Observations of Mating, Birthing and Parental Behaviour in Three Subspecies of Slender Loris *(Loris tardigradus* and *Loris lydekkerianus)* in India and Sri Lanka

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Key Words

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Abstract

Studies of the life history parameters of slender lorises in captivity have led to conflicting results regarding gestation length, birth seasonality, interspecies variation in litter size and the degree of parental care given to offspring. During the course of field studies of *Loris lydekkerianus lydekkerianus, L. l. nordicus* and *L. tardigradus tardigradus*, data were collected on these life history variables, as well as on behaviours relating to mating. All 3 taxa displayed courtship behaviour involving the pursuit of a female by multiple males. Mating corresponded closely with captive observations, with a period of prolonged single intromissions lasting 3–11 min. One gestation period of 163 days was calculated for *L. l. lydekkerianus*. Births for all 3 taxa were distributed throughout the year, and males were seen mating throughout the year. All 3 taxa gave birth to singletons and twins; no subspecific pattern in litter size was evident. Females carried infants for the first 4 weeks of life and were regularly attended by males, which groomed both the mother and her offspring. After infants had been parked, female *L. l. lydekkerianus* and *L. l. nordicus* rarely returned before dawn, though males visited and played with infants. Female *L. t. tardigradus* maintained proximity with their infants, whilst males were not observed in proximity to infants during the night. All 3 taxa slept in social groups. High-energy milk, in combination with male care, may aid in the potentially high reproductive output of 4 infants per year.

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Introduction

The Lorisinae are the least-studied of all prosimians, particularly in the wild [Rasmussen, 1997]. The African lorisines have now been the topic of two in-depth reports [Charles-Dominique, 1977; Pimley, 2003]; the Asian lorisines, however, have only recently become the subjects of long-term field studies [Kar Gupta, 1995; Nekaris, 2001a, 2003; Radhakrishna, 2001; Wiens, 2002]. Several species of slow loris are now recognised, as are at least 2 species of slender loris [Groves, 2001]. The conservation status of all the mainland Asian forms is considered data deficient, whereas the slender lorises of Sri Lanka are considered endangered or critically endangered [Hilton-Taylor, 2002; Nekaris et al., in press].

Despite a lack of field observations, the slender loris (genus *Loris*) has been studied in captivity for many years. Interest in this primate has been due to a remarkable assemblage of derived morphological, physiological and behavioural characteristics. Amongst these are retia mirabilia of the proximal limb vessels, extreme slenderness of limbs, small hands in comparison with feet that possess shortened second digits, a unique non-saltatory locomotor pattern, the closest orbital approximation amongst all primates, digestive specialisations for toxic prey and an unusually low basal metabolic rate [Osman Hill, 1953; Mueller et al., 1985; Demes et al., 1990; Miyake et al., 1991; Sellers, 1996; Rasmussen and Nekaris, 1998; Nekaris, 2001a]. Although all of these issues have been addressed to some degree in captive studies, predominant among them have been those dealing with slender loris reproduction. Anatomical research relating to reproduction has focused on various changes in the internal anatomy of the male reproductive system, spermatogenic cycles, changes in seasonal testicular volume and the biochemistry of the female reproductive tract [Ramakrishna and Prasad, 1962, 1967; Ramaswami and Anand Kumar, 1965; Manjula and Kadam, 1980; Swayamprabha, 1983; Manjula, 1984; Manjula and Kadam, 1984; Sarma and Kadam, 1984]. A second line of inquiry has attempted to resolve issues of evidence of birth seasonality, gestation length, litter size and other life history variables for both Indian [Ramaswami and Anand Kumar, 1962; Manley, 1966, 1967; Kadam and Swayamprabha, 1980; Izard and Rasmussen, 1985; Rasmussen and Izard, 1988] and Sri Lankan slender lorises [Osman Hill, 1935; Nicholls, 1939; Nieschalk and Meier, 1984; Goonan, 1993; Schulze et al., 1994]. These studies have come to contradictory conclusions with regard to whether the presence or absence of seasonality is an artefact of captivity and also to whether or not differences in gestation length, time of weaning and litter size are due to phylogenetic or environmental effects.

Even fewer studies on captive individuals have addressed infant development and adult-offspring relationships. The slender loris has been difficult to breed in captivity and even more difficult to maintain in captive social groups, despite living in relatively gregarious social aggregations with daily sleeping groups of 2–7 individuals in the wild [Nekaris, 2001b, 2003; Bearder et al., 2002]. Thus, observations of infant development and parent-offspring relationships have been difficult. Notable exceptions are the colonies at Duke University Primate Center (DUPC) in the USA and Ruhr University, Bochum, in Germany, where excellent breeding success has been achieved and subsequent related behaviours described [Rasmussen, 1986; Izard and Rasmussen, 1987; Rasmussen and Izard, 1988; Schulze and Meier, 1995].

A recent study has described infant development and some aspects of life history in the wild for the Mysore slender loris (*Loris lydekkerianus lydekkerianus*) [Radhakrishna, 2001]. Detailed descriptions of the interactions between parents and their offspring, however, were limited. Furthermore, no field study has addressed any of these topics for Sri Lankan lorises.

Since 1997, I have conducted one 14-month study of *L. l. lydekkerianus* and three short-term studies totalling 7 months of 2 taxa of Sri Lankan slender lorises (*L. l. nordicus* and *L. t. tardigradus)* in their natural habitats. Over the course of these field trips, I have collected numerous observations relating to the life history parameters discussed above. Although many of the results are preliminary, the current conservation status of the slender loris renders it important to provide information on the reproductive parameters of these animals. Such information is vital not only for their well-being in the wild and for improved captive management, but it will also contribute to an expanding database on the mating, birthing and rearing strategies of the slender loris as more long-term studies are conducted. Furthermore, taxonomic differences in these variables may aid in the resolution of questions regarding slender loris taxonomy. In this paper, I present data on timing of births, litter size and adult-offspring interactions for 3 taxa of slender loris.

Methods

Study Species

The slender loris is endemic to Sri Lanka and southern India. Variation amongst populations of slender loris has long been acknowledged, and therefore the number of recognised species and subspecies within the genus *Loris* has varied [Osman Hill, 1953]. For the purposes of this paper, I follow, with one exception, the taxonomy of Groves [2001], who, based on detailed re-evaluation of museum specimens, recognised 2 species within the genus *Loris*, one of which is monotypic, while the other comprises at least 4 subspecies. Mounting behavioural, genetic and biogeographic evidence supports this view [Nekaris and Jayewardene, 2003]. Both species, and 2 subspecies of one of them, are included in this study.

The Mysore slender loris (*L. l. lydekkerianus;* fig. 1) is distributed in southern India in the eastern Ghats in Tamil Nadu, Andhra Pradesh and Orissa [Rao, 1994; Singh et al., 1999, 2000]. Adult body weights range from 260 to 350 g, with males (295 g) being significantly larger than females (260 g) [Nekaris, 2000]. The behaviour of this subspecies was studied in detail at Ayyalur Interface Forestry Division in Tamil Nadu [Radhakrishna, 2001; Nekaris, 2001a, b, 2003; Nekaris and Rasmussen, 2003].

The northern Ceylonese slender loris (*Loris l. nordicus;* fig. 2) is the most widely distributed of the Sri Lankan subspecies. It is found in the lowland dry zone throughout the north central and northern provinces, including Jaffna as well as some areas in the northeastern and Uva provinces [Osman Hill, 1953]. Many areas of its range fall within a similar ecological zone to that inhabited by *L. l. lydekkerianus*. It is the heaviest of the Sri Lankan subspecies, averaging 235 g [Osman Hill, 1933, 1953; Phillips, 1980]. Although observations in the wild are limited [Hladik and Petter, 1970; Petter and Hladik, 1970; Nekaris and Jayewardene, 2003], this subspecies is well known from captivity [Nieschalk and Meier, 1984; Schulze and Meier, 1995].

The south-western Ceylonese slender loris (*L. t. tardigradus;* fig. 3) is distributed in the south-western wet zone of Sri Lanka but is scarce or absent in most of its formerly known range [Nekaris and Jayewardene, 2003]. It is the smallest of the lorises, weighing only 85–162 g [Osman Hill, 1953; Nekaris and Jayewardene, 2003]. Some information is available from captive groups regarding its behaviour, along with some preliminary field observations [Still, 1905; Phillips, 1931; Goonan, 1993; Nekaris and Jayewardene, 2003].

Fig. 1. Parked infant *L. l. lydekkerianus* at Ayyalur Interface Forestry Division.

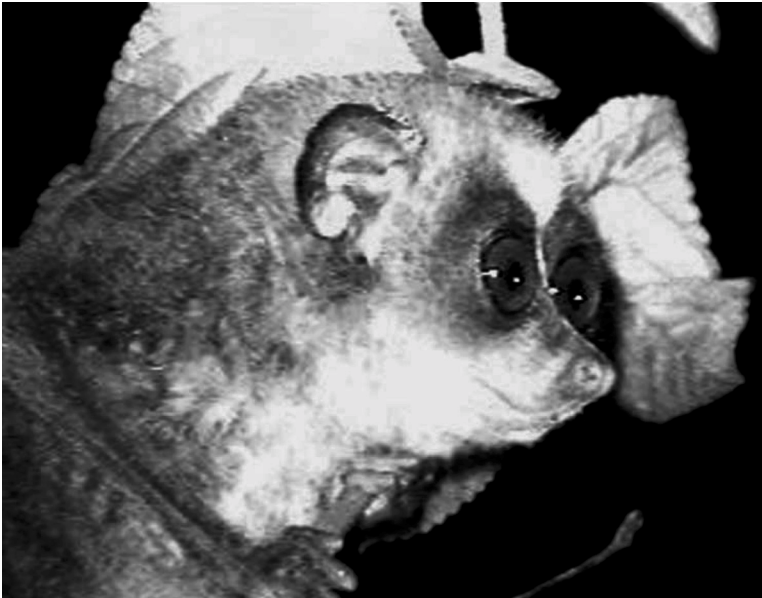**Fig. 2.** Parked infant *L. l. nordicus* at Giritale.

Fig. 3. Parked infant *L. t. tardigradus* at Masmullah.

Study Sites

Behavioural observations were conducted principally at 4 study sites. For *L. l. lydek-kerianus*, I conducted a 10.5-month study at Ayyalur Interface Forestry Division (fig. 4) from October 1997 to August 1998, as well as a 3.5-month survey [Nekaris, 1997]. Details regarding this dry scrub jungle in Tamil Nadu, South India, are published elsewhere [Bearder et al., 2002; Nekaris, 2001a, 2002, 2003; Nekaris and Rasmussen, 2003].

Preliminary field research in Sri Lanka was carried out from May to August 2001, March to April 2002 and August to September 2002. *L. l. nordicus* was observed at the Smithsonian Primate Research Camp in Polonnaruwa and at the Minneriya Giritale Sanctuary, Sri Lanka. *L. t. tardigradus* was observed at the Masmullah Proposed Forest Reserve, a monsoon rain forest in the southern province of Sri Lanka. Details of these sites are published elsewhere [Nekaris and Jayewardene, in press]. Additional observations in Sri Lanka were made at Anuradhapura Town, Trincomalee Town, Mihintale Strict Nature Reserve, Maimbulakanda Forest Reserve and Kanneliya Forest Reserve (fig. 4).

Behavioural Observations

All occurrences of social behaviour between adults and infants were recorded ad libitum during the course of surveys or during systematic observations of general activity [Nekaris, 2001a]. The results presented here are primarily descriptive; quantitative data regarding social behaviour are reported elsewhere [Nekaris, 2001a; Bearder et al., 2002]. Data for *L. l. lydekkerianus* are derived from 1,173 h of observation, as well as from general surveys of areas surrounding the principal field site. Data for the Sri Lankan forms are fewer, with 190 h of direct observation for *L. l. nordicus* and 120 h for *L. t. tardigradus*. Infants were spotted during surveys as well as during observations, and although they were not always observed at length, general characteristics (e.g. litter size, approximate age) were noted. Animals were located by spotting the bright red or orange reflection of the tapetum lucidum and followed for as long as possible. For all observations, headlamps and torches
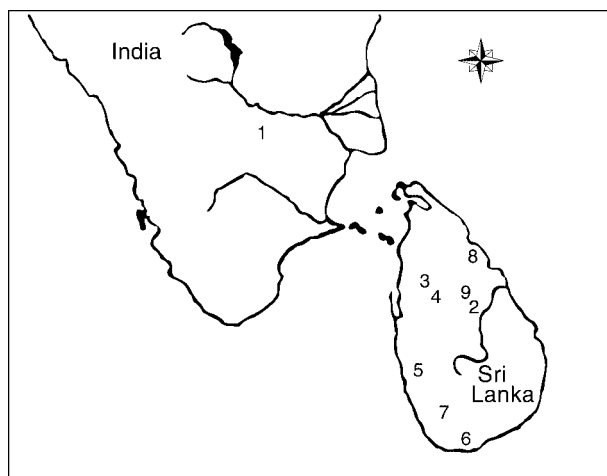
Fig. 4. Map of the study sites. 1 = Ayyalur Interface Forestry Division, India; 2 = Polonnaruwa Smithsonian Primate Research Camp; 3 = Anuradhapura Town; 4 = Mihintale Nature Reserve; 5 = Maimbulakanda Nature Reserve; 6 = Masmullah Proposed Forest Reserve; 7 = Kanneliya Forest Reserve; 8 = Trincomalee; 9 = Minneriya Giritale Sanctuary.

covered with a red filter were used because the animals showed signs of stress in the presence of white light [Nekaris, 2003].

Sex, approximate age of slender lorises, stage of female sexual receptivity and presence or absence of a descended scrotum in males were noted. These features were determined by comparison with figures developed by researchers with long-time experience of lorises [Fitch-Snyder and Schulze, 2001] in combination with my own observations of both wild and captive lorises of both sexes at various stages of development.

The age of slender lorises is determined based on a combination of characteristics. Newborn infants cling to the belly of the mother and often keep their eyes closed. Infants from about 4–8 weeks are fluffy with large heads relative to their bodies; they sleep much of the night. Juveniles of 2–3 months are characterised by fluffy pelage, colouration different to that in adults and clumsy locomotor skills. Adults are characterised by full adult body size, adult colouration and, in some cases, scars or healed wounds. Multiparous females were designated by scarring and long nipples. Females were considered primiparous when they still had some subadult colouring, nipples that did not protrude from the belly and were free of scars [Schulze and Meier, 1995; Fitch-Snyder and Schulze, 2001; Nekaris, 2001b, 2002].

With experience, sexing is not difficult in adults, as external female and male genitalia are easily visible from a distance of about 3 m. Female lorises, however, may be regarded as males because the clitoris superficially resembles a penis and females may show a dark fur pattern which, without experience, can be mistaken for scrotal pigmentation [Schulze et al., 2002]. Unlike pottos, however, loris females never show a prominent 'pseudoscrotum' [Osman Hill, 1953]. In Sri Lanka, sexing was made easier by a night vision video camera (Sony Hi-8), which emphasised the pigmented skin of the male scrotum. Sexing of immature lorises is almost impossible unless one is within 1 m of them. In India, animals were so fearless that it was possible on occasion to get within a few centimetres of them. In Sri Lanka, only 3 infants were caught and sexed; for the others, sex remains undetermined. Details of individual identification are provided elsewhere [Nekaris, 2001a, 2003; Nekaris and Rasmussen, 2003; Nekaris and Jayewardene, 2003].

Visibility of animals was excellent at all sites occupied by *L. lydekkerianus* due to sparse dry zone vegetation [Nekaris and Rasmussen, 2003; Nekaris and Jayewardene, 2003]. Observations of *L. t. tardigradus* were more difficult due to dense vegetation, inaccessible sections of the forest and the distinct rapid movement of this species, which allows them to depart quickly from view [Nekaris and Jayewardene, 2003].

Results

Courtship

Courtship behaviour related to oestrous swelling in a female was observed for all 3 taxa. Courtship bouts involving 1 or more males were observed on at least 8 separate nights for *L. l. lydekkerianus*. Three females in the area came into oestrus and were the objects of attention of 4 identified males and at least 3 unknown males who were not seen regularly in the study area. Three of the known males were observed to travel between the 3 females, grooming them all in turn in 1 night during the months when conception must have occurred (see births below). During courtship behaviour, only 1 male at a time was ever seen in a tree with an oestrous female, although on 3 occasions additional males lingered within a 25-metre radius and groomed the female later in the night, after the first male had left.

On at least 9 occasions, 3 of the identified adult males and 1 juvenile male were observed to engage in a 'sit-and-run' strategy. All of these males sat at low heights (less than 2 m) in a bush, remaining still for 1–3 h, followed by sudden rapid movement over a distance of up to 300 m to join a female in a grooming session. These sessions occurred between males and both oestrous and non-oestrous females. On 8 of these occasions, an adult male joined a female who had previously been his grooming partner. In the last case, a juvenile (sexually immature) male met the female in his sleeping group. No sound was heard prior to this movement.

Similar behaviour was observed for *L. l. nordicus*. At Polonnaruwa in mid-June 2001, an adult female was exhibiting clear signs of oestrus. Over 3 days, she was visited by at least 3 males – twice independently, once by 2 of them simultaneously, and on one occasion by 3 adults, 2 of whom were clearly identified as males.

During both interactions when only 1 male was present, males began by pursuing the female through a series of trees. When they were within reach of the female, they sniffed her anogenital region. On both occasions, the female moved through the trees for several minutes with the male in pursuit, until she allowed him to groom her. Grooming was mutual, lasting for 45 min, before the female pushed the male away and he retreated. Grooming was interspersed with co-feeding (the male and female foraging for insects in the same tree) and with bipedal play wrestling [Schulze and Meier, 1995].

During the 2 visits when 2 males were present, different patterns were observed. During the first visit, mutual grooming with the first male lasted about 20 min; the second male observed the pair from a neighbouring tree located 5 m distant. After 20 min, the female moved into the tree containing the second male; at this point all lorises moved out of view. During the second visit, though all 3 animals were in the same tree, they were not observed to groom the female at the same time. The 3 animals were watched for a period of 45 min.

During the visit by 3 males, the subadult never entered the tree, but appeared and reappeared 15–20 m from the female, during the 1.5 h of observation. No ag-

gression between male *L. l. nordicus* was observed, even when they were in the same tree as the female.

A male who participated in the first dyad described above had been seen earlier in the evening grooming a mother and her twins. After leaving this female, he was then seen to engage in the sit-and-run strategy. He sat almost motionless in a fence of tangled vines for nearly 2 h; then, with no audible signal, he scaled a tree trunk and ran over 100 m in less than 10 min to join another female.

Only 1 observation of courtship was observed for *L. t. tardigradus*. Two males with scrotal testicles were observed to pursue a female exhibiting an oestrous swelling; the animals were followed for 38 min before they moved out of view. Throughout the pursuit, a defensive 'chitter' was uttered, followed by a low-intensity whining click, reminiscent of the 'krik' call of *L. lydekkerianus* [Schulze and Meier, 1995]. No comparable behaviour was observed over the following days.

Male Reproductive Cycle

During the study of *L. l. lydekkerianus,* it was noted that the size and shape of the males' testes differed from night to night. Later comparison with figures of captive animals [Schulze et al., 1994] clarified that the testicles of males were descending on some nights and were inguinal on others. Descended, or scrotal, testes were more visible, and the visibility of the pigmented area surrounding the testes was enhanced. The number of times that the testes were either inguinal or scrotal was not quantified, as it became taken for granted that they would change in appearance about every other night.

A similar phenomenon was noted for Sri Lankan *L. l. nordicus*. Over 10 days at Polonnaruwa, 2 males were observed almost nightly and showed the same pattern of 'flat versus three-dimensional' testes every other night. These males groomed females even when their testes were in the inguinal stage.

One adult male *L. t. tardigradus* was hand caught and measured. This same male had been seen 3 days previously, in pursuit of an oestrous female (described above). His testes were scrotal and exuded a pungent smelling sticky fluid. Furthermore, the pigmented area was raised from the skin, forming a honeycomb reticulated pattern, described for *L. t. tardigradus* by Osman Hill [1953] and by Charles-Dominique [1977] for pottos.

Copulation

Only 1 copulation event was witnessed. The bout occurred on December 7, 1997, between an adult female and at least 1 adult male *L. l. lydekkerianus*. The female was observed foraging for 4 h before an identified adult male was spotted at 22.10 h pursuing her. He followed her for nearly an hour, during which time she cuffed him away several times. This behaviour did not deter him, and still he frantically pursued her. At 23.15 h, she finally allowed him to copulate with her in a suspended posture on a horizontal branch at a height of 2.5 m [Izard and Rasmussen, 1985]. Penetration lasted for 5 min, at which time 2 other males appeared in neighbouring trees, producing whining vocalizations. Before either of them had the chance to physically harass the copulating male [Dixson, 1998], the focal male chased the nearer male whilst 'growling', followed by a 'monosyllabic whistle' [for details on vocalisations, see Schulze and Meier, 1995]. They grappled with one

another and fell out of the tree while the female resumed feeding. The focal male then returned to the female and resumed copulation. The female hung, suspended upside down, with the male clinging to her. At times the male was supported only by his hold on the female. The male clung to the female's back, wiping his chin back and forth on it, a behaviour seen in captivity [Schulze and Meier, 1995].

During a 39-min period between 23.38 and 0.17 h, I observed 5 intromissions with durations of 11, 3, 3, 4 and 7 min (mean = 5.6 min). Most pauses were momentary and were caused by the female pushing the male away whilst uttering an intense 'chitter'; she was otherwise silent throughout the episode. The copulating male made a grunting sound throughout all intromissions. He also emitted a 'chitter' when he momentarily ceased copulating to chase away other males.

At 0.17 h, another male approached. The focal male 'whistled' and momentarily ceased copulating with the female to chase him away; she again resumed feeding. This was followed by another 6-min intromission session, during which the male put all his body weight on the female. In no intromission was the adult male ever observed to 'wiggle' his pelvis at the end of a bout, nor was the female observed to eat a copulatory plug, a second sign that the male had achieved ejaculation, though this is not to say that it was not achieved.

After this intromission, at 0.30 h, the focal male chased another male into a neighbouring tree, and the female followed. Two adult males entered this tree, and a fight ensued between all 4 males with more 'chittering' and fighting on the ground. This resulted in 3 of the males running off in different directions. The female and an unidentified adult male were relocated copulating in a 1-metre-tall shrub 10 m from the original tree. At 1.07 h, another fight between the males occurred, followed by more copulation between the female and the original male. Observations ceased at 3.00 h. The associated copulatory vocalisations could still be heard, resulting in a total copulation session of at least 4 h. No further sexual behaviour was seen in the days that followed.

Birthing and Behaviour during Carrying

Estimated birth dates of infant *L. l. lydekkerianus* are summarised in table 1. Three of these births were to females that were observed almost nightly, either during intensive behavioural observation or in nightly checks of individuals in the study area [Nekaris, 2001a, 2003]. One female was first seen with newborn twins on May 19, 1998 – 163 days after copulation. She had been seen on May 15 without infants. Other infants were first seen on March 24, 1998, and April 24, 1998. Estimation of the March birth is accurate, as the female had been seen the night before with no infants. For the April birth, the female had not been seen since April 11, but the single infant was the same size as those observed for the other 2 females and had her eyes closed (see below).

Although it was not possible to calculate any gestation lengths for Sri Lankan slender lorises, some preliminary information can be presented regarding birth seasonality and litter size. Estimated birth months are reported in table 1. Both newborn and parked infants of *L. l. nordicus* and *L. t. tardigradus* were observed. For the most part, age was estimated based on physical appearance or behaviour; only 3 animals were caught and measured. The body weight of 2 parked infant *L. l. nordicus* (100 and 110 g) corresponded to those of captive 2-month-old *L. l. nordicus* [Fitch-Snyder and Schulze, 2001; data by B. Meier]. An infant of the smaller-

Table 1. Months during which births were recorded and litter size for 3 taxa of slender lorises

	Inferred month of birth	Number of instances of each type of birth
L. l. nordicus	February	singleton: 1
	April	singleton: 1
	May/June	singletons: 4
		twins: 1
	August	singletons: 2
	October	singleton: 1
	Nov./Dec.	singleton: 1
L. t. tardigradus	Dec./Jan.	singletons: 3
	March	singletons: 2
	June	twins: 2
	July	singleton: 1
L. l. lydekkerianus	March	twins: 1
	April	singletons: 2
	May	twins: 1
	June	singleton: 1
	October	singleton: 1

bodied *L. t. tardigradus* weighed only 56 g, yet showed all the same signs of behavioural development of a typical 2-month-old *L. lydekkerianus*.

In all taxa, infants were carried for the first 4 weeks of life. The mother was the only individual observed carrying the very young infants. Infant carrying was observed for all taxa: *L. l. lydekkerianus* (n = 55), *L. l. nordicus* (n = 38) and *L. t. tardigradus* (n = 5). The observation length varied from a few minutes to all-night follows. Infants are capable of gripping the fur of their mother immediately after birth and are also capable of opening their eyes, though they usually keep them shut for the first week of life [Goonan, 1993]. After approximately 1–2 weeks, infants still remain on their mother's back or belly but begin to scan the environment. For all taxa, twins ride laterally side by side on the mother's belly, in staggered positions on the belly or with one on the back and one on the belly; two sets of nipples [Osman Hill, 1953] allow for increased variation in the position of twins while suckling (fig. 5). An infant at this age was never observed trying to leave the mother.

Despite their heavy burdens, mothers of all 3 taxa were agile and moved swiftly while carrying infants. Infants held tight to their mothers during travelling and foraging. Mothers were not seen to share food with infants during this time period or to transport infants with their mouths. On occasion, the infant was pulled away from the mother's body for grooming, otherwise mothers had very little hand contact with their infants during nightly travel.

Mothers groomed their infants with their tongue or toothcomb during periods of rest (fig. 6). Infants were also groomed regularly by adult males. Adult male and female grooming sessions occurred almost nightly for all 3 taxa [Bearder et al.,
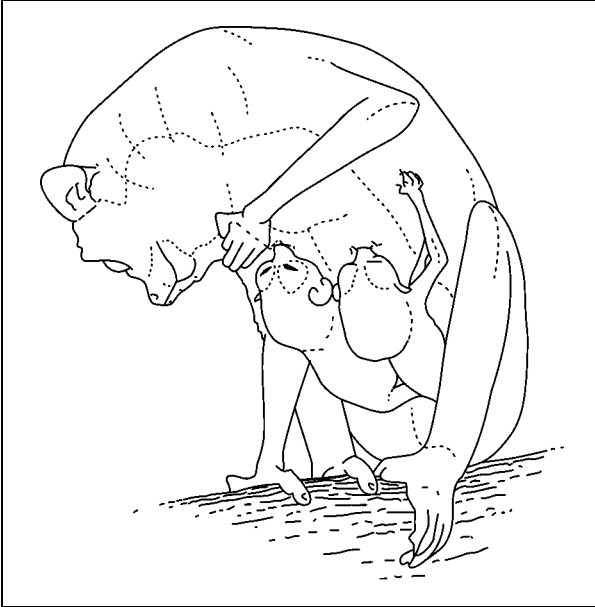
Fig. 5. Mother slender loris carrying twins (by H. Schulze).

Fig. 6. Mother slender loris grooming infant (by H. Schulze).

2002; Nekaris and Jayewardene, 2003]. Presence of the infant did not deter an adult male from seeking out a female grooming partner, and in fact, the infant often supplanted the female as the focus of the male's attention. For *L. l. lydekkerianus* and *L. l. nordicus*, males who were not members of the sleeping group groomed both the mother and her infants. Males were seen to travel directly from a grooming bout with one female with offspring to another. Males intermittently groomed infants and their mother with their toothcomb or by licking them but were never observed to try to remove an infant from the mother's body. On 1 occasion, an *L. l. nordicus* male was observed to play-wrestle with a mother and her twins with such enthusiasm that all 4 of them fell out of the tree.

Rearing and Behaviour during Parking

Parking [Kappeler, 1998] was observed in detail for the Mysore slender loris. One multiparous female began parking her twins at 4 weeks; it was at this point that one of them disappeared due to unknown causes. After the death of the infant, the female only returned to her parked infant before the typical retrieval time of dawn on 1 occasion. The female infant of a second multiparous mother was seen parked throughout the night 4.5 weeks after her suspected date of birth. The behaviour of these females contrasted with that of a primiparous female who gave birth to twins in March. She parked her infants for part of the night as early as 2 weeks and then began to park them in separate trees at 4 weeks, during which time one of them disappeared and was not seen again. By 6 weeks of age, her remaining infant was parked for the whole night. The difference in the timings between the multiparous females and the primiparous one might be due to the inexperience of the latter.

Although mothers rarely returned to their infants before dawn, males showed a marked interest in parked infants. During the period of infant parking observed during this study (from late April to late July), adult and subadult males were observed in the same tree with infants or within 5 m of them on 46 occasions. These 'neutral' occasions were generally accompanied by non-vocal communication, including curious staring accompanied by head cocking and scent marking. During 24 of these occasions, the male groomed or played with the infant. On 1 occasion, 1 subadult and 1 juvenile male joined together and play-wrestled with an infant. Infants responded positively to this behaviour and on several occasions, when the male was departing, the infant followed him 3 trees beyond its normal nightly range. Males of all age classes who played with the infants after they had been parked were always also part of the infant's sleeping group [Nekaris, 2003]. In future studies of slender lorises, genetic tests may resolve whether or not these affiliative males are indeed fathers or in some other way closely related to the infants (e.g. elder brothers).

Although age at first parking in the Sri Lankan lorises was not known, 3 parked infants of *L. l. nordicus* exhibited fur quality, colouration, body size and mannerism consistent with an age of 7 weeks to 2 months. Two *L. l. nordicus* infants observed on several nights were never visited by another loris, although both an adult female and adult male were seen foraging within 20 m for several minutes.

On 1 occasion, a 4-month-old parked juvenile was involved in a gregarious behavioural session, lasting nearly 3 h, involving at least 9 other animals. I observed a mother with twins and the 4-month-old juvenile together in one bush. Two

adult males joined them within minutes. Another adult male was observing the interaction from 10 m away, and another mother and singleton were foraging 15 m from him. Grooming occurred between the mother with twins and the juvenile, the males and the mother with twins, and the males with the juvenile. The mother with a singleton maintained a distance from the mother with twins but was visited by the males in turn. Eventually, all animals gathered into one bush where they groomed and play-wrestled. This continued until they moved as a group into an impenetrable part of the forest.

Of 4 parked *L. t. tardigradus* infants, 3 were seen in the vicinity of adult females. The females engaged in foraging, interspersed with grooming of the infants. Only 1 of these females was a *confirmed* mother, retrieving the infant and carrying it to the sleeping site. This female was seen near her infant at least once an hour over 14 h of observation on 6 separate mornings and evenings. Two days after the infant had been caught and measured, the mother was observed to retrieve her infant rapidly and carry him out of view of approaching observers. This behaviour might have been due to the lack of habituation of this female or from a motivation to prevent his recapture. The infant was not heard to call earlier than 30 min before sunrise. Males were not observed to visit the infant in the night.

Dusk Dispersal and Dawn Assembly

The assembly behaviour of *L. l. lydekkerianus* at dawn was observed 57 times and has been described in terms of group composition and habitat use elsewhere [Bearder et al., 2002; Nekaris and Jayewardene, 2003]. When infants are being carried, the mother joins the rest of the sleeping group while carrying her infants with her. It is important to note that females habituated to observation were not necessarily habituated to being followed to their sleeping sites. One female in particular showed signs of stress, including folded corners at the mouth, urine washing and refusal to return to her sleep site in the presence of observers. In order to habituate the female to my presence while she was carrying the infants, I began to follow her from a greater distance and ceased observation 30 min before dawn so that she could proceed to her sleeping site undisturbed. Eventually, I was not perceived as a threat and could follow her all the way to her sleeping site.

When parking of the infant begins, at dusk dispersal, the mother loris leaves her infant(s) in the sleeping tree. During the course of the night, the infant may move up to 20 m from the location where the mother left it. Approximately 30 min before dawn, it alerts the mother to its presence by uttering a series of 'zic' calls [Schulze and Meier, 1995]. The mother is usually within visual range when the calls begin. Mothers of *L. l. lydekkerianus* reacted differently to their calling infants. Two mothers immediately retrieved their offspring, seemingly stimulated by infant calls. As infants grew older, the time at which they were retrieved was later. A third habituated female was slower to retrieve her infant, which on several occasions uttered frantic 'zic' calls for more than 30 min. Finally, a non-habituated mother warily retrieved her infant, which actually had to move 50 m towards the mother before she picked it up.

Once at a sleeping site, social interactions between all group members continued until full light. This gregarious period ranged from 20 to 35 min before dawn [Nekaris, 2001a, 2001b]. The infant(s) sleep(s) with the mother; suckling can be clearly seen upon contact with their mother. An infant is usually tucked between its
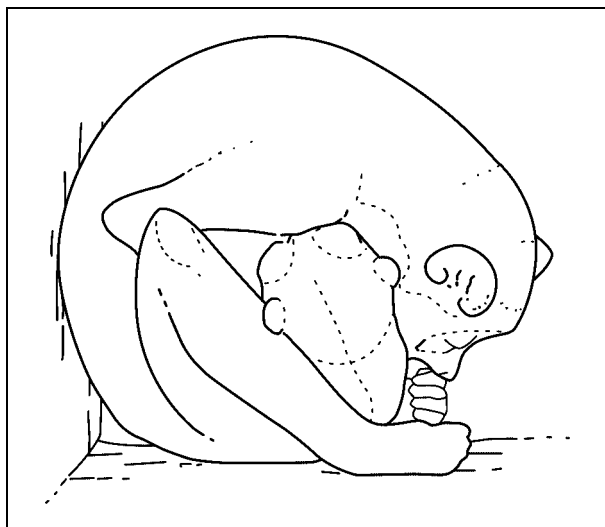
Fig. 7. Mother and infant slender loris in typical sleeping posture (by H. Schulze).

mother's legs and chest or cradled on her legs with its knees pointing sideways (fig. 7); other group members huddle close to the mother and her offspring.

For *L. l. nordicus*, dawn assembly has been observed only 4 times. A mother with twins and an adult male shared one sleeping site, used each day. Another female and her infant shared a sleeping tree with an adult male. Animals assembled approximately 45 min before dawn, playing, grooming and feeding together before moving into their sleeping tree; males directed grooming to infants and the mother.

Dawn assembly was observed 6 times for one group of *L. t. tardigradus*. Poor visibility made it difficult to count the daily participants of the sleeping group, although an adult male and female with her infant were present. On one night, a third adult loris joined the group at dawn, having approached from a different direction. Upon entering the sleeping tree, animals groomed and played. Approximately half an hour before dawn, the infant began to utter 'zic' calls, summoning the mother within 15 min. When she reached her infant, it climbed onto her belly and she moved to the sleeping tree. Up to 4 animals were seen emerging from sleeping trees at dusk, confirming that these animals sleep in communal groups.

Discussion

Although the results presented in this study are preliminary, they allow for interesting comparisons with captive studies. Overall, studies from the wild and captivity concur; however, important differences suggest ways in which captive animal husbandry might be improved. For example, slender lorises should be given greater opportunities for sociality and for infant parking. This might be achieved by larger cage size with many branches, which would allow for the species-typical

continuous locomotion and would also allow animals to meet, but, if given a variable enough series of supports, they would not be forced to be in permanent contact. The two species (*L. lydekkerianus* and *L. tardigradus*) should be housed and reared differently in some respects, possibly with regard to male access to infants.

These observations also offer important suggestions regarding habituation of mothers rearing infants that may assist in future field studies. Captive mothers with infants should be carefully observed for signs of stress and should even be protected from prebirth stress. For example, Schweigert (in Fitch-Snyder and Schulze [2001]) found that increased stress levels in captive *L. t. tardigradus* almost always resulted in infanticide.

Although male and female *L. l. lydekkerianus* were social throughout the year [Bearder et al., 2002], the interest of males in females during oestrus was qualitatively more fervent, with a greater variety of male vocalisations occurring more often. This same interest was exhibited by male *L. l. nordicus*. Male interest in females also increases during oestrus in captivity; in particular, increased sniffing of the anogenital region in connection with appeasing 'krik' calls by the male are common [Izard and Rasmussen, 1985; Schulze and Meier, 1995]. Males of other prosimian species, including some bushbabies and pottos, have been shown to exhibit heightened interest in females during oestrus, increasing their 'courtship' visits as well as their grooming behaviour [Petter-Rousseaux, 1964; Charles-Dominique, 1977; Bearder and Martin, 1980; Nash, 1993; Dixson, 1995]. It is thought that these visits by males aid in establishing social relationships or allow a male to monitor female reproductive status. Young [1961] suggests that male activity may increase in the days or weeks preceding sexual receptivity.

The unusual sit-and-run behaviour exhibited by male slender lorises might be an example of an increase in male behaviour relative to female sexual receptivity. Petter and Hladik [1970], in a 10-day study of *L. l. nordicus*, remarked how animals move less than 10 m in a night. They further noticed on their transects that an animal would often be located in the same place as it had been a few hours earlier [Petter and Hladik, 1970]. Perhaps had they watched these individuals for a longer period, they too would have noticed the sudden burst of energy following a long period of inactivity.

The timing of the males' 'run' to a female is an area that warrants further investigation. Dixson [1995] suggests that olfactory cues may serve a broadcast function. Male jaunts were not preceded by audible sounds; perhaps they picked up on an olfactory message from the female instead [Wyatt, 2003]. It is also possible that an ultrasonic sound precedes male movement toward a female. A recent study of the loud calls of 3 taxa of slender loris revealed that the upper frequency of the call is at the upper end of human hearing [Coultas, 2002]. Researchers with captive experience have speculated that lorises may be capable of ultrasonic vocalisations [Schulze and Meier, 1995].

The heightened interest of males in oestrous females has been described as serving a mate guarding function [A. Clark, cited in Bearder, 1987; Dixson, 1998]. Unfortunately, the month during which the copulation was witnessed was at the beginning of the long-term study, at which time fewer individuals had been identified. It was not possible, therefore, to assess whether the male that engaged in most (or all) of the intromissions had previously been a favoured social partner of the adult female, or if he only began to 'court' her in the weeks prior to tumescence.

The short-term study in Sri Lanka also precluded the collection of such information.

Males of all 3 taxa showed a pattern of shifting testicular conditions, from inguinal to scrotal. Osman Hill [1953] observed that animals in his colony (*L. t. tardigradus*) also became inguinal overnight and that pigmentation was more noticeable. In their captive *L. l. lydekkerianus*, which were freshly caught from the wild, Ramaswami and Anand Kumar [1962] found no evidence of seasonality in the pattern of testicular volume. Ramakrishna and Prasad [1962, 1967] showed that descended scrota are associated with presence of sperm in the seminiferous tubules and that this descent could occur over any season. These studies support the preliminary conclusions made here regarding the lack of evidence for seasonality in slender lorises.

Alternatively, the testes of captive *L. l. nordicus* at Ruhr University regularly looked enlarged with somewhat tight and pink skin when ambient temperatures were high, which may serve to help cool the animals. Similar enlargement of these parts was not regularly observed during mating [Schulze and Meier, 1995]. Further studies of lorises in the wild might carefully monitor changes in ambient temperature in correlation with physical changes of male testes.

Mating behaviours observed during this study correspond closely to those recorded in captivity and extend the captive observations. Pairs in captivity copulate while suspended upside down on horizontal branches. Oestrus is thought to last for less than 24 h [Izard and Rasmussen, 1987]. Behaviours associated with copulation may last for 5 h and include playing, fighting, wrestling and repeated mounting by the male. Slender lorises are capable of multiple, but prolonged, intromissions. A single prolonged intromission lasts 3–16 min but may be interrupted if the female is aggressive [Dixson, 1998]. Goonan [1994] reported several of these single prolonged intromissions over 3 h, while Rasmussen [1986] found them to last over 5 h. Schulze and Meier [1995] suggest that a sign that a consummatory phase of copulation has been reached is the self-licking of the genitals by both males and females, followed by no further copulation. The male uses pelvic thrusts, but with no genital lock. Copulation often concludes with a wiggle of the male pelvis and the presence of a hardened vaginal plug produced by the male, which females may remove with their mouths. A whitish copulatory plug, which keeps the vagina closed, may be visible for some time after copulation. Later, usually the next day, it is removed with the mouth.

Throughout copulation males emit appeasing 'krik' calls, and females may emit aggressive calls [Rasmussen, 1986; Goonan, 1994; Schulze and Meier, 1995]. Based on this copulation pattern, Dixson [1995, 1998] predicted that lorises might have a multi-male multi-female mating system. The clarification of this pattern in the wild, in combination with a pattern of home range overlap consistent with a multi-male, multi-female social organisation, supports this view [Nekaris, 2003].

Another characteristic of Mysore slender loris copulation was the consistent interruptions of intromission when the focal male chased away harassing males. Although males did not physically harass the copulating pair, they sat within 1–5 m of them, producing a loud vocalisation. Such behaviour has been observed in more than 30 primate species, including some bushbabies and slow lorises [Elliot and Elliot, 1967; Neimeyer and Anderson, 1983; Dixson, 1998]. This behaviour has not, however, been observed in captivity in slender lorises, though female aggres-

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sion occurs [Narayan Rao, 1927; Rasmussen, 1986; Schulze and Meier, 1995]. Because slender loris females are rarely housed with more than 1 male, chances for harassment or interruption during copulation, such as those seen in the wild, are limited. Future studies of slender loris behaviour might take into account the numerous hypotheses proposed for the function of harassment [reviewed by Dixson, 1998].

Manley [1967, p. 80] pointed out that the 'nocturnal habit and retiring nature of these primates almost invariably preclude the observation of copulation', and it follows from this that the duration of gestation cannot be determined. Observation of copulation among non-Malagasy nocturnal primates in the wild is rare [Dixson, 1998]. Therefore, even the single gestation length obtained from this study is valuable for comparison with estimates from captivity.

The gestation period of 163 days calculated for *L. l. lydekkerianus* in this study was in line with those reported from captivity. Most notably, it approximates the duration reported by Manley [1967] of 160–166 days for *L. l. lydekkerianus* and 166–169 days for small red lorises at the DUPC (although classified as *L. l. malabaricus,* stud book keepers suspect that they are of Sri Lankan origin) [Izard and Rasmussen, 1985; Fitch-Snyder and Schulze, 2001]. Two subsequent births at the same field site were also estimated at 165 days [Radhakrishna, 2001]. Notably, estimates for the smaller *L. tardigradus* are higher than those for *L. lydekkerianus*: 174 days (*L. t. nycticeboides*) and 167–175 days (*L. t. tardigradus*) [Nicholls 1939; Goonan, 1993]. Goonan [1993] studied 2 taxa, which he diagnosed (with some reservation) as *L. 'tardigradus' grandis* and *L. 't.' tardigradus.* An offspring produced by this pairing did not reproduce.

Whether or not slender lorises breed seasonally has been another area of contention. Researchers collecting large numbers of wild *L. l. lydekkerianus* for physiological studies made general observations of whether or not females were pregnant or infants were present [Ramakrishna and Prasad, 1962; Ramaswami and Anand Kumar, 1965; Manjula and Kadam, 1984; Sarma and Kadam, 1984]. In particular, Ramaswami and Anand Kumar [1965] collected more than 170 animals and, based on the pattern of pregnancies, suggested that 2 birth peaks occurred, one in July and one in October. Subsequent statistical analyses of these data showed no significant evidence for this assertion [Preuschoft and Lonardini, in Smith, 1986]. Osman Hill [1937], who maintained colonies of Sri Lankan slender lorises over many years (particularly *L. t. tardigradus*), also suggested that lorises exhibit long periods of anoestrus interspersed with periods of oestrus. Radhakrishna [2001] found evidence of biannual breeding in *L. l. lydekkerianus*, with a birth peak in April-May and a second birth peak in October-December; however, the study was based on a small sample size, and sampling was not done in all months of the year. The general consensus from these studies has been that lorises are biannual breeders; the timing of the two breeding periods has been the main source of contention.

Detailed observations from captive populations offer contradictory results. No evidence for seasonal breeding was found in either the Bochum (*L. l. nordicus*) or DUPC colonies (*L. l. 'malabaricus'*) [Nieschalk and Meier, 1984; Izard and Rasmussen, 1985; Schulze et al., 1994]. Schulze et al. [1994] suggested that the nearly 6 months gestation length may provide the semblance of biannual breeding when in fact no real seasonality occurs. Izard and Rasmussen [1985] found both spermatogenesis in males throughout the year and non-seasonal variation in scrotal pigmen-

tation. They postulate that discrepancies might be due to taxonomic differences, whereas Goonan [1993] suggests that it is interbreeding of different taxa in captivity that might cause the discrepancy.

The data presented in this study also show no evidence for seasonality, with births occurring throughout the year. At Polonnaruwa, a female *L. l. nordicus* was in oestrus when 2 other females neighbouring her home range were both carrying infants. Though sample size is too small for any firm conclusions, the fact that births are distributed throughout the year suggests, at the very least, that there is no strict breeding season, although as more data are collected, a peak in births may become evident. Radhakrishna [2001] has made this suggestion for *L. l. lydekkerianus*, linking a greater number of infants born during the wet season with periods of food abundance, although no measure of food abundance was conducted.

Slender lorises are capable of producing 1–3 offspring per litter in captivity [Kadam and Swayamprabha, 1977; Fitch-Snyder and Schulze, 2001]. Variation in litter size has been considered by some authors to be a sign of taxonomic variation, with twinning more common among the large grey forms (*L. lydekkerianus*) and singletons more common among the smaller red lorises (*L. l. tardigradus*) [Phillips, 1931; Pocock, 1939; Fitch-Snyder and Schulze, 2001]. Ramaswami and Kumar [1965] concluded that the ratio of twins to singletons in slender loris births was almost equal; of 86 pregnancies, 56% were twins and 44% were singletons [Schulze and Meier, unpubl. data]. In the captive colony at Ruhr University, singletons tend to be more common: of 106 births, 88% were singletons and only 12% were twins. In this study, all 3 taxa gave birth to both twins and singletons, though singletons were more common than twins. It is important to note that, during the study in India, 1 member of both sets of twins was lost during parking, presumably to predation [Bearder et al., 2002]. The percentage of twin births may therefore actually be higher. Regardless, at this stage no evidence for taxonomic differences in litter size is evident.

All 3 taxa were observed to park their infants by as early as 4 weeks of age and certainly by 2 months. The more detailed observations for *L. l. lydekkerianus* included only 2 exceptional cases where the mother returned to the infant before dawn. Tilden and Oftedal [1997] showed that Lorisoidea, including slender lorises, produce the richest and highest energy-dense milk of all primates, deviating from the more common low-energy and low-protein milk of most primates. They suggested that the nutritional quality of this milk would allow for longer periods of parking, followed by increased ingestion of milk when the mother returns. This prediction is in accordance with the style of parking exhibited by *L. lydekkerianus*, which is followed by close infant-mother contact at the sleeping site. It is also supported because hand-reared slender lorises (*L. l. nordicus*) require milk with extraordinarily high amounts of fat [Christie, 1992].

Three captive animal studies, on the other hand, found no concrete evidence for infant parking [Rasmussen, 1986; Goonan, 1993; Schulze and Meier, 1995]; rather, studies on captive individuals report independent movement from the mother by the age of 6 weeks to 2 months. Captive infant *L. l. nordicus* used 'zic' calls to summon their mothers before the end of the dark cycle [Schulze and Meier, 1995]. Wild slender loris mothers move within home ranges averaging 1.6 ha [Nekaris, 2003; Nekaris and Jayewardene, 2003], whereas such distances are not available to captive mothers.

Of the 3 taxa, *L. t. tardigradus* is the only one for which there is evidence that mothers maintain proximity to their infants during the night rather than parking them entirely alone. In this subspecies, although infants are indeed parked, suspected mothers were seen to re-engage with the infant after short bouts of foraging, as well as engaging in protective behaviour of the infant. It would not be unreasonable to conjecture that, at one third the body size of *L. lydekkerianus*, a smaller home range size may also play a role in maintaining the proximity of mothers to their offspring.

Slender loris mothers always returned to their own infants by dawn and did not approach the parked infants of other females. This behaviour contradicts some captive observations that suggest that no mutual recognition exists between mothers and infants and that, once separated from one another, mothers would not recognise their infants and would even drop them when they returned [Osman Hill, 1937, 1953; Swayamprabha and Kadam, 1980]. Schulze et al. [1994] report the dropping of infants (*L. l. nordicus*) that could not cling properly to the fur of the mother, with the result that the mother must carry the infant in her hands. On other occasions, a mother has been observed removing a baby from her chest as if to groom it but instead dropping it. The babies that fell down repeatedly did not survive, even after being retrieved by the mother. In such cases, heightened stress may increase the frequency of dropping in this excitable species [Schulze et al., 1994].

In this study, highly habituated females showed signs of stress when they were carrying newborn infants; they also showed reluctance to nest in the presence of an observer. Although *L. lydekkerianus* mothers did not return to their infants during the night, they still groomed them during carrying and played with them at the sleeping site. This contradicts observations by several authors who found them to pay little or no attention to their infants [Narayan Rao, 1927; Osman Hill, 1953; Swayamprabha and Kadam, 1980]. Furthermore, slender loris infants began to issue 'zic' calls when their mother was in view and not to any other animal in the sleeping group. This observation differs from those of Swayamprabha and Kadam [1980], who remarked that slender loris infants would accept the attention of any mother, although the authors did not take into account that their study placed the infants under unusual duress.

In *L. lydekkerianus*, males play a role in the social development of the offspring through allogrooming, playing with and visiting them throughout the night. All slender loris taxa slept in groups, most of which contained at least 1 male. This is in contrast to other lorisines, which sleep alone or in mother-infant pairs (e.g. *Perodicticus potto* and *Nycticebus coucang*) [Wiens, 2002; Bearder et al., 2003; Pimley, 2003]. Captive male *L. l. nordicus* maintained in stable family groups have also expressed interest in newborns, and males and older offspring sometimes carry them. Only in the first days after birth are mother lorises apprehensive towards other group members with interest in their infants [Schulze et al., 1994; Schulze and Meier, 1995]. Similarly, captive *L. l. 'malabaricus'* males spent significantly more time with their offspring than either galagos (*Galago moholi*) or slow lorises (*N. coucang*). In captivity, as well as in the wild in both India and Sri Lanka, mothers tolerated grooming of infants by males while they carried them. In fact, allogrooming and play with males constituted 10–40% of the activity budget of young lorises in captivity (*L. l. malabaricus*) [Rasmussen, 1986; Nekaris and Rasmussen, 2003].

Caretaking of infants by adult males is rare amongst primates in general. Four patterns of positive adult male caretaking among diurnal primates have been recognised: intensive caretaking, affiliation, occasional affiliation and tolerance [Whitten, 1987]. In this study, paternity of caregivers was not confirmed by genetic analyses; it was clear, however, that more than 1 male (adult and subadult) from the same sleeping group might interact with infants in the night, and thus care was not restricted to fathers per se. This type of care corresponds most closely to the pattern described as 'affiliation'. This relationship is characterised mostly by frequent spatial proximity, with infants initiating contact with males that approach them. Males may also serve as babysitters, when mothers are away, may nuzzle or groom infants and are tolerant of infant play [Whitten, 1987]. In diurnal primates, where touch and visual stimulation are pronounced, such features of behaviour may occur at a greater frequency than they might in a nocturnal primate with a different array of sensory perceptions [Charles-Dominique, 1977]. Such behaviour has rarely been documented in nocturnal prosimians, and the incidence of all of the above behaviours among *L. lydekkerianus* suggests that males of this species can be described as affiliative caregivers.

Because slender loris mating is promiscuous, males are not guaranteed confidence of paternity. Presence of complex penile morphology and deposit of a copulatory plug are indicative of intense sperm competition for this species [Dixson, 1995]. Whereas penile spines may enhance sperm uptake, a plug may prevent insemination by additional males. However, a copulatory plug offers no guarantee that the female will not remove it and mate again with another male. Though a copulatory plug was not observed in this study, it has been reported for *L. l. lydekkerianus* by Radhakrishna [2001]. It is also present in captive *L. t. tardigradus, L. l. 'malabaricus'* and *L. l. nordicus* [Izard and Rasmussen, 1985; Schulze and Meier, 1995; Fitch-Snyder and Schulze, 2001]. In captive *L. l. nordicus,* attempts of a male to copulate with a female with a vaginal plug failed [H. Schulze, pers. commun.]. If a female is capable of entering oestrus only twice a year, and if more than 1 male has mated with her, then paternal uncertainty may be relevant in ensuring good relationships between the males and infants as well as between adult males and females. Affiliative caregiving, as described above, may be a reproductive strategy for males competing for females with a short reproductive window. Future studies of slender lorises might consider examining this behaviour in the light of affiliative bonds between the caregiving males and the mothers, duration of courtship of the mother throughout the year followed by subsequent care of the infant or dominance of the male to other males in the area [Whitten, 1987].

It has been shown that both Indian [Ramaswami and Kumar, 1965; Izard and Rasmussen, 1985] and Sri Lankan [Osman Hill, 1937; Phillips, 1980] female slender lorises are capable of giving birth to twins twice per year and may become pregnant again while lactating. In some cases, weaning of infants corresponds with the next birth in *L. l. nordicus* [Schulze and Meier, unpubl. data]. The cost of lactation is high [Rasmussen and Izard, 1988; Tilden and Oftedal, 1997]. Captive female slender lorises fed on a rich diet during lactation may still lose weight [Schulze et al., 1994], and females in the wild increase foraging during pregnancy and lactation [Nekaris and Rasmussen, 2003]. *L. lydekkerianus* differs from galagos and tarsiers in its pattern of all-night parking and also in that the females of this species transport their infants for the first month before parking them [Bearder, 1987; Gursky,

1994]. Perhaps nocturnal visits to infants by males of the sleeping group, rather than by mothers, aids in reducing the energetic burden that would be placed upon the mother if she had to constantly return to check her offspring rather than engage in the vital task of foraging.

In marmosets and tamarins, where a similar pattern of birthing is prevalent, the energetic burden of carrying infants during lactation (yielding low-fat milk) is alleviated by male helpers [Power, 1999; Tardiff, et al., 2001]. Many species of callitrichids, like slender lorises, can become pregnant during lactation and are capable of giving birth to 2 sets of offspring per year. Increased affiliation of female slender lorises and their young with males, both during nightly activities and at sleeping sites, might serve similar functions to those hypothesised for callitrichids. Namely, male care reduces the energetic burden on the female, allowing greater reproductive output. For instance, by huddling together with females and their offspring at sleeping sites, males may help with thermoregulation [Power, 1999]. All of these topics are worthy of further examination.

More information needs to be collected on *L. t. tardigradus*; preliminary evidence presented in this paper suggests that it may have a different pattern of parental care from *L. lydekkerianus*, with males playing a smaller role. The only recent captive study of this species found that the mother showed a high level of aggression when another animal approached the infant. Carrying lasted for 3–5 weeks, and there was no paternal grooming or interest in the infant, although group members were seen to affiliate and play-wrestle with infants after 120–150 days when the offspring were fully weaned [Goonan, 1993].

Conclusion

During the first international conference dedicated to the study of prosimians, Doyle and Martin [1972] pointed out that field work is not only indispensable for the understanding of evolutionary processes in unique environments, but also provides information that is difficult or impossible to replicate in a captive environment. At this same conference, the vital importance of basic field studies for species conservation was also emphasised [Osman Hill, 1972]. It is hard to imagine that, 30 years hence, many nocturnal prosimians have still not been studied in detail in the wild. Though the many hypotheses generated from the current study are intriguing, an understanding of the basic ecology of the slender lorises still ranks of top priority.

The data presented in this paper are open for elaboration and refinement but provide a starting point for comparison with future studies. Those prosimians least studied in the wild also often fare poorly in captivity [Klopfer and Boskoff, 1979], and this is true of the slender loris [Schulze and Meier, 1995]. An understanding of the life history of the species in the wild can lead to successful captive breeding programmes and effective management of these endangered primates in their natural habitats.

Acknowledgments

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