

Behavioural variation in the Mysore slender loris *Loris lydekkerianus lydekkerianus*

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The Mysore slender loris, *Loris lydekkerianus lydekkerianus* is a nocturnal strepsirrhine primate endemic to India. As with other lorine species, there have been few studies on this taxon and much still remains unknown about it. During a 21-month study on a Mysore slender loris population in Tamil Nadu, southern India, we collected data on the ecology and behaviour of 32 identified individuals. Certain aspects of diet and social behaviour of lorises in this population vary from what is already known for the Mysore slender loris in another part of southern India, offering a new perspective into behavioural variations in this taxon. Evidence for behavioural variation in the Mysore slender loris is significant for two reasons – one, there are few instances of clearly documented intraspecific variation in wild nocturnal primate species and two, this flexibility, it would appear, allows the Mysore slender loris to inhabit and survive in degraded and disturbed habitats across southern India, an adaptability that is thus critically linked to its conservation status.

Keywords. Behavioural variation, conservation, habitat loss, Mysore slender loris.

INTRASPECIFIC variation in social organization and social behaviour has been reported in many primate species; several cercopithecine and colobine monkey species, for example, exhibit variable social organization and reproductive patterns in different sites across their geographical range^{1,2}. Primatologists have typically linked such within-species variation to the influence of ecological factors like distribution and type of food resources, demographic conditions, habitat modification, predation pressure and conspecific threats^{3–10}. Most studies on this topic, however, have tended to focus on the diurnal, group-living primates; less is known about within-species differences in the nocturnal solitary primates, largely because of the lack of long-term socio-ecological studies on many nocturnal strepsirrhine primates.

Nocturnal primates, in comparison to their diurnal counterparts, are less-documented and tend to be dismissed as a homogeneous, primitive group. Yet, studies in the recent past clearly attest that they are remarkably

diverse species that operate on complex social networks^{11,12}. Studies on the nocturnal mouse lemurs (*Microcebus* spp.) show that although they occupy a range of habitats and environmental gradients in Madagascar, habitat plasticity differs between species – some may inhabit many habitat/forest types, whereas others are more specialized^{13,14}. Intraspecific variation in the number of birth seasons and litter size has been reported for *Microcebus murinus*; very little difference, however, has been reported in social grouping patterns and mating systems of different populations of the species^{14,15}. Data available on the social systems of sportive lemurs (*Lepilemur* spp.) indicate a great deal of variation both within and among taxa. Initial studies on the white-footed sportive lemur, *Lepilemur leucopus* reported the species to be solitary^{16,17}. A subsequent study on the same population observed male–female and female–female pairs resting during the day, and duos or trios of individuals feeding together at night¹⁸. Similarly, Petter *et al.*¹⁹ characterized *Lepilemur edwardsi* as solitary, whereas Warren and Crompton²⁰ observed two or more individuals sleeping together during the night and three or four animals feeding together in the same tree in their study site in Ampijoroa, Madagascar. Accordingly, the latter defined the social system of the species as ‘noyau’ or dispersed harem system. On the other hand, Thalmann’s studies^{21,22} on the same population led her to describe the species as living in dispersed family groups, possibly even pair-bonded. Asian pottos (*Perodicticus potto*) and pygmy lorises (*Nycticebus pygmaeus*) have seasonal breeding patterns in the wild. But when maintained under captive conditions in the northern hemisphere, pottos often turn polyestrous, whereas the breeding patterns of pygmy loris remain seasonal²³.

Slender lorises (*Loris tardigradus* and *L. lydekkerianus*) are nocturnal strepsirrhine primates that are endemic to India and Sri Lanka²⁴. Despite the slew of studies on their behaviour and ecology in the last decade, they still remain among the least known of all primate species¹². The Mysore slender loris *L. lydekkerianus lydekkerianus* is endemic to India and inhabits a range of habitats, from deciduous forests and scrub jungles to croplands and urban forests in the southern part of the country^{25,26}. Data from two studies on the behavioural ecology of the taxa report that the species is predominantly solitary, arboreal

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and insectivorous, with a preference for thin and oblique substrates^{27–29}. Adult males and females have individual home ranges and sleeping group associations are usually composed of a female and her offspring^{30–32}.

Studies on geographically separate populations of the same species provide unique opportunities to examine the effect of ecology on the social organization of a species or the form and extent of behavioural flexibility displayed by the species¹. Two studies on a Mysore slender loris population in Ayyalur, southern India, provide interesting data on the ecology, behaviour and reproductive biology of *L. lydekkerianus lydekkerianus*^{27,28,30–35}. In the present study we examine the feeding ecology and social behaviour of a geographically separate Mysore slender loris population, also in southern India, and evaluate the differences between the two populations in terms of variation in diet and social behaviour. The results of this study are significant for two main reasons: (i) it represents evidence of intraspecific variation and adaptability in a little-known endemic primate, (ii) it broadens our understanding of the behavioural ecology of wild, nocturnal primates.

Methodology

Study area

The present study was conducted in a 7.2 ha area of open scrub land (10.05°N, 78.13°E) in Malapatti (henceforth

referred to as site M), Tamil Nadu, southern India (Figure 1). The study site was a mosaic of small farms, thickets, and tamarind and fruit orchards; the main tree species were *Prosopis*, *Tamarindus*, *Cocos* and *Syzygium*. Farm boundaries were marked by *Euphorbia* hedges or thick layers of *Prosopis* and *Acacia* branches, and these were the main pathways used by the lorises as they traversed across the study area. High anthropogenic disturbance in the form of constant cattle and movement of people, browsing and grazing by cattle, felling of *Prosopis* bushes and regular alterations in the farm boundaries created a highly disturbed and unstable habitat for the lorises.

One of us (S.R.) had previously conducted a study on the behaviour and ecology of a geographically separate Mysore slender loris population in Ayyalur, Tamil Nadu, southern India. Ayyalur (henceforth referred to as site A), lies about 50 km north of Malapatti (Figure 1), and both study areas fall within the same broad forest type of Tropical Thorn Forest³⁶. However, there were some ecological differences between the study sites in terms of size, human movement and diversity of plant species. The 16 ha site A comprised of State-protected Reserve Forest in one part, where the vegetation was largely dominated by *Acacia*, *Euphorbia* and *Albizzia* species, and orchards and croplands in the other part, where the main plant species were *Tamarindus* and *Eucalyptus*^{27,28}. Human and cattle movement was partially restricted in the Reserve Forest, but was higher in the orchards and croplands. The



Figure 1. Map of southern India showing the Malapatti and Ayyalur study sites.

loris study population here included 28 individuals²⁸. In comparison, site M being composed almost wholly of orchards and farms, had low tree species diversity and experienced constant human and cattle movement. Despite the smaller size of this site, the loris study population here comprised 32 individuals.

Behavioural observations

The study extended from October 2005 to June 2007. The study methods used were similar to those followed in site A^{28,30}. We located slender loris individuals by their distinctive eyeshine and followed focal animals through the night from 1800 to 0600 h using red cellophane paper-covered Petzl headlamps. We individually identified study animals through distinctive physical markings on their bodies and locomotory idiosyncrasies^{27,28}. We employed instantaneous sampling technique with 5-min intervals to record the behavioural data of study individuals, and *ad libitum* sampling to collect information on sleeping group compositions, mating events, and all instances of feeding and social interactions³⁷. Duration of gestation was calculated from the date of copulation of the female to the date of birth of her offspring. Allogrooming, play-wrestling, maintaining spatial proximity (autogrooming, locomoting/sitting beside each other or within 5 m of each other) and sniffing another individual without eliciting an aggressive reaction were considered affiliative social interactions, while repeated vocalizations (whistles, chitters and/or growls) directed at another individual/s, lunging at, chasing, wrestling and biting another individual were considered agonistic interactions. We collected data for a total of 899 h of observation on 32 identified individuals. Study individuals comprised 11 adult females, 10 adult males, seven subadult and juvenile individuals, and four infants. Only data relating to feeding records, social interactions and reproductive life-history schedules of the study individuals are presented in this article.

Results

Feeding ecology

Site M: We collected a total of 62 feeding records during the course of the study. Loris individuals fed on insects, seeds, fruits, small vertebrates and plant exudates. Insects contributed to 60% of the animals' diet, whereas flowers and exudates comprised 13%, fruits and seeds 24%, and animal prey 3% of the diet. Lorises fed on the flowers of *Madhuca longifolia*, pods and seeds of *Prosopis juliflora*, and fruits of *Psidium guajava*, *Syzygium cumini* and *Pithecellobium dulce*. They also consumed dried gum or sap from the outer surface of *Prosopis* and *Tamarindus* pods and less frequently, from the branches of *Prosopis*.

They did not scrape tree trunks to exude gum flow. On two occasions, an adult female caught and ate a mouse and a gecko. Vertebrate feeding appeared to be opportunistic and we did not observe lorises foraging or hunting for small vertebrates.

Site A: Insects formed a predominant part of slender loris diet at 91.48%, with plant material and gum forming 6.61% and 1.9% respectively. Study individuals fed on the fruits of *Securinega leucopyrus* and *Ziziphus oenoplia*, and on gum from the bark of *Albizia* and *Acacia* tree species²⁸.

Social behaviour

Site M: We recorded a total of 115 social interactions; 53% of these were affiliative and 47% of them agonistic. Affiliative interactions ($n = 61$) largely occurred between mother and offspring (45.9%), siblings (18.0%), adult males and females (16.4%) and between adult males and offspring of the resident females (18.0%). Most of the agonistic interactions ($n = 54$) occurred in the context of female territoriality (46.3%), when adult females vocalized/fought with neighbouring females or their offspring during range intrusions. Agonistic interactions also occurred between adult males and females (14.8%) when females vocalized to deter male advances, between males (13.0%) in mating contexts or when they vocalized at each other from the resident females' ranges, and between adults and juveniles (9.3%) when females rejected attempts by offspring to feed at the nipple or adults rejected attempts by juveniles to allogroom or play.

We obtained data on adult male–female associations on the basis of social interaction patterns and sleep-group compositions of four females and four males. Adult females interacted and slept together with only a single adult male at any period of time; adult males, however, attempted to associate with more than one female during the same period of time (Table 1).

Site A: Social interactions between loris individuals were largely affiliative (98%) and rarely agonistic (2%). Affiliative interactions occurred between mother and offspring (39.1%), siblings (28.7%), adult males and females (8.6%), juveniles and adults (14.7%), and subadults and adults (8.9%). The majority of agonistic interactions (48%) occurred between adult males and females, when the latter rejected male advances. Agonistic interactions also occurred between adult females during territorial conflicts (13%), and between adult males in mating contexts or when they vocalized at each other from their home ranges (19.4%). Adult males and females slept together and socially interacted with more than one female and male partner respectively, at the same period of time³¹.

Table 1. Adult male–female associations in Malapatti

Male–female pair	Social interaction			Social interaction between male and offspring of the female (SI Tog + Af Int)	Duration of association
	SI Tog	Af Int	Agg Int		
♀WI–♂ST	5	2	–	8	October 2005–August 2006
♀VI–♂JA	5	5	3	4	February 2006–May 2007
♀MA–♂CL	4	–	–	2	April 2006–January 2007
♀PB–♂CL	–	2	2	–	August 2006; March–May 2007
♀WI–♂CH	3	1	–	–	September 2006–April 2007
♀PB–♂JA	–	–	1	–	June 2006

SI Tog, Sleep together; Af Int, Affiliative interaction; Agg Int, Aggressive interaction.

Table 2. Comparison between the Ayyalur and Malapatti populations

Parameter	Ayyalur site	Malapatti site (the present study)
Dietary composition	Insects: 92%; plant material: 7% and gum: 2% (ref. 28)	Insects: 60%; flowers and exudates: 13%; fruits and seeds: 24% and animal prey: 3%
Social behaviour	98% interactions affiliative and 2% agonistic ³¹	53% interactions affiliative and 47% agonistic
Agonistic interaction	48% between adult males and females for deterrence of male advances; 13% between adult females during territorial conflict and 19% between adult males ³¹	15% between adult males and females for deterrence of male advances; 46% between adult females during territorial conflict and 11% between adult males
Adult male–female social associations	Adult females socially associated with more than one male at a given period of time ³¹	Adult females socially associated with only one adult male at a given period of time
Mating system	Promiscuous ³⁴	Promiscuous
Litter size	Twins and singletons ³⁴	Twins and singletons
Gestation period (month)	5.5 (ref. 34)	5.3
Inter-birth interval (month)	7 (ref. 34)	9
Age of infant parking (weeks)	3 (ref. 35)	6
Age of weaning (month)	3.8 (ref. 35)	3.9

Reproduction

Site M: We observed one mating event in December 2006, when three males engaged in physical interactions for access to an adult female. We only recorded births ($n = 11$) in January, May, June and July, with the highest number of births occurring in May ($n = 5$). Births did not differ significantly across different months of the year (χ^2 test: $\chi^2 = 0.00094$, $df = 11$, n.s.). We did not collect sufficient information to check for patterns of estrus seasonality. Four females gave birth twice during the study period; based on these data, we calculated the gestation period to be 5.3 months, and the mean inter-birth interval to be approximately 9 months ($n = 4$, range = 5.4–12.0 months, mean \pm SD = 8.9 ± 3.3 months).

Site A: The mating system was observed to be promiscuous with 3–4 males competing for mating access to a female during copulatory events. Reproductive seasonality occurred in this population, with a significant peak in estrus and birth during April–June and October–December. Gestation lasted 5.5 months and a mean inter-birth interval of 7 months was recorded³⁴.

Parking and weaning

Site M: The studied females parked their infants when they were about six weeks old ($n = 5$, range = 37–49 days, mean \pm SD = 41.8 ± 4.4 days). Infants were parked at the sleeping site at dusk and retrieved the next morning. Weaning, documented in the case of a pair of twins, began when the infants were 118 days (3.9 months) old.

Site A: Parking began when infants were three weeks old, and weaning when offspring were about 115 days (3.8 months) old³⁵.

Behavioural variation

A comparison of the behavioural patterns displayed by the Ayyalur and Malapatti populations reveals significant variations in feeding ecology, social behaviour and reproductive life-history schedules (Table 2). The two loris populations differed in their diet, social behaviour, social structure and age of parking, but were similar in their mating system, litter size, duration of gestation and age of weaning.

Discussion

Primate species respond in many ways to alterations in their habitat – changes in population density, breeding success, feeding ecology, group size, and juvenile/infant mortality rate have been reported to occur under conditions of habitat disturbance such as logging, hunting, food scarcity and fragmentation^{38–41}. Primate populations experiencing high-density pressures also show marked changes in social structure and behaviour; these effects, however, tend to be mediated by environmental or species-specific characteristics and rarely follow a common trajectory^{42–46}.

The findings of this study present new perspectives on behavioural variation in the Mysore slender loris. Comparisons between the population in the present and that in the Ayyalur study^{27,28,30–35} reveal several differences in diet, social behaviour and reproductive biology. The Mysore slender loris has been previously described as an insectivorous species, feeding almost exclusively on insects^{28,29}. Loris individuals in the present study population were primarily insectivorous; however, they also included large amount of plant material, particularly fruits and seeds in their diet. Plant species diversity and composition strongly influence insect abundance and diversity^{47,48}, and it is likely that the agricultural mosaic, sparse habitat and low tree species diversity in site M corresponds to low insect density and diversity. The greater catholicity in diet exhibited by the loris population in site M may thus be in response to such a potentially low insect diversity.

The high rate of aggressive encounters, particularly female territorial aggression, as well as the longer inter-birth interval and delayed age of infant parking observed in the Malapatti population are likely related to the higher density of lorises at the site and the consequent effects of crowding. We argue that another significant variation which occurs in the Malapatti population, viz. the unimale social association for females, as apposed to the multimale social association pattern seen at Ayyalur, is also a product of similar ecological factors. Due to poor habitat quality and the resulting competition for food resources, it would be more beneficial for females in Malapatti to limit the presence of males in their ranges to one^{49,50}. Hence females may not actively resist residency of a single male and may indeed prefer to socially associate with one male⁵⁰. Inter-population variations in *L. l. lydekkerianus* diet, social behaviour and life-history schedules thus appear to be related to the different habitats of the two populations and the environmental stresses caused by overcrowding and habitat instability in Malapatti.

Previous studies on the reproductive biology of the Mysore slender loris have differed in their conclusions on reproductive seasonality in the taxa^{51–57}. For example, Swayamprabha⁵⁷ concluded that the slender loris was not

a seasonal breeder, whereas others^{52,54,55} claimed seasonality, but disagreed on their identification of the breeding months and duration of the estrus cycle. In all these studies, the study animals were collected near the city of Bangalore in southern India. Our present findings indicate that the discrepancies between the results of these studies may be due to variations between loris populations in response to local ecological conditions.

The most puzzling question raised by this study refers to the ‘attractiveness’ of site M as a slender loris habitat. Despite the poor habitat quality, the site density was much higher than that of site A. We discerned no particular advantages in site M that might make it a more loris-suitable habitat than site A. This suggests that site M may be an ecological trap^{58,59}. Primate species adapt differently to disturbances in the habitat, and factors that allow some species to persist or survive well, while others are adversely affected, are still poorly understood⁶⁰. The Mysore slender loris occupies a range of habitats across southern India. The taxon also seems to thrive near human occupation; some of the highest densities for *L. l. lydekkerianus* are from disturbed and degraded habitats near human habitations^{25,26}. With its apparent preference for human-modified habitats and ability to colonize new sites or adapt successfully to habitat alterations, *L. l. lydekkerianus* possesses the hallmark of a pioneer species^{61,62}. In today’s global scenario of increasing loss in forest cover and fragmentation, adaptation to a range of habitat types increases the chances of survival of a species. Furthermore, in the absence of hunting pressures, tolerance or preference for disturbed habitats and proximity to humans may even improve the conservation status of a species⁶³. However, existence of species in forest fragments and disturbed habitats carries its own costs^{40,63} and the long-term consequences of this, as well as ecological traps such as Malapatti, on *L. l. lydekkerianus* are yet to be fully understood. Comparative studies on different loris populations and behavioural adaptations within these populations will throw better light on the long-term survival ability of the species and the management regimes that need to be adopted for it in India and Sri Lanka.

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