

Activity Budget and Positional Behavior of the Mysore Slender Loris (*Loris tardigradus lydekkerianus*): Implications for Slow Climbing Locomotion

K.A.I. Nekaris

Department of Anthropology, Washington University, St. Louis, Mo., USA

Key Words

Loris tardigradus lydekkerianus · Lorisidae · Nocturnal prosimian · Activity budget · Social behavior · Positional behavior · Crpsis

Abstract

Both predator defense and feeding ecology models have been proposed to explain the relatively slow climbing locomotion of the Lorisinae. During a study of the socioecology of the Mysore slender loris (*Loris tardigradus lydekkerianus*) in Tamil Nadu, India, six categories of behavior and eleven different postures were recorded to estimate a general activity budget for the slender loris, and are examined here particularly in relation to slow climbing locomotor strategies. Reactions to potential predators are also described. The main study population was composed of 15 animals. Activity budgets were compiled in three ways: all instantaneous point samples collected over 1,173 h pooled ($n = 13,717$), the means of individual lorises ($n = 15$) and behavior at the moment of first contact ($n = 357$). No significant difference was found between these three data sets. Approximately 45% of the activity budget was spent in inactive behaviors including sitting vigilant, resting and sleeping. Foraging and traveling comprised nearly half the activity budget, with the rest of the time spent grooming. The most common postures assumed by lorises were sitting and quadrupedal walking. Individual lorises were relatively gregarious and spent up to half their activity budget with other animals. Unlike pottos and angwantibos, lorises did not freeze, head butt or drop from branches in reaction to potential predators, but either ignored them, fled or made loud calls. Cryptic and slow climbing locomotion were used before traveling on open ground between discontinuous substrates, thereby supporting hypotheses relating to predator pres-

KARGER

Fax + 41 61 306 12 34
E-Mail karger@karger.ch
www.karger.com

© 2001 S. Karger AG, Basel
0015-5713/01/0724-0228\$17.50/0

Accessible online at:
www.karger.com/journals/fpr

Dr. Anna Nekaris
Department of Anthropology, Southern Illinois University
Mailcode 4502, Carbondale, IL 62901-4502 (USA)
Tel. +1 618 453 5017, Fax +1 618 453 5037
E-Mail titania@nocturnalprimate.org

sure, and also before capturing fast moving insect prey, supporting hypotheses relating to diet. It is proposed that a divergence in foraging strategies between bushbabies and lorises may be the best adaptive explanation for their behavioral and morphological differences, including predator defense mechanisms.

Copyright © 2001 S. Karger AG, Basel

Introduction

The slender loris (*Loris tardigradus*) is a small nocturnal prosimian inhabiting Sri Lanka and South India [1–3]. Until recently, virtually nothing was known about its behavior and ecology in the wild. Even the distribution of these animals is only beginning to be studied [4–6].

The slender loris is a member of the family Lorisidae, which includes the fast leaping galagos (Galaginae) and slow climbing lorises and pottos (Lorisinae). In addition to extreme differences in locomotor repertoire, behavioral differences separate these subfamilies. Galagos are generally thought to rely more on hearing, tend to be more vocal and more gregarious and include higher quality evasive prey in their diet. Lorises are thought to rely more on olfaction, make few to no loud calls and rely more heavily on slow-moving 'toxic' prey. Social interactions are dispersed with few physical interactions between individuals [7–9]. Slow movement in the lorises is thought to limit social interactions, as animals may not be fast enough to meet often in the night or to meet at communal sleep sites at dawn [10]. All of the lorisids studied to date have fully nocturnal activity rhythms [11].

Two hypotheses have been put forward to explain the locomotor differences between these subfamilies. Charles-Dominique [10, 12] has argued that the stealthy locomotion of lorises helps them to evade predators, as opposed to galagos which use speed to flee. This anti-predator strategy led secondarily to other features of diet and social behavior. However, increasing evidence suggests that adaptive divergence in foraging strategies is the key to explaining differences between galagos and lorises. Hunting for fast moving, high-energy insects may have selected for leaping, prominent ears and emphasis on sound in bushbabies. Slow-moving insects, insects containing high levels of toxic compounds, head-down olfactory exploration of resources and faster-moving vertebrates caught by stealth have all been implicated as having affected the behavioral repertoire of the lorises [7, 9, 13, 14].

From October 1997 to August 1998, I conducted a socioecological study of the Mysore slender loris, *Loris tardigradus lydekkerianus* in Tamil Nadu, India. I have shown previously that the slender loris is almost exclusively insectivorous and relies heavily on pungent and toxic prey items [15]. The slender loris is distinct from other lorises in that it emits a loud whistle frequently throughout the night and it sleeps socially in groups of up to six animals [16, 17]. In this paper, I present the first information on the general activity budget of this subspecies, including activity rhythm, percentage of time slender lorises engaged in various behaviors, and positional behavior and its context. Reaction of slender lorises to potential predators is also discussed briefly. This information is then interpreted in relation to the following questions. Is slender loris locomotion related more to foraging behavior or predator avoidance? In what context does the slender loris move 'cryptically'? Does slow locomotion limit social interactions with other lorises?

Methods

The Study Site

This study was carried out in a semi-protected dry deciduous *Acacia-Euphorbia* scrub forest, Ayyalur Interface Forestry Division (AIFD), in Dindigul District, Tamil Nadu, South India (77° 54'–78° 17' E and 10° 04'–10° 40' N) from October 1997 to August 1998. The 1-km² study site was located in the foothills of the Eastern Ghats. Temperatures in January through March range from 35 to 40 °C, becoming hotter from April to June (40–49 °C). Temperatures drop again in July, leading to the monsoon in September to November during which time temperatures fall to 30–35 °. The total rainfall for the 11-month duration of this study was only 956 mm.

The study site contained patchily distributed acacia trees and cacti and was bordered by croplands and fenced-in orchards. Most of the vegetation consisted of thorny bushes and short trees that were separated from one another by up to 15–20 m of scrubby undergrowth [see 16, 18 for more details on vegetation].

Habituation and Nocturnal Observation

Most lorises at AIFD, when approached by an observer for the first time, remained immobile for several minutes, staring at the observer. Most animals were habituated within 1 h and could then be approached by any observer; they were considered habituated when they did not freeze at the sound of footsteps, or when they carried out their activities without staring at the observers. Other researchers have experienced such easy habituation with lemurs in Madagascar [R. Sussman, pers. comm.].

Animals were observed from a distance of 1–7 meters with the aid of hand held lights and headlamps covered with red cellophane to reduce disturbance to the animals. Lorises possess a reflective layer on the eye called the *tapetum lucidum*, the brilliant orange light reflected back from this layer could be seen from over 100 m away [19]. With the exception of some dense clumped shrubs, it often was possible to walk 360° around most vegetation. Except when animals entered dense cacti or shrubs, visibility was excellent, allowing for fine resolution of the details of loris behavior. In addition, observation was made relatively easy by the fact that, throughout the entire study, for 61% of sightings lorises were 3 m or lower and for 90% of sightings they were below 5 m; they could, indeed, frequently be watched at eye level by the observers.

Most studies of nocturnal primates now incorporate radio-tracking [e.g. 20–24]. However, during this study in India, radio-tracking and live trapping of mammals were not permitted, therefore locating specific individuals was not guaranteed. Whenever possible, animals were followed from their regular sleeping sites. Because lorises slept in groups, it was possible to choose a different animal to follow on many nights [17, 18]. If animals had emerged from their sleeping sites prior to my arrival, the first animal spotted was then observed.

Behavioral Sampling

The first month of the project was spent constructing an ethogram based on one developed for captive lorises [25]. Data were collected using focal-animal instantaneous point sampling at 5-min intervals for 1,173 h [26]. Upon spotting a loris, it was followed for as long as possible. The mean follow time was 6.2 ± 3.2 h and the mode was 10.5 h ($n = 149$ nights); 57% of all observation sessions were ≥ 7 h long; 38% of all sessions concluded with following an animal to its sleeping site. The minimum follow time was 25 min and the maximum was 11 h.

During each observation session, the name, age and sex of the animal, its activity and positional behavior were recorded. Identification of individuals is described below. Behavioral categories included: inactive (rest, stand or sit motionless, sleep); travel (directed movement when the animal is not looking for food); forage (movement associated with looking for food); feed (actual consumption of a food item); groom (autogroom or allogroom); and other (vocalize, urine wash, scent mark, play hang).

In addition to these categories, I also recorded whether an animal was alone or gregarious. I defined gregarious behavior as a physical or visual interaction (groom, play, fight, copulate, forage or travel together, stare) between two or more animals within 5 m of one another. I did not include deferred communication such as scent marking or vocalizations in this definition unless either of these categories occurred in obvious connection with another animal (i.e. scent marking a conspecific while

grooming it, growling during a fight). Proportion of time spent gregarious was calculated in two ways: proportion of sample points any loris was gregarious with another (including infants) and proportion of sample points that adult and subadult lorises spent together (excluding infants).

The eleven locomotor postures and modes recorded were sit, sleeping ball ('Schlafkugel'), quadrupedal stand, quadrupedal walk, bipedal stand, bipedal hang, cling, climb up, climb down, bridge and other. The category of other was used for unusual postures that were seen after the project ethogram had been established. These postures included tripedal hang, quadrupedal hang and variations in the style of sitting which were distinct from the drawings in Schulze and Meier [25].

Data on reaction to potential predators were recorded ad libitum.

Contact Records

Some authors believe that data collected at the first moment an animal is seen are the least biased [e.g. 10]. Therefore, contact records were collected in addition to point sampling [27]. Whenever an animal was first seen, either the focal animal or animals spotted during routine walks throughout the study area that subsequently were not followed, a contact record was recorded containing the same ecological variables as in an instantaneous sample point ($n = 357$). These data are used in comparison to the general activity budget. If two animals were spotted at the same time, the behavior of each animal was recorded as a separate sample point, though they were additionally designated into the category 'gregarious'. Contact records were recorded throughout the night.

Data Analysis and Statistics

A common problem in the study of animal behavior is that data points collected continuously are neither random nor independent from one another. They may also be more heavily weighted towards certain individuals [28]. I accounted for this problem in three ways.

First, data were compiled using the entire data set of 13,717 instantaneous sample points. This data set was used to determine the percent of observations of different sexes and individuals and of mean duration of follow time. Secondly, to account for variability across individuals, particularly those animals that were observed more than others, data were first compiled by individual, with each individual mean representing a datum. Thirdly, contact records, which are independent from one another and reflect the behavior of numerous individuals, were also used for analyzing activity budgets and habitat use. These three data sets are compared below for each research question. Data were analyzed using Microsoft Excel 1997 and JMP for Macintosh. Significance for χ^2 analysis was set at $p \leq 0.05$ level.

The Study Animals

The Mysore slender loris (*L. t. lydekkerianus*) is the largest of six recognized subspecies [1–3, 29]. Body weights from animals weighed during preliminary surveys [5] and in an animal market produced the following results: adult males (294.4 ± 25.1 g, $n = 4$); adult females (259.7 ± 26.6 , $n = 7$); subadult males (197.5 ± 32.2 g, $n = 4$); subadult female (215 g, $n = 1$). Sample size is too small for statistical comparison, but males are generally larger than females. Dorsally, the fur is a medium grey, fading to a light brown or fawn on the lower back and sides. The belly is white. Pronounced circumocular patches and a dorsal stripe of mixed brown and grey are present, and are characteristic of this subspecies [1, 29]. The ears were pale fawn or brown, unlike the black ears sometimes reported for this subspecies [30]. The fur of infants was paler and fluffier than the woolly fur of adults.

Twenty known animals were observed during this study. On more than 40 occasions, animals could not be identified to individual and were, consequently, placed in the category of 'unknown' male, female, or individuals of unknown sex. Because of the excellent visibility mentioned above, it was possible to identify each individual by failsafe features, including missing or mutilated fingers and toes, shape and size of the nose, distinct facial masks, notches in the ears, and location in the study area.

Sex of the individual was easy to distinguish; an area of dark fur surrounds the male scrotum, while the females exhibit elongated clitorises distinct from male genitalia. In addition to these features, each loris had a unique behavioral pattern that distinguished it from other animals. Age was determined by size and pattern of pelage. Younger animals tended to be smaller in body but with a proportionately large head, paler and fluffier, they also had fewer visible scars and ear notches. The age of

Table 1. Identification, sex, age class and number of sample points recorded for animals observed in this study

Name	Sex	Age class	Total sample points and percentage of all five min samples
Titania	F	A	2,348 (17.1%)
Morgaine	F	A	1,627 (11.9%)
Ygraine	F	A	413 (3%)
Halva	F	A	142 (1%)
Fanny	F	A	78 (0.6%)
Ophelia	F	S	310 (2.3%)
Ava	F	J	12**
Donald	M	A	781 (5.7%)
Mickey	M	A	140 (1%)
Billie blue	M	A	352 (2.6%)
Sudden	M	A	343 (2.5%)
Vladimir	M	S	312 (2.3%)
Arcadio	M	A	12 (0.1%)*
Scary	M	I/J	728 (5.3%)
Chakki	M	I	3,119 (22.7%)
Isadora	F	I	1,066 (7.8%)
Puck	F	I	362 (2.6%)
Hill baby	U	I	74 (0.5%)*
Chaku	U	I	390**
Bottom	U	I	96**
Unknown adult	M	U	507 (3.7%)*
Unknown adult	F	U	960 (7.0%)*
Unknown	U	U	43 (0.3%)*

F = Female, M = male, A = adult, S = subadult, J = juvenile, I = infant, U = unknown; * animals were excluded from individual analysis; ** animals were identified to individual but were excluded from all analyses.

three females was determined by their elongated nipples (suggesting that they were at least primiparous), and the later presence of infants confirmed that these females were adults.

Data used in individual analysis comes from fifteen animals: five adult females, four adult males, one subadult female, one subadult male, one male who was observed from the age of about three months until the age of about 14 months, two female infants and one male infant (table 1). Five animals observed during only one observation session were excluded from individual analysis, as was the behavior of infants when carried by their mother during the first weeks of life.

Of 13,717 instantaneous sample points, males were observed 46% of the time ($n = 6,292$), females were observed 51% of the time ($n = 6,946$), and individuals of unknown sex comprised another 3% ($n = 479$). Age classes included adults ($n = 6,881$, 50%), infants ($n = 4,621$, 34%), juveniles ($n = 1,102$, 8%) and unknown ($n = 1,113$, $n = 8\%$).

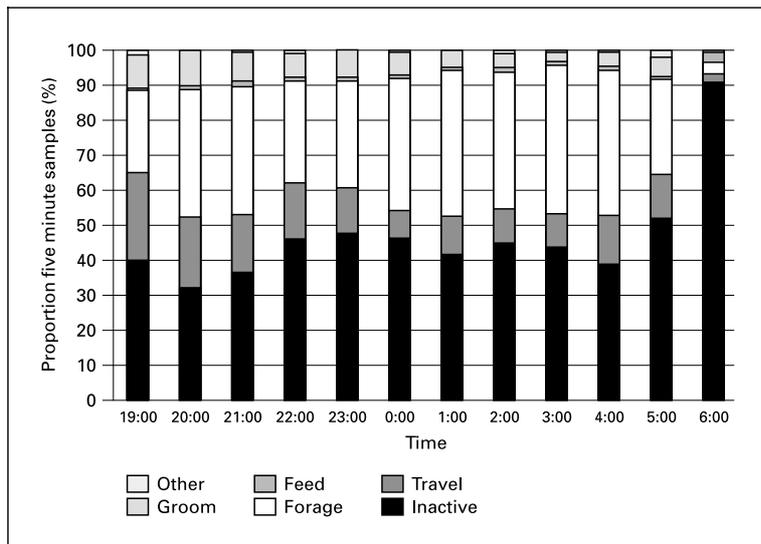


Fig. 1. Activity of the slender loris throughout the night shown through comparison of proportion of instantaneous sample points.

Results

Activity Rhythm

Slender lorises at AIFD were nocturnal. They awoke at dusk (between 18.00 h and 19.00 h) and ceased their behavior almost as soon as the sun rose (between 5.00 h and 6.00 h). No analysis of light levels was conducted during this study, but by the early morning hours of 5.00 h and 6.00 h, lorises showed a clear decrease in activity (fig. 1).

Using the instantaneous point sample data set, a significant relationship between activity and time of night was found ($\chi^2 = 196.86$, d.f. = 10, $p \leq 0.001$). Lorises became significantly more active between 20.00 h and midnight. No further significant relationship was found between time and activity until 4.00 h when they again became significantly more active, followed by a significant decrease in activity in the hour before dawn. The relationship between behavior and moonlight is described in Bearder et al. [17]. No significant difference in behavior and time of night is found using the contact data ($\chi^2 = 59.05$, d.f. = 48, $p \leq 0.13$); however, this lack of significance may be due to too small a sample size in the hours between midnight and dawn ($n = 59$).

General Activity

Table 2 shows activity records for each type of data collection. No significant difference in activity budgets was found between the three data collection techniques ($\chi^2 = 363.6$, d.f. = 10, $p \leq 0.173$).

Lorises spent about 43% of sample points engaged in inactive behaviors. This behavioral category is termed inactive rather than 'rest' because inactive lorises were not necessarily resting. The most common inactive behavior was simply sitting or stand-

Table 2. General activity budget for each type of behavioral observation

Activity	Total sample points (n = 13,717)	Individual lorises, mean (n = 15)	Contact data (n = 357)
Inactive	0.436	0.43 ± 0.18	0.364
Travel	0.149	0.223 ± 0.13	0.356
Forage	0.335	0.27 ± 0.11	0.26
Feed	0.008	0.009 ± 0.008	0
Groom ¹	0.064	0.06 ± 0.04	0.012
Other	0.008	0.008 ± 0.007	0.008

¹ Grooming was observed 823 times during instantaneous point sampling and included allogrooming (17%, n = 142) and autogrooming (83%, n = 681).

ing while the animal was alert, often scanning its surroundings, sometimes for hours at a time (see below). Sleeping during the night was more common for infants, which slept for several hours at a time. Adults infrequently napped, closing their eyes for approximately 10–15 min, before again becoming alert.

In all three data sets, lorises spent more than half of their active time either traveling or foraging. Traveling was directed movement. Though no calculation of pacing was carried out during this study, traveling was swifter than foraging. It was almost always accompanied by scent marking, either urine marking or marking substrates with scent glands [25, 31]. Traveling was more common on the perimeters of the home range, and may have a territorial function. Traveling was also used to gain access to opposite sex conspecifics. On several occasions, an animal became active after 2 or 3 h of remaining relatively motionless. Without any sound audible to the observers, that animal moved in a direct line, often more than 50 m, to an animal of the opposite sex and began a grooming session.

Foraging was distinct from traveling. Slender lorises were almost exclusively faunivorous, and would spend up to 2 h in one or two trees feeding on insects [15, 16]. Rapid climbing and walking back and forth in one tree or among a series of trees for 1–2 h was commonly associated with foraging. Lorises often engaged in head down foraging, similar to that described for pottos [7], sniffing a substrate as they moved along it. Lorises consumed their most common prey items, ants and termites, by picking them up as they walked along. However, when a faster prey item was discovered, movement slowed considerably, the loris flattened its ears against its head and then quickly grabbed the item.

Feeding occurred during foraging. Though actual ingestion was observed on 1,238 occasions, it was observed infrequently on a sample point, thus resulting in a low proportion of sample points (<1%) reflecting feeding [15, 16]. It was often accompanied by urine washing, particularly when an insect containing secondary compounds was consumed [15, 16].

Grooming, comprising 1–6% of the activity budget, included autogrooming and allogrooming. Autogrooming sessions lasted up to 1 h, and included cleaning the fur with the toothcomb, tongue and toilet claw. This behavior corresponded closely to that seen in captivity [see 25 for a detailed illustrated description]. Allogrooming included 2–7 conspecifics grooming each other. Because lorises slept communally, dawn and dusk were periods of intense social grooming. Allogrooming also occurred during the night between all age and sex classes, including adult males and infants.

Other behaviors were less frequent or difficult to record. 'Auto play hanging' involved a lone animal twisting and flipping around a branch while making the same play face used while playing with another loris [31]. Vocalizing was also included in the category 'other'; though the distinct loud whistle of the loris was recorded on 1,214 occasions, whistles rarely occurred on a sample point [17]. Urine washing and scent marking occurred almost constantly and were, thus, difficult to record. However, intense urine washing after consumption of toxic insects and prolonged marking of a substrate with the chin or by rhythmic micturition were more pronounced and prolonged, and thus were included in this category [15, 16, 31].

Lorises were seen most frequently in trees averaging 5.6 ± 0.05 m ($n = 8,515$) in height, though they used trees as tall as 12 m ($n = 28$) and were also observed on the ground ($n = 244$). The average height of the animals in these trees was 3.4 ± 1.4 m ($n = 13,633$).

Proportion of Time Spent Gregarious

Mothers carried their infants for 3–4 weeks after they gave birth. For 3–5 weeks they carried them part of the night, parking them for a portion of the night. After 6 weeks, mothers cached their infants almost the entire night. When all observations are analyzed ($n = 13,717$), including mothers carrying their infants during these first weeks, lorises spent 82% of their active time alone and were seen with one or more animals 18% of the time. When mothers with infants are excluded from this analysis ($n = 12,289$), slender lorises spent 88% of their time alone and 12% of their time with other animals. Animals were encountered alone 77% ($n = 275$) of the time and were encountered together 23% ($n = 82$) of the time.

All age/sex classes exhibited gregarious behavior. In most cases when two animals were encountered together, one of them immediately departed. On several occasions when a male/female pair were encountered grooming, the male departed and then silently reappeared within 20 min to resume grooming. The amount of time each focal animal spent in association with other animals is presented in table 3. When only the 15 known individuals are considered ($n = 12,121$), males were significantly more social than females ($\chi^2 = 269.08$, d.f. = 2, $p \leq 0.001$), even when mothers carrying their infants are taken into account. Details of social interactions between slender lorises are available elsewhere [16–18].

Positional Behavior

Postural modes assumed by slender lorises are shown in table 4. Once again, no significant difference was found between the three data sets ($\chi^2 = 196.86$, d.f. = 20, $p \leq 0.20$). However, there was a non-significant trend for quadrupedal walking to be recorded more often and sleeping less often upon first contact. These differences can be explained in that the eyes of an animal that is quadrupedally walking are facing in a direction more likely to be detected by a torch. In contrast, it is nearly impos-

Table 3. The proportion of sample points during which each individual was seen in association with other animals, both including and excluding mother/infant interactions

Individual	Gregarious excluding mother/infant	Gregarious including mother/infant
Billie blue (n = 352)	0.32	0.32
Mickey (n = 140)	0.06	0.06
Donald (n = 781)	0.11	0.11
Sudden (n = 343)	0.08	0.08
Vladimir (n = 312)	0.22	0.22
Scary (n = 728)	0.24	0.24
Titania (n = 2,348)	0.108	0.11
Ygraine (n = 413)	0.12	0.18
Fanny (n = 78)	0.02	0.02
Morgaine (n = 1,627)	0.21	0.52
Ophelia (n = 310)	0.14	0.14
Halva (n = 142)	0.53	0.53
Chakki (n = 3,119)	0.03	0.09
Puck (n = 362)	0.20	0.45
Isadora (n = 1,066)	0.04	0.08

Table 4. Proportion of observations in which each posture or locomotor mode was used during each type of behavioral observation

Positional behavior	Total sample points (n = 12,793)	Individual mean (n = 15)	Contact data (n = 339)
Sit	0.30	0.30	0.28
Quadrupedal walk	0.21	0.22	0.32
Sleeping ball	0.11	0.10	0.006
Bridge	0.08	0.11	0.06
Climb up	0.07	0.07	0.16
Climb down	0.06	0.06	0.03
Quadrupedal stand	0.04	0.04	0.04
Cling	0.04	0.05	0.05
Bipedal hang	0.02	0.01	0.01
Bipedal stand	0.003	0.004	0.003
Other	0.001	0.001	0

sible to spot a sleeping animal, as the *tapetum lucidum* is not visible. Positional behavior was also analyzed in relation to different activities. These results are described below.

Lorises exhibited several stationary postures. The most characteristic of these is the sleeping ball or Schlafkugel [25, 29, 31–33]. The animal sleeps with its head tucked into

its chest and its arms wrapped around its legs. At a sleeping site, up to seven animals sleep huddled together in this posture.

During sitting, the most common posture used by slender lorises, an animal sat semihunched, with its long legs brought up on either side of its body. Sitting also occurred when an animal positioned its rump on a branch, with its legs hanging free over the side of the branch. Quadrupedal standing involved standing on a substrate with all four limbs in contact. Quadrupedal standing or sitting often occurred when a loris needed to use the ground to travel between two supports. This act was done with wariness, an animal sometimes scanned the surrounding area for up to 45 min before moving between substrates. Ground use was almost always a last resort, though slender lorises used it frequently and with great speed and agility. Bipedal standing was done with the hind limbs and was assumed most often during hunting for flying insects. Clinging involved an animal vertically clinging to a more or less vertical substrate.

Five locomotor modes were used. During quadrupedal walking, the most common of these, animals advanced keeping at least three limbs on a substrate. It was used during feeding, foraging, traveling, and grooming. Bipedal hanging was assumed often during feeding, particularly when an animal captured prey from the undergrowth. Bipedal hanging also occurred during play, when two animals dangled from a branch and play wrestled. Climbing up and climbing down were directed up or down movements; climbing up occurred more than climbing down because animals more often used slow diagonal bridging to descend a tree, and directed quick movement to ascend it.

The fifth locomotor mode, bridging, was particularly important in loris locomotion, as lorises are incapable of leaping [13, 35]. Bridging was used most during traveling, but also during foraging and feeding. On several occasions, an animal remained stationary in a bridging posture for 10 or more min. During bridging, the loris used its entire long body length to move between supports. This was done by grasping a terminal branch of the next tree and the loris pulling the branch towards itself until it held enough of the branch to support its body weight. If a gap between substrates was too wide, animals would still attempt to reach a neighboring branch by thrusting themselves forward. This procedure was sometimes done several times until a connecting branch was eventually grasped; however, on one occasion, an unsuccessful animal fell out of the tree. All the postures and locomotor modes described here are illustrated in detail in [25].

Reaction to Potential Predators

Few other animals were found at AIFD. The most common animal was the spotted owl (*Athene brahma*). Spotted owlets are too small to prey upon adult lorises, though infant lorises fall within their size range. In fact, slender lorises shared a cactus as a daytime sleeping site with a pair of spotted owlets, suggesting the owlets are a minimal danger. However, infants which were exposed on terminal branches of trees moved to unexposed areas deeper in trees when owlets called. Reactions of infants to owl calls are described in detail elsewhere [17].

Slender lorises encountered non-conspecifics on only 12 other occasions and they mostly showed no reaction. Other animals were seen so infrequently that they could rarely be identified. On one occasion, a focal female ignored a large lizard. Snakes were seen on three occasions: a female literally walked over a pit viper, 2 young animals were

parked in a cactus with a vine snake and a young male walked past a vine snake as if it were a branch. A large sleeping bird was ignored by another female.

However, fear responses in slender lorises were seen on some occasions. Once, a loris was stranded on an electrical wire and emitted an extremely loud fear cry, rivaling the fear cries of bushbabies. On four occasions, when lorises were spotted at their daytime sleeping sites, animals awoke and the entire group fled upwards to the highest point of a tree or bush. Animals are caught from their sleeping sites in this area for the pet trade and the Ayurvedic medicine trade [35]; it is possible that they are more wary of humans in the daytime. A small cat (possibly *Felis chaus*) was seen in the study area five times. The cat was always seen on the ground, and the thorny trees probably served as good protection against it. On three of these occasions, lorises ignored the cat. Once, the cat walked past three focal animals that were within 20 m of one another; only one animal cast a look at the cat and then continued in its movements. On the final occasion, a loris was seen being chased up a tree by the cat, while it uttered the very loud fear cry. The loris scaled the thorny *Acacia* tree trunk with considerable speed and the cat was unable to follow.

Circumstantial evidence suggests this cat was an actual predator of the slender loris. The cat had been seen in the study area for two days in a row, corresponding to the lopping of a bush for firewood by a local villager. The infant Chakki used this bush as an essential 'bridge'. Chakki disappeared on the second day the cat was spotted and was never seen again. His remains were not found.

Discussion

'It toils not, neither does it do anything much except go to sleep [36].' This quote, and others like it, is consistently applied to the lorises. It certainly does not apply to the slender loris. In fact, the use of the term 'slow' to describe the movement of lorises is misleading and reinforces the view of these animals as highly cryptic. Pottos and slow lorises in both the wild and in captivity have been shown to be capable of a rapid pace [7, 31, 37, 38]. Though lorises do not leap, they are capable of moving quickly and fluidly through their environment with steady hand over hand walking.

Slender lorises are similar to other lorises in their general movement. Their positional behavior is typified by slow climbing, during which at least three limbs hold fast to a substrate, and by suspension from two or three limbs, in which they engage during feeding and social interactions, including mating and play wrestling. However, they are much more social than any lorise studied to date, spending 10–20% of their time with other animals throughout the night, as compared to the 2–4% reported for West African lorises [10]. Furthermore, they sleep communally [17, 18], as opposed to other Lorises, which sleep alone or in mother-infant dyads. This suggests that their locomotor pattern limits neither social behavior nor the ability to congregate for sleeping.

The slender loris was seen to move very slowly in two contexts. The first of these involved very cautious sitting, standing and bipedal hanging before crossing through undergrowth. Once the animal dropped to the ground, locomotion to the nearest substrate was very swift. Both pottos and angwantibos have been shown to freeze for hours when alarmed. Both of these genera also produce no loud alarm call [10]. With the exception of wariness towards humans during initial habituation, lorises did not freeze in the presence of potential predators. Even the most likely predator of the slender loris,

the jungle cat, did not elicit freezing, but rather the potential victim emitted loud alarm calls. These calls were made only when a loris was on the ground; arboreal lorises ignored the cat altogether. Slender lorises also regularly emit territorial loud whistles at regular intervals throughout the night [17], a behavior absent in the West African lorises. Slender lorises spent more than half their time traveling or foraging; animals that remained still usually appeared to be resting or relaxing rather than frozen in fear.

Pottos are equipped with a spinal process on their nuchal region, termed the defensive shield [10]. Animals may butt potential predators with this shield and it is also thought to protect the vulnerable area around the neck, particularly during head-down foraging [7]. The nuchal skin of slender lorises also is thickened [25]. Though butting was not observed towards conspecifics or any of the other animals lorises came into contact with, it could be elicited from infants if a clipboard or pencil was directed towards them. It has also been seen in captivity [25].

Another defense used by pottos, angwantibos and, possibly, slow lorises is dropping from a tree when menaced [10, 39]. This was not observed in slender lorises, which always held at least one limb fast to a substrate. During preliminary surveys [5], animals were caught to be weighed and measured. It is possible to pick the animals directly off a branch; rather than dropping, animals held tight to a branch until pried off of it. Similar observations were made by Petter and Hladik [40].

AIFD provides an interesting testing ground for hypotheses regarding slow locomotion and predator defense. Very few potential predators were available; however, the area is heavily disturbed, and only twenty miles away a much richer fauna is found. It is unlikely that slender lorises have been isolated at AIFD long enough to lose their predator defenses completely. In Madagascar, where extinctions of some key avian predators occurred many centuries ago, lemurs still show reactions to potential aerial predators, even in captivity where aerial predators are not a threat [41].

Though slow movement may play a role in predator defense to some degree, behavioral and morphological changes associated with foraging behavior may be a better adaptive explanation for the locomotor pattern exhibited by the slender loris. Slender lorises specialize on insects, concentrating on slow-moving prey items including repugnant insects containing toxic compounds, such as ants, termites and some beetles [15, 16]. The West African lorises include similar types of prey in their diet, including stinging caterpillars and sphingid moths [10]. However, lorises also included a wide variety, but smaller proportion, of higher quality crickets, grasshoppers, moths and dragonflies in their diets. Slow and chameleon-like movements were associated with quick-moving, less toxic prey that was more likely to escape if not stalked carefully. No nutritional analyses were run on the prey items eaten by lorises. However, the locomotor strategy of lorises might be a compromise between high quality and toxic food types.

As noted above, an adaptive divergence in foraging strategies might account for the physical and behavioral differences among lorises and galagos. Most evidence points to a common ancestry between West African lorises and bushbabies, with Asian lorises branching off at a later date [9].

Slender lorises, and lorises in general, have basal metabolic rates lower than those predicted for animals of their body size [9, 42, 43]. Adaptation to a toxic diet by lorises may have eliminated competition between the ancestors of lorises and bushbabies. Whereas bushbabies pursue prey by active leaping and listening, lorises rely on stealth and a lowered basal metabolism to detoxify otherwise unpalatable prey items. However, this does not limit their ability to move rapidly to supplement their diet with more

energy-rich or more easily digestible prey items. Evidence from the AIFD supports this view, but due to the lack of predators at the study site, the role of predation in selecting for unique lorisine adaptations cannot be excluded. More studies are needed of slender lorises in a variety of habitats with a greater diversity of predators and competitors to further test this hypothesis.

Acknowledgements

Dr. Charles Southwick and the Indo US Primate Project helped me to begin my study. This project could not have been carried out without the invaluable aid and generosity of Dr. M. Singh and his colleagues from the University of Mysore, especially Sindhu Radhakrishna. I thank District Forest Officer Abass, Range Forest Officer Rajagopal, and the staff of AIFD; my field assistants, Santiago, Sesu Mary, C.A. Buzzell and S.M. Heinrichs; and the staff and students from University of Wisconsin in Madurai. D.T. Rasmussen, R.W. Sussman, S.K. Bearder, H. Schulze, J. Losos, J. Phillips-Conroy, T.M. Gleason, R.J. Smith, L. Green and two anonymous reviewers provided comments on this manuscript. E. Hill and S. Ford helped with statistics. Finally, S.K. Bearder provided critical advice on field methods for this project. Financial support was provided by One with Nature of the Philadelphia Zoo, Sophie Danforth Conservation Biology Fund, Primate Conservation Inc., Bruce Wulff, Wenner-Gren Foundation, and NSF (SBR-9714870).

References

- 1 Osman Hill WCO: A monograph on the genus *Loris*. Ceylon J Sci (B) 1993;XVIII:89–129.
- 2 Jenkins PD: Catalogue of primates in the British Museum (Natural History) Part IV: Suborder Strepsirrhini. British Museum (Natural History), London 1987.
- 3 Schulze H, Meier B: The subspecies of *Loris tardigradus* and their conservation status; in Alterman L, Doyle G, Izard MK (eds): *Creatures of the Dark: The Nocturnal Prosimians*. New York, Plenum Publishing, 1995, pp 193–210.
- 4 Nekaris KAI: A preliminary survey of the slender loris *Loris tardigradus* in South India. *Am J Phys Anthropol Suppl* 1997;24:176–177.
- 5 Singh M, Lindburg DG, Udhayan A, Kumar MA, Kumara HN: Status survey of the slender loris in Dindigul, Tamil Nadu, India. *Oryx* 1999;33:31–37.
- 6 Singh M, Kumar MA, Kumara HN, Mohnot SM: Distribution and conservation of slender lorises in Southern Andhra Pradesh, South India. *Int J Primatol* 2000;21:721–730.
- 7 Oates J: The niche of the potto. *Int J Primatol* 1984;5:51–61.
- 8 Sussman RW: *Primate Ecology and Social Structure*, vol I: Lorises, Lemurs and Tarsiers. Needham Heights, Pearson Custom Publishing, 1999.
- 9 Rasmussen DT, Nekaris KAI: Evolutionary history of the loriform primates. *Folia Primatol* 1998;69(suppl 1): 250–285.
- 10 Charles-Dominique P: *Ecology and Behaviour of Nocturnal Primates*. London, Duckworth, 1977.
- 11 Bearder SK: Physical and social diversity among nocturnal primates: A new view based on long-term research. *Primates* 1999;40:267–282.
- 12 Charles-Dominique P: Vie sociale de *Perodicticus potto* (Primates, Lorises). *Etude de terrain en forêt équatoriale de l'ouest africain au Gabon. Mammalia* 1974;38:355–379.
- 13 Walker AC: The locomotion of the lorises, with special reference to the potto. *E Afr Wildlife J* 1969;7:1–5.
- 14 Glassman DM, Wells JP: Positional and activity behavior in a captive slow loris: A quantitative assessment. *Am J Primatol* 1984;7:121–132.
- 15 Nekaris KAI: Diet of the slender loris (*Loris tardigradus lydekkerianus*) in Dindigul District, Tamil Nadu, India. *Am J Phys Anthropol Suppl* 1999;28:209.
- 16 Nekaris KAI: The Socioecology of the Mysore Slender Loris (*Loris tardigradus lydekkerianus*) in Dindigul Dt, Tamil Nadu, South India. PhD Thesis, Washington University, St. Louis, 2000.
- 17 Bearder SK, Nekaris KAI, Buzzell CA: Are some nocturnal primates afraid of the dark?; in Miller L (ed): *Eat or Be Eaten: Predator Sensitive Foraging*, in press. Cambridge University Press.
- 18 Nekaris KAI: The spacing system of the slender loris and its implications for social organization. *Am J Phys Anthropol* 2000;51:77.
- 19 Charles-Dominique P, Bearder SK: Field studies of loriseid behaviour: Methodological aspects; in Doyle GA, Martin RD (eds): *The Study of Prosimian Behaviour*. New York, Academic Press, 1979, pp 567–629.

- 20 Bearder SK, Martin RD: The social organization of a nocturnal primate revealed by radio tracking; in Amlaner CR Jr, Macdonald DW (eds): A Handbook on Biotelemetry and Radio Tracking. Oxford, Pergamon Press, 1980, pp 663–648.
- 21 Crompton RH: Foraging, habitat structure, and locomotion in two species of *Galago*; in Rodman PS, Cant JGH (eds): Adaptations for Foraging in Non-Human Primates. New York, Columbia University Press, 1984, pp 73–111.
- 22 Gursky SL: Group size and composition in the spectral tarsier, *Tarsius spectrum*: Implications for social organization. *Trop Biodiv* 1995;3:57–62.
- 23 Fietz J: Mating system of *Microcebus murinus*. *Am J Primatol* 1999;48:127–133.
- 24 Mueller AE: Aspects of social life in the fat-tailed dwarf lemur (*Cheirogaleus medius*): Inferences from body weights and trapping data. *Am J Primatol* 1999;49:265–280.
- 25 Schulze H, Meier B: Behaviour of captive *Loris tardigradus nordicus*: A qualitative description including some information about morphological bases of behaviour; in Alterman L, Doyle D, Izard MK (eds): Creatures of the Dark: The Nocturnal Prosimians. New York, Plenum Publishing, 1995, pp 221–250.
- 26 Altman J: Observational study of behavior: Sampling methods. *Behaviour* 1974;49:227–265.
- 27 Rasmussen DT: Primate origins: Lessons from a neotropical marsupial. *Am J Primatol* 1990;22:263–277.
- 28 Thomas DH: Refiguring Anthropology: First Principles of Probability and Statistics. Chicago, Waveland Press, 1986.
- 29 Osman Hill WC: Primates. Comparative Anatomy and Taxonomy. I. Strepsirrhini. Edinburgh, Edinburgh University Press, 1953.
- 30 Seth PK: Preliminary observations on slender lorises. *Anthropologist* 1963;7:45–51.
- 31 Rasmussen DT: Life History and Behavior of Slow Lorises and Slender Lorises. PhD Thesis, Duke University, Durham, 1986.
- 32 Narayan Rao CR: Observations on the habits of the slow loris *Loris lydekkerianus*. *J Bombay Nat Hist Soc* 1927;32:206–208.
- 33 Subramonian S: Some observations on the habits of the slender loris (*Loris tardigradus*). *J Bombay Nat Hist Soc* 1957;54:387–398.
- 34 Sellers W: A biomechanical investigation into the absence of leaping in the locomotor repertoire of the slender loris (*Loris tardigradus*). *Folia Primatol* 1996;67:1–14.
- 35 Mohnot SM: On the primate resources of India. *J Bombay Nat Hist Soc* 1978;75:961–969.
- 36 Glinn B: The slow loris. *Life* Oct 8, 1951;31:179–180.
- 37 Barret E: The Ecology of Some Nocturnal, Arboreal Mammals in the Rainforests of Peninsular Malaysia. PhD dissertation, Cambridge University, 1984.
- 38 Dykyj D: Locomotion of the slow loris in a designed substrate context. *Am J Phys Anthropol* 1980;52:577–586.
- 39 Tenaza R, Fitch H: The slow loris. *Zoonooz* 1984;57:10–12.
- 40 Petter JJ, Hladik CM: Observations sur le domaine vital et la densité de population de *Loris tardigradus* dans les forêts de Ceylon. *Mammalia* 1970;34:394–409.
- 41 Goodman SM, O'Connor S, Langrand O: A review of predation on lemurs: Implications for the evolution of social behavior in small nocturnal primates; in Kappeler PM, Ganzhorn JU (eds): Lemur Social Systems and Their Ecological Basis. New York, Plenum Press, 1993, pp 51–56.
- 42 Mueller EF: Energy metabolism, thermoregulation and water budget in the slow loris (*Nycticebus coucang*). *Comp Biochem Physiol* 1979;64A:109–119.
- 43 Mueller EF, Nieschalk U, Meier B: Thermoregulation in the slender loris (*Loris tardigradus*). *Folia Primatol* 1985;44:216–226.