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Infant development in the slender loris (*Loris lydekkerianus lydekkerianus*)

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In this article we present data on infant development in wild slender loris, a nocturnal primate species. The behavioural ecology of the grey slender loris *Loris lydekkerianus lydekkerianus*, a nocturnal strepsirrhine, was studied for 21 months (October 1997–June 1999) in a scrub jungle in Dindigul, south India. A total of 22,834 scans were collected during 2656 h of observation on identified and unidentified lorises using instantaneous point and *ad libitum* sampling methods. Developmental schedules were observed for twelve individuals born during the course of the study period. A greater number of twin births were observed than singleton births and more isosexuals than heterosexuals. Infants were parked at the age of 3 weeks and weaned by 5 months of age. Individuals showed significant developmental differences in their activity schedules. Females appeared to reach sexual maturity by 10 months of age. Social interactions with related conspecifics decreased with age and adult slender lorises did not show differences in social time spent with related and non-related conspecifics.

MEMBERS of the suborder Strepsirrhini (Order Primates)¹ are distinctive in their retention of primitive anatomical and behavioural characteristics and short life-history schedules. Some of the significant variables that measure infant development in nocturnal strepsirrhines are litter size, mode of infant carriage, presence or absence of infant parking, period of lactation and age at sexual maturity. Within the infraorder Loriformes (angwantibos, pottos,

lorises and bushbabies)¹, the lorids (angwantibos, pottos and lorises) typically have lower developmental and reproductive rates in comparison to similar-sized galagos (bushbabies)^{2–4}. Litter size in lorids and galagos appears to be linked to the stability of the habitat more than body size: species occupying harsher environments tend to have higher reproductive rates^{3,5}. Strepsirrhine neonates are carried for short periods following birth and mode of infant transport can be oral (*Galagos* bushbabies, *Cheirogaleus* dwarf lemurs, *Microcebus* mouse lemurs) or the abdominal fur of the mother (*Loris* slender loris)^{3,6,7}. Infant parking is typical of the Loriformes, wherein infants are left alone in the nest or near the sleeping site while the mother forages. Females may return to nurse the offspring and move it from one site to another^{3,8}. Ages of weaning and sexual maturity are not well represented in the nocturnal strepsirrhines; limited information details that cheirogaleids are weaned when 5–6 weeks old, galagos at 6–12 weeks and lorids at 12–26 weeks. Cheirogaleids are reported to attain sexual maturity when 9.5 months old, lorids at 17–21 months and galagos at 8–24 months^{3,9,10}.

The slender loris (Strepsirrhini: Loridae)¹, a nocturnal lorine, inhabits the forests of south India and Sri Lanka. Recent taxonomic revisions recognize the existence of two species – the red slender loris (*Loris tardigradus*) in southwestern Sri Lanka and the grey slender loris (*Loris lydekkerianus*) in south India and Sri Lanka¹. Field information on their behavioural ecology is meagre, and the little that is available is due to recent efforts^{11–16}. Observations in captivity show that the neonate is born with its eyes open but tends to keep them closed most of the time

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for the first few days¹⁷⁻¹⁹. Infants display righting, holding and climbing reflexes from birth, and cling onto the mother's fur without any assistance from the latter¹⁷. Females groom their infants intensely for the first 3 days following birth, but thereafter, only when the infant vocalizes^{17,19}. Litter sizes have been reported to be single²⁰, usually twins²¹, equal distribution of twins and singletons²² and a higher incidence of singletons²³. According to some authors, infant parking is absent¹⁹ or uncommon²⁴, while others observe that infants were parked when a month old^{2,25}. Disparate conclusions also characterize records on duration of lactation: Hill²⁶ and Ramaswami and Kumar²⁷ claim that it is long, while Goonan¹⁹ gives a period of 4–5 months. Lactating females have been described to exhibit a prominent lacteal tract^{22,23,28}. Ramakrishna and Prasad²⁹ estimate that a slender loris female attains sexual maturity at 12–15 months of age, while Izard and Rasmussen²³ calculate the same to be 10 months of age. A male slender loris is said to be sexually mature when 10–11 months old²⁹. This article presents data on infant development in wild slender lorises from a dry scrub habitat. As the study was strictly observational, particulars on litter size, age of infant parking, period of lactation, age of sexual maturity, and differences in activity schedules and social relations are described to show developmental changes in the slender loris.

Methods

The study was conducted at the Beerangi Karadu hill range (10°29'N and 78°10'E), Dindigul district, Tamil Nadu, south India. For location and detailed description of the study area, see Radhakrishna and Singh¹⁶.

The study began in October 1997 and concluded in June 1999. Study animals were individually identified by distinctive physical markings on their bodies and locomotory idiosyncrasies¹². They were followed during the night and observed using red cellophane paper-covered^{8,30} Petzl headlamps. The average follow-time of an animal based on 187 all-night (from the sleeping site at dusk to the sleeping site at dawn), and partial-night (more than five continuous hours) follows was 9.7 h. Five-minute instantaneous scan and *ad libitum* sampling techniques were used on focal animals usually chosen randomly. A total of 22,834 scans were collected during 2656 h of observation; 21,019 on 28 identified individuals and 1815 scans on unidentified individuals.

The five-minute instantaneous scan sampling^{31,32} was used to record habitat variables and the behavioural categories of the focal animal and the *ad libitum* sampling to record complete sequences of social interactions and feeding bouts of focal individuals. Six main behavioural categories were recognized: locomotion (active behaviour that occurred without an obvious immediate goal); exploration (activity by the animal to investigate the environ-

ment); feeding (ingestive behaviour), inactivity (passive behaviour); social behaviour (behaviour engaged in while in physical contact with, or in the same/adjacent tree as one or more conspecifics), and self-directed behaviour (activities performed by the animal on itself).

Study females carried their infants ventrally when they retrieved them at dawn in order to suckle them. The offspring could not suckle if they were not allowed access to the mother's abdomen or chest. Hence when the females refused to carry their offspring when they joined them to sleep or stopped sleeping with them, it was assumed that weaning had begun. Time spent by a female carrying her infant before parking indicates biological dependence of the infant, and hence was not included for calculations of social behaviour. Age of sexual maturity in study females was determined based on physical signs of estrus in the females, and change in the behaviour of resident and neighbouring males towards them. Bigger body size and elongated nipples distinguished multiparous females from the primiparous ones.

Four main age categories, viz. 0–3 months infant, 3–9 months juvenile, 9–12 months subadult and 12 months + adult were recognized, based on the physical and social development of the animal. These four main age classes were subdivided into 12 categories (3rd week to 1 month, 4–6 weeks, 6–8 weeks, 2–3 months, 3–3.5 months, 3.5–4 months, 4–4.5 months, 4.5–5 months, 5–7 months, 7–9 months, 9–12 months, 12 + months) for analyses of social relations with respect to developmental changes.

Data were analysed using non-parametric tests³³. The Wilcoxon's matched pairs signed ranks test and the Mann-Whitney *U* test were used to compare differences in developmental schedules across age classes. χ^2 and Wilcoxon's matched pairs signed ranks tests were applied to test for significant differences in social time spent with related and non-related conspecifics across age classes. Kendall's rank correlation test checked for correlations between social time spent with related or non-related conspecific and age of animal. Twin births were considered as single datapoints when basic statistics was calculated for parking and weaning, as twin infants were parked and weaned at the same time. All analyses were performed using the software Statistica, ver 4.5 and Microsoft Excel 2000.

Results

Birth

Among the twelve infants born in the study area, ten were twins and two were singletons (Table 1). Two infants (CU and BO) died before their sex could be identified. At the end of the study period, only five of them were present in the study area. The rest had disappeared from the study area (IS and AN) or had died (CU-CH, PU-BO and KI).

Table 1. Identity and sex of infants

Infant identity	Sex	Year of birth	Singleton/ twin	Birth type		When last seen	
				Isosexual/ heterosexual	Identity of mother	Age (months)	Status
CU	?	Mar 1998	Twin	?	MO	1	Dead
CH	M	Mar 1998	Twin	?	MO	4	Dead
IS	F	Apr 1998	Singleton	–	IN	12	Disp
PU	F	May 1998	Twin	?	TI	12	Dead
BO	?	May 1998	Twin	?	TI	1	Dead
KI	F	Jul 1998	Twin	Isosexual	GA	6	Dead
AN	F	Jul 1998	Twin	Isosexual	GA	10	Disp
LA	F	Nov 1998	Twin	Isosexual	IN	7	Alive
KU	F	Nov 1998	Twin	Isosexual	IN	7	Alive
SL	M	Nov 1998	Singleton	–	MO	7	Alive
GE	M	May 1999	Twin	Isosexual	MO	1	Alive
SE	M	May 1999	Twin	Isosexual	MO	1	Alive

Disp, Disappeared from study area.

For the first two days following parturition, neonates had their eyes closed for the major part of the night. They clung onto the ventral fur of the mother and were carried unsupported by her for the entire pre-parking period. Females rarely groomed their infants during the time they carried them in the pre-parking stage; allogrooming was usually confined to the sleeping sites at dusk and dawn. Individuals other than the mothers were never seen to carry infants, nor make any attempt to do so.

Parking

Study females usually began parking their infants when they were three weeks old ($n = 4$, mean \pm SD = 22.75 \pm 8.18, range = 14–33 days). Infants were parked at the sleeping site at dusk and retrieved the next dawn. Individual differences were seen in the duration and pattern of parking practised by the females. Female MO ‘part-parked’ (park one night and carry the following night or park for a few hours and carry the remainder of the night) her twin infants CU–CH for the first few weeks. CU died aged 1.5 months, and CH was completely parked when 2 months old. Female TI also practised part-parking once – she visited her infant PU during the night and carried her away at 3.00 a.m. Separate parking, i.e. independent parking of twin infants for the first few days following commencement of parking was seen with twin infants LA–KU and SL–GE.

Developmental schedules

Infants did not differ from juveniles, nor did juveniles differ from subadults in the time spent in the behavioural categories of locomotion, exploration, feeding, inactivity, social and self-directed behaviour. (Infants and juveniles:

Wilcoxon’s matched pairs signed ranks test: $n = 7$, ns; Loc: $T_s = 7$, Expl: $T_s = 5$, Feed: $T_s = 3$, Inac: $T_s = 3$, Soc: $T_s = 10$, Self: $T_s = 7$. Juveniles and subadults: Wilcoxon’s matched pairs signed ranks test: $n = 3$, ns; Loc: $T_s = 0$, Expl: $T_s = 0$, Feed: $T_s = 0$, Inac: $T_s = 0$, Soc: $T_s = 0$, Self: $T_s = 0$.) Subadults differed from adults significantly only in the time spent on self-directed behaviour. (Mann–Whitney U test: $n = 5$, 10; Loc: $U = 11$, ns, Expl: $U = 25$, ns, Feed: $U = 13.50$, ns, Inac: $U = 13$, ns, Soc: $U = 20$, ns, Self: $U = 6$, $P < 0.05$.)

Post parking, infants slept for short periods during the night ($n = 37$, mean \pm SD = 1.88 \pm 1.09, range = 0.5–5.5 h). This decreased with age, and usually infants older than 2.5 months ($n = 5$, mean \pm SD = 2.5 \pm 0.71, range = 2–3.5 months) stopped sleeping during the night. This is reflected in the activity schedules of the age classes – infants spend most of their time (43%) inactive and are most inactive in comparison to the other age classes. Subadults spend the most time on exploration, and adults the least; the reverse is true for feeding. In the social category, infants spend the most time and adults the least (Figure 1).

Weaning

Among study individuals, weaning usually began when the offspring was about four months old ($n = 5$, mean \pm SD = 115.20 \pm 10.66, range = 99–125 days). It lasted about a month ($n = 5$, mean \pm SD = 30 \pm 9.62, range = 16–41 days) and all offspring were completely weaned by 5 months of age. The first sign of weaning lay in the female’s refusal to carry the offspring when she joined her/him to sleep at dawn. A week or so later, she would stop joining her offspring to sleep and this marked the end of weaning. Post-weaning, when the female rejoined the offspring to sleep, the offspring would make no attempt to climb onto the female’s abdomen.

Females with twin offspring displayed a distinct lacteal tract during the lactating period, though this was not observed in females who gave birth to singletons.

Social relations

Time spent with related and non-related social partners significantly differed as slender loris infants developed to adulthood (Wilcoxon's matched pairs signed ranks test, $n = 12$, $T_s = 4$, $P < 0.01$; Figure 2). A significant negative correlation was seen between time spent socially with related conspecifics and age of the individual (Kendall's rank correlation: $n = 12$, $\tau = -0.78$, $P < 0.01$) and significant positive correlation between time spent socially with non-related conspecifics and age of the individual (Kendall's rank correlation: $n = 12$, $\tau = 0.80$, $P < 0.01$).

Until 6 weeks old, study infants spent 100% of their social time with related conspecifics. From 6 weeks to

4.5 months of age, individuals significantly spent more time with related conspecifics (χ^2 test: $df = 1$, $P < 0.01$; 6–8 weeks: $\chi^2 = 35.37$; 2–3 months: $\chi^2 = 265.79$; 3–3.5 months: $\chi^2 = 115.28$; 3.5–4 months: $\chi^2 = 44.29$; 4–4.5 months: $\chi^2 = 13.89$). From 4.5 to 9 months of age, there was no significant difference between time spent with related and non-related conspecifics (χ^2 test: $df = 1$; ns, 4.5–5 months: $\chi^2 = 1.68$; 5–7 months: $\chi^2 = 0.60$; 7–9 months: $\chi^2 = 1.02$). Subadults significantly interacted more with related conspecifics (χ^2 test: $df = 1$; $\chi^2 = 9.85$, $P < 0.01$). No significant difference was seen in time spent by adults with related and non-related individuals (χ^2 test: $df = 1$, $\chi^2 = 0.49$, ns).

Twins spent 75.03% of their social behavioural time with each other and 16.28% with the mother. Female KI spent 68.10% of her social behavioural time with female twin AN and AN spent 58.87% of her time with KI. Twins LA–KU spent 86.67% of their total social behav-

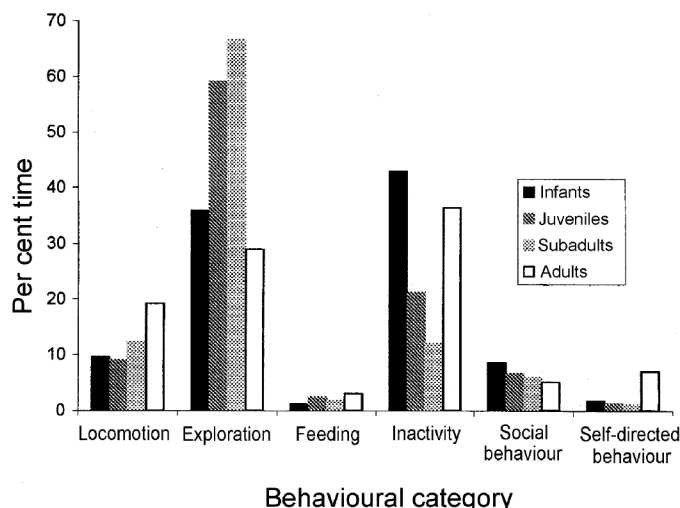


Figure 1. Developmental changes in activity schedule.

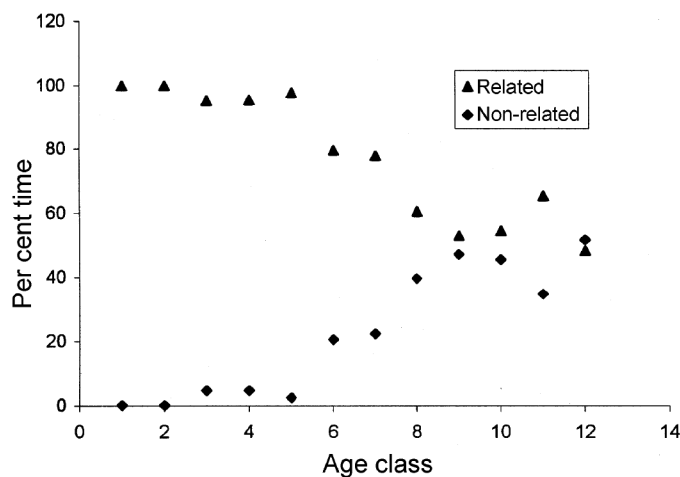


Figure 2. Time spent with related and non-related partner in different categories.

Table 2. Sexual maturity in slender loris females

Identity of female	Age of female (months)	Evidence	
		Behaviour of female	Behaviour of male
IS	9.5	Reddening of genitalia; ranges outside natal range and sleeps alone there	
	10.5	Reddening of genitalia	
	11.5		Male from neighbouring range approaches for the first time
	11.5	Reacts aggressively to resident male's approach	
	11.5	Allogrooms with male from neighbouring range; hereafter disappears from natal range	
AN	9.5		Resident male grooms and sniffs her
	10	Disappears from natal range	

journal time with each other. Infant twins met frequently during night to play. This decreased as they grew older and by the time they were three months old, social interactions were limited to allogrooming and playwrestling at dawn and dusk. Social interactions were also observed between subadult and juvenile siblings, if present at the same time in the home range.

Sexual maturity

Study females appeared to attain their first estrus when they were about 9 to 10 months old. Clearly discernible signs leading to assumptions of the age of sexual maturity are presented for two females IS and AN in Table 2. Signs of sexual development were also accompanied by changes in ranging patterns in the two females, and both of them disappeared from the study area when they reached 10–11 months of age. Taking into account the gradual change in ranging pattern and the attainment of sexual maturity, it is assumed that the disappearance of the females was due to migration from the natal range.

Female PU was 11.5 months old when she died. No obvious signs of sexual maturity were observed in her; however, a few days prior to her death, PU began to range and sleep outside her natal range.

Discussion

Birth and developmental schedules

In the present study, twin births occurred more often than singletons, and isosexuals more than heterosexuals. Though the sample size is too small to arrive at any conclusions about slender loris birth ratios, it is interesting that an earlier study²² concluded that the ratio of twins and singletons in slender loris births was almost equal, and that there were as many isosexuals as heterosexuals.

Parking of study infants began when they were three weeks old. Female MO's unusual practice of early part-parking followed by complete parking when the offspring was 2 months old, was most likely due to her primiparous stage. This hypothesis is supported by the observation that MO parked her later offspring when they were 3 weeks old. Charles-Dominique⁸ also comments that a potto (*Perodicticus*) mother may park her infant during one night and carry it the following night. The separate parking of twin offspring by all the study females in the early stages of parking is particularly noteworthy. Infants move very little in the first couple of days of parking, and in case of a predator attack, would not be able to defend themselves. The costs of maternal investment require that potential losses be kept to the minimum, and this could explain the occurrence of initial separate parking. Separate parking of twins has also been seen in galagos³⁴.

Meier and Preuschoft³⁵ note that the first independent locomotion of slender loris infants begins only when they are around 5 to 7 weeks old. According to Goonan¹⁹ however, infants first begin to leave their mothers at the age of 21 days. This fits in with the present observations that infants are parked when 3 weeks old. Nekaris¹¹ reports that slender loris females park infants for a portion of the night from the third to the fifth week, and for the entire night when the offspring is six weeks old. The potto and the angwantibo have been reported to park their infants suspended beneath a branch within 3–8 days following birth^{8,36}. Study infants were never observed to follow the mother, as has been documented for the *Perodicticus* (potto) and *Galago demidovii* (Demidoff's bushbaby) by Charles-Dominique⁸. Similar behaviour has been recorded in wild slow lorises too, and Wiens³⁷ notes that slow loris infants did not at any time follow their mothers or other conspecifics. However, Nekaris¹¹ reports that after a period of parking, slender loris juveniles followed the mother around the home range.

Izard and Rasmussen²³ describe a lactation period of 5–7 months, while Goonan¹⁹ interprets infants being carried

only occasionally when they were 2 months old as the beginning of weaning. According to Goonan¹⁹, weaning began when the infant was 2 months old and ended when it was about 4–5 months old. Schulze (pers. commun.) discovered a slight lengthening of the lactation period in females if they gave birth to twins. While lactation usually lasted for about 5 months, it lengthened to 5.8 months in the case of twins. Infants observed in the present study were observed to catch their first insects by the time they are three weeks old. However, they continued to suckle until they were about 4–4.5 months old. Lemur infants also continue to sleep with their mothers and suckle even after they begin to take solid food³⁸.

In this study, females with singleton offspring did not exhibit the naked lacteal tract, though Izard and Rasmussen²³ report that their study females with singleton offspring displayed it. Izard *et al.*¹⁰ observe that slow lorises do not exhibit the naked lacteal tract.

Development does not appear to bring about any significant changes in the time spent in various behaviours. The time spent by subadult individuals on exploration is a reflection of their ranging patterns. Study subadults enlarged their home ranges by including areas outside the mother's range, and later migrated from the natal range too^{15,16}. A combination of several factors – mother–offspring interactions, sibling interactions and social interactions of the infant with other co-sleeping partners – accounts for the greater social behaviour shown by infants in comparison to the other age classes¹⁶. Schulze (pers. comm.) notes that development is faster in slender loris singleton infants than twins raised alone (sibling dead after birth) and proposes that better nutrition during pregnancy might be a contributing factor.

Social relations and sexual maturity

Until a month-and-a-half old, study infants interacted only with the mother and the twin and older sibling, if present. Even post-parking, for the first few weeks, males did not join female-offspring sleep groups. Hence the exclusivity of social interactions with related conspecifics until 6 weeks old. Once males began joining the female-offspring sleep groups, infant social interactions with non-related members increased, though greater amount of social interactions was with the mother, twin and sibling. This explains the significantly high social relations with related members in slender loris juveniles until they are 4.5 months of age. When juveniles were 5 months old, weaning was completed and with this the regular presence of the mother decreased steeply. Older siblings, if present, also migrated by this time. Social interactions with adult males – both resident and immigrant stranger – were now more frequent¹⁴. Hence the increase in social relations with non-related members in the age stage 4.5 to 5 months. In the subadult stage, the significantly higher

time spent with related social partner reflects an increase in social interactions with the mother and younger siblings. Apart from time spent with the offspring, for reasons of infant dependence, adult slender lorises spent about equal time interacting socially with related and non-related individuals.

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