during the night and sleep during the day. They are almost completely arboreal and prefer to move on thin branches that can be grasped by the digits of their limbs. Insects like ants, termites, walking sticks, and grasshoppers are eaten most often, though fruits of particular plant species like *Securinega* and *Ziziphus*, and gum from tree species like *Acacia* are also consumed. Typically, there is little direct contact between conspecifics during the night. Individuals however monitor each other's positions through indirect means of communication like vocalisations and urine-markings.

Home Range Overlap: Slender loris males have relatively large home ranges that overlap those of two or more females. Each female home range is also overlapped by more than one male's range. This kind of a range overlap system indicates that both males and females have access to multiple mates. While females usually do not trespass into other female ranges, movement of males into the home ranges of other males is more variable. Thus, while some males intrude, others do not; again, some

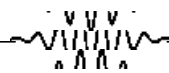


males are aggressively attacked for intruding, while others are not. The fact that females do not intrude into each other's home ranges may be an indicator of intense female-female competition. Males occasionally compete for females, but details of male-male competition are not clearly understood. Similar inter-male competition also occurs in certain species of galagos, and it has been hypothesised that, in these species, the regulating factor could be dominance rank (as indicated by body size), with males preventing similar-sized males from gaining access to females without wasting energy on smaller males. Another intriguing possibility, never really explored in wild primates including prosimians, is that personality and temperament differences between individuals could be responsible for differences in competitive strategies and individual behavioural patterns.

Sleeping Groups: Slender lorises sleep alone or in sleeping groups that consist of 2-6 members. Although individuals forage and explore alone during the night, members of a sleeping group meet up at particular trees (sleeping sites) at dawn and sleep together. Sleeping partners may be related, like mother-offspring-siblings, or they could be an unrelated male and a female. Females carry their offspring for the first few weeks following birth; after that they 'park' or leave their infants at the sleeping sites and forage alone during the night. At dawn they return to the sleeping site to sleep with the infants.

A sleeping group association is temporary and tends to be correlated with estrus cycling and the duration of lactation in females. Females usually come into estrus when they have been lactating for two months and male presence in sleeping groups increases significantly during this time. Hence, during the breeding season, the more common sleep group compositions are a lactating female and her offspring as well as adult male-female pairs and groups. With the end of lactation, females stop sleeping with their offspring regularly. However, if the offspring are twins, they continue sleeping together even in the absence of the mother. Even more noteworthy, the older sibling, if still present in the natal range, also groups up to sleep with them. The male

Slender lorises sleep alone or in sleeping groups that consist of 2-6 members. Although individuals forage and explore alone during the night, members of a sleeping group meet up at particular trees at dawn and sleep together.

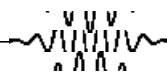


One of the more unusual aspects of social relationships in the slender loris is the relationship between the adult male and the female offspring of an adult female.

who had been sleeping with the female may now join the female's offspring to sleep together with them, even though sometimes the female may herself be absent in this association.

In fact, one of the more unusual aspects of social relationships in the slender loris is the relationship between the adult male and the female offspring of an adult female. Male and female slender lorises regularly exhibit dispersal away from their home ranges. Offspring may emigrate from their natal range as soon as they reach adult status, or they could move after reaching adulthood. Such migration is probably aimed at increasing reproductive success, as well as avoiding inbreeding, and crowding of the natal range. When immigrant males move into a range already occupied by a female and her offspring, they try to establish social relations with the offspring by playing and sleeping with it. Such overtures appear to be aimed at eventually establishing access to the adult female, for migrations significantly increase during breeding periods. But interestingly, even in the absence of the mother, the male sleeping partner continues to meet the female offspring to sleep with and allogroom her. Although the reasons behind such associations are not immediately clear, perhaps they represent strategies of males to establish social bonds with future mating partners?

Allogrooming/Play-wrestling: Apart from home range overlap and sleeping associations, allogrooming and play-wrestling sessions are significant indicators of inter-individual relationships. Although individuals meet up occasionally during the night to allogroom each other, such sessions are more common at dusk and dawn, when the animals either split from the sleeping group or meet to sleep together. Allogrooming sessions are sometimes interspersed with play-wrestling where two individuals hang upside down from a branch and mock-wrestle and play together. Inclusion of play-wrestling in an allogrooming session is idiosyncratic – some individuals never play-wrestle, while others habitually do. As in the case of male competitive strategies outlined above, is this variation in play-wrestling bouts also indicative of individual differences in temperament? Mirroring



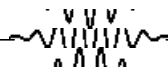
the variation in sleep group composition, allogrooming sessions can take place between mother-offspring pairs, siblings (siblings in this article refers to offspring of the same mother; whether they are full- or half-sibs is usually not known), unrelated adult males and females, as well as between an adult male and the offspring of an adult female.

Mother-infant and sibling-sibling interactions: The majority of social interactions in the slender loris are those between a female and her offspring and between siblings. A female sleeps with her offspring regularly until the beginning of weaning, and may also play-wrestle with and allogroom them. Even after the offspring is completely weaned, mother and offspring do meet to sleep together, though not as often as earlier. Offspring remain in the natal home range until they are 10-11 months old; thereafter, either the female or her offspring moves out of the home range.

Twin births are a common occurrence in the slender loris. Twin infants are parked separately for the first few days following commencement of parking, after this they are left parked together. Even though they explore and forage separately, they often meet up during the night to play. Comparatively, twins spend more time interacting with each other than they do with their mother. Twins playing together are reminiscent of gambolling kittens, as they suspend and swing themselves from tree branches, pounce on one other and grab and pull the playing partner's ankles. As they grow older, meeting up to play during the night gradually decreases, and twins older than 3 months do not meet up during the night to play. They continue to sleep together, however, and even when the mother stops sleeping with them (during and after weaning), twin offspring often continue to sleep together.

Apart from the close association between twins, older and younger siblings also often interact socially. Slender lorises are potentially able to give birth twice a year, in April-May and October-December. If the older offspring is still present in the home range when the female gives birth again, the older and younger

The majority of social interactions in the slender loris are those between a female and her offspring and between siblings.



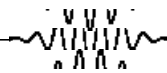
Male-female associations are likely to be strongly influenced by reproductive necessity on the part of the male to ensure first mating access to the female.

siblings share the home range with the mother and sleep together with her. What is intriguing here is that, not only do the older and younger offspring play-wrestle and allogroom at dawn and dusk when the group gathers to sleep together, but the older offspring also visits the younger siblings during the night to play with them. Even in the absence of the mother (as when she stops sleeping with the younger offspring during and after weaning), the older sibling joins the younger siblings to sleep with them. This association eventually terminates when the older sibling moves out of the natal home range. It is not known if emigrating individuals return to the natal range in the slender loris (emigrating males may return to the natal range in a bushbaby species), but it is interesting to speculate that in the eventuality of a return to the natal range, past associations between siblings may foster kin recognition in the future and facilitate sharing of range resources.

Reproductive Behaviour: Mating in the slender loris is promiscuous, with three to four males mating with one female in succession during a single mating session. Males constantly fight for mating access to the female, and it is possible that the male who mates first might be more successful than the others. As a corollary, it would appear that male-female associations are likely to be strongly influenced by reproductive necessity on the part of the male to ensure first mating access to the female. Male-female pairs that share greater home range overlap, sleep together and allogroom more often than do other pairs. Such an association, however, does not ensure first mating access to the female for the male. Whether other benefits accrue to either partner from such associations, or whether established 'friendships' between males and females result in mating preferences much later in time, remain to be discovered.

Future Research

The slender loris appears to be the archetype of a solitary primate species, with most of the intra-specific social interactions occurring in biological contexts like reproduction and



parental investment. However, certain aspects of its social behaviour excite attention and demand further research. One of these concerns the relationship between siblings. The bushbaby-like matriarchal grouping of females does not occur in the slender loris. However, it is notable that associations between siblings - older and younger, as well as twins - sustain themselves even in the absence of the mother. Taking into account that offspring are most likely to emigrate on reaching adulthood, this leads to some interesting questions: would a pair of twins, provided both survive to the same age, emigrate from the natal range together? If they did so, at what stage would they terminate their relationship, especially under conditions of competition for food and mates?

Other issues that would profit from more field research would be the long association between adult males and females, and the relationship between the adult male and the female offspring of the female sleeping partner. In the case of a male who was present in the range before the birth of the offspring, paternity, or at least its high probability, might partially explain investment in the association on the part of the male. However, this cannot explain the case of males who immigrated into the range after the birth of the offspring. It would also be interesting to test if similar relationships also develop between the adult male and male offspring of the female sleeping partner.

Suggested Reading

- [1] J G Fleagle, *Primate Adaptation and Evolution*, Academic Press, New York, 1988.
- [2] P Charles-Dominique, *Ecology and Behaviour of Nocturnal Primates*, Duckworth, London, 1977.
- [3] M L Roonwal and S M Mohnot, *Primates of South Asia: Ecology, Sociobiology and Behaviour*, Harvard University Press, Cambridge (Mass.), 1977.
- [4] S Radhakrishna and M Singh, *Social behaviour of the slender loris (Loris tardigradus lydekkerianus)*, *Folia Primatologica*, Vol. 73, pp.186-191, 2002.

It is notable that associations between siblings - older and younger, as well as twins - sustain themselves even in the absence of the mother.

Address for Correspondence
Sindhu Radhakrishna
National Institute of Advanced
Studies, IISc Campus
Bangalore 560 012, India.
Email:sindhu@nias.iisc.ernet.in

