

## RESEARCH ARTICLE

# Not All Lorises Are Slow: Rapid Arboreal Locomotion in *Loris tardigradus* of Southwestern Sri Lanka

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The unique slow-climbing quadrupedalism of Asian lorises has been the subject of numerous studies; however, qualitative observations of more rapid locomotion have occasionally been reported. Field studies of the red slender loris have revealed the habitual use of unexpectedly high-speed locomotion by the so-called “sloth of the primate world.” Novel video footage permitted the first quantitative kinematic analysis of rapid quadrupedalism in wild lorises. Observations revealed that this previously unexplored behavior is far from infrequent, with 26% of red slender loris locomotor activity being dedicated to high-velocity arboreal quadrupedalism. This locomotor pattern may represent a primitive retention of the rapid, scrambling quadrupedalism that is observed in other strepsirrhines, or it may constitute a more recent specialization of this smallest loris taxon. *Am. J. Primatol.* 69:112–120, 2007. © 2006 Wiley-Liss, Inc.

**Key words:** arboreal locomotion; velocity; quadrupedalism; primate behavior

## INTRODUCTION

Asian lorises have long been characterized by a form of slow arboreal locomotion that is unique among primates [Jones, 1795; Osman Hill, 1953]. The earliest descriptions of *Loris* and *Nycticebus* emphasized this singular locomotor pattern; indeed, early taxonomists were so struck by similarities in movement and suspensory postures between slender lorises and sloths that they suggested

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that the two groups share taxonomic affinities [Osman Hill, 1933]. Cautious movement in lorises has often been attributed to their distinctive morphology [Walker, 1979]. A medley of morphological specializations, such as relatively long limbs, retia mirabilia of the limb vessels, and shortened second digits of the hands and feet, are thought to enable slow climbing/bridging behaviors and strong grasping [Osman Hill, 1953; Rasmussen & Nekaris, 1998].

The extraordinary locomotor pattern of these primates has not gone unstudied in the laboratory. Kinematic and kinetic research has quantitatively characterized the nonsaltatory locomotion of Asian lorises as “smooth, slow and deliberate” [Ishida et al., 1992, p 147]. Average speeds of 0.59 m/sec have been recorded for a large number of strides ( $n = 300$ ) of captive slender lorises moving at their preferred speeds on substrates ranging in size, orientation, and compliance [Stevens, 2002, 2003; Stevens & Heesy, 2002; Stevens et al., 2001]. Higher average velocities have been reported for smaller samples of strides on horizontal-only substrates [Schmitt & Lemelin, 2004], with animals occasionally reaching speeds of 1.65 m/sec in the laboratory when urged vocally, with a conspecific, or with a food reward [Demes et al., 1990]. This speed approaches those used by galagos, which can travel at 2.2 m/sec [Crompton et al., 1993].

Interestingly, field observations of both *Nycticebus pygmaeus* [Duckworth, 1994] and *Loris lydekkerianus* [Nekaris, 2001] have also noted the occasional ability of these taxa to move quickly during particular behaviors, such as courtship. However, it is the strikingly *regular* use of rapid locomotion by *L. tardigradus* that Nekaris and Jayewardene [2003] used as a key feature to distinguish this taxon from congeners in the field. The red slender loris (*L. t. tardigradus*) is the smallest member of the loris subfamily, averaging 130 g. It occurs only in southwest Sri Lanka, where it is endangered [Baillie et al., 2004]. Groves [1998] recently distinguished this taxon from other slender lorises on the basis of body size, pelage differences, and metric variation in museum specimens. A range of behavioral and ecological parameters, such as distinct vocalizations and life-history strategies, further validate this distinction [Coultas, 2002; Nekaris, 2003a; Nekaris & Jayewardene, 2003].

## MATERIALS AND METHODS

To quantify previously unexplored rapid locomotor behavior, we compared locomotor velocities for strides obtained from red slender lorises (*L. t. tardigradus*) in the wild, and slender lorises (the taxonomic affinities of which are currently under study) housed at the Duke University Primate Center (DUPC). In both settings, habituated animals were filmed in a lateral view moving at their chosen speeds (without urging) on a broad range of arboreal substrates varying in diameter, orientation, and flexibility.

Field observations were carried out from 2001 to 2004 in a 40-ha plot of the Masmullah Proposed Forest Reserve in Sri Lanka’s southern province [Nekaris et al., 2005]. Identified and measured subjects were filmed ad libitum at a distance of at least 5 m to reduce the effects of parallax, using a Hi-8 Sony USA Handycam with the Nightshot© option enabled. Since red lorises in the natural setting are often obscured by dense vegetation, a multicamera kinematic data-collection setup was not feasible. Nonetheless, on different occasions we were able to collect 15 strides from two adult red slender lorises (*L. tardigradus*, one male (161 g) and one female (148 g)) using 2D field kinematic methods as detailed in Stevens et al. [2006].

The field data were compared with 375 strides collected on two adult captive slender lorises, *L. lydekkerianus*, one male (200 g) and one female (165 g), housed at the DUPC. To reduce the effects of the captive experimental setting on the subjects' performance, animals with regular access to varied substrates were acclimated to experimental supports in their naturalistic enclosures for a number of days prior to the experiments. In the captive setting, standard 2D kinematic techniques, which were approved by the IACUC and were similar to those described by Rollinson and Martin [1981], were employed. Two Panasonic AG-195 VHS professional video cameras were positioned at a distance of 4.5 m to reduce problems associated with parallax [Plagenhoef, 1979; Spencer & Spencer, 1995], and synchronized using a Videonics Digital Video Mixer MX-1 NTSC. The animals were filmed walking over simulated arboreal supports that varied in size, orientation, and compliance. Supports were constructed from 8-ft-long PVC pipes and covered with a nonslip surface. Additional methodological details are described in Stevens [2003]. Between June 1999 and November 2000, 56 experiments were conducted in an indoor enclosure at the DUPC, yielding 92 hr of kinematic data.

All kinematic data were collected by importing video clips into Peak Motus software (version 5.1.6), and frame rates were optimized by splitting the 30-Hz fields to achieve 60 Hz. Only steps in which there were no visible changes in speed or direction were included. Strides were analyzed frame by frame, and anatomical landmarks on subjects (e.g., the center of the foot was identified as a highly visible anatomical landmark in both experimental and natural settings) were manually digitized at touchdown events. Stride durations were defined as the time interval between consecutive ipsilateral hindlimb contacts. Stride lengths were defined as the distance in meters between consecutive ipsilateral hindlimb contacts. Distances were calibrated on experimental supports with marks made at 5-cm intervals, whereas measurements were carefully made on natural supports using steel forestry tape. Absolute velocities were calculated by dividing the stride length by the stride duration. The results discussed herein are limited to data obtained on symmetrical quadrupedal strides. Because of differences in the sample sizes of strides collected in the laboratory and field settings, we did not use statistical approaches to compare maximum velocities in the two loris species. It should be noted that we used a conservative approach by including a vastly larger sample of captive loris strides in order to maximize their opportunities to employ high-velocity locomotion. It is our impression after collecting nearly 400 strides that the captive lorises in this study would not have selected to use higher velocities on any of the supports without considerable urging.

To explore the frequency and context of rapid locomotion in wild red slender lorises, we recorded independent behavioral data points on locomotor activity and support use in the Masmullah Proposed Forest Reserve at the first moment an animal was contacted by observers (following Charles-Dominique and Bearder [1979]). Locomotor categories included fast quadrupedalism, slow quadrupedalism, vertical ascent, vertical descent, and cantilevering/bridging, with support diameters and orientations also recorded as in Nekaris [2001]. Since fast quadrupedalism is categorically distinct from the other locomotor modes, in that it consists of rapid scrambling behavior rather than the deliberate walking commonly observed in lorises, we were able to confidently distinguish it in the field. Because of the dense vegetation, it was not always possible to collect all substrate parameters during a given observation. We recorded the path lengths of animals by flagging trees through which they passed every 3 min, and pacing the distance in the daylight with a measuring tape and pedometer. Field behavioral data were analyzed with SPSS V.11.0, with probability set at  $P \leq 0.05$ .

**RESULTS**

The average speeds of wild red slender lorises far outpaced those of slender lorises in the laboratory setting. Indeed, the maximum velocities for red slender loris strides collected in the wild are over twice those observed for its larger congener (Fig. 1a). This pattern is retained in all branch types. Despite the larger body size and longer absolute limb lengths of the captive slender lorises, and the higher number of strides we were able to collect for them in the laboratory setting, in no strides did their speeds approach those used by the wild red slender lorises (Fig. 1b). The rapid locomotion reported herein is not atypical for red slender lorises, and it was commonly observed in all seven subjects that were

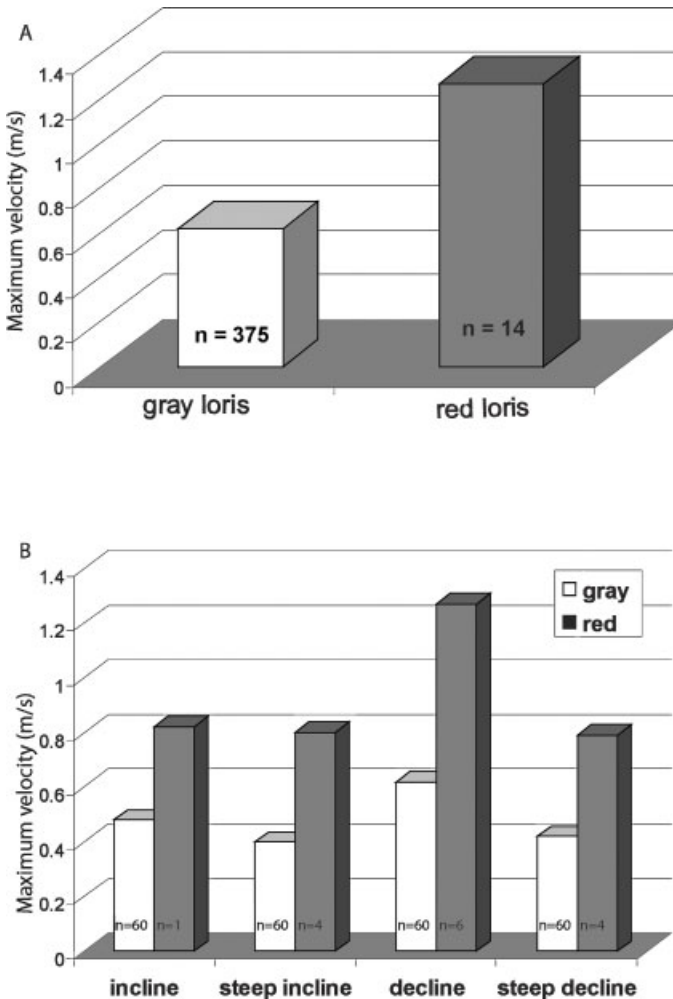


Fig. 1. Quantification of slender loris maximum velocities. **A:** Maximum velocity of gray slender lorises in captivity (n = 375 strides) vs. red slender lorises in the wild (n = 15 strides). **B:** Maximum velocity as above by substrate type. Note that even a few strides obtained for red slender lorises on supports in the wild can exceed the velocity of all strides obtained in the lab for their congeners. No attempts were made to urge animals in either setting to move more rapidly, hence all strides included in this study reflect the chosen speeds of habituated animals.

habituated at the time of this study. Qualitatively, these animals are capable of moving much more rapidly, such as when pursuing a female in estrus.

A closer examination of locomotor behavioral categories in the wild reveals that the red slender lorises engaged in rapid arboreal quadrupedalism in more than one-fourth of the observed locomotor bouts ( $n = 69$ ; Fig. 2).

Within a secondary tree fall zone setting, red lorises are small-branch specialists ( $n = 61$  substrate size observations), most often moving on supports less than 5 cm in diameter ( $\chi^2 = 23.793$ ,  $df = 3$ ,  $P \leq 0.0001$ ), and only occasionally selecting branch clusters, or substrates larger than 5 cm (Fig. 3a). Overall, they do not exhibit strong preferences with respect to branch orientation, as no significant differences were observed in their choice of substrate angle during movement ( $n = 61$  substrate orientation observations,  $\chi^2 = 4.164$ ,  $df = 2$ ,  $P = 0.125$ ; Fig. 3b). Rapid quadrupedalism ( $n = 17$ ) is used on arboreal supports of all diameters (Fig. 3c) and orientations (Fig. 3d), but was never observed in animals moving on the ground. It should be noted that a more detailed study of 12 additional marked and habituated individuals is currently under way, and that rapid quadrupedalism clearly constitutes either the most common or the second most common form of locomotion used by all individuals (Nekaris, personal observations; Bernede, unpublished data).

Travel distances for wild gray slender lorises were recently reported [Nekaris & Jayewardene, 2003], and although kinematic data are not yet available, it appears that they do not rely on rapid quadrupedalism to the same extent as do the red slender lorises. Although a comparison of travel paths over time suggests that the faster speeds used by *L. tardigradus* may also be reflected in longer travel distances (Table I), it is clear that more observations would be required to confirm such a pattern.

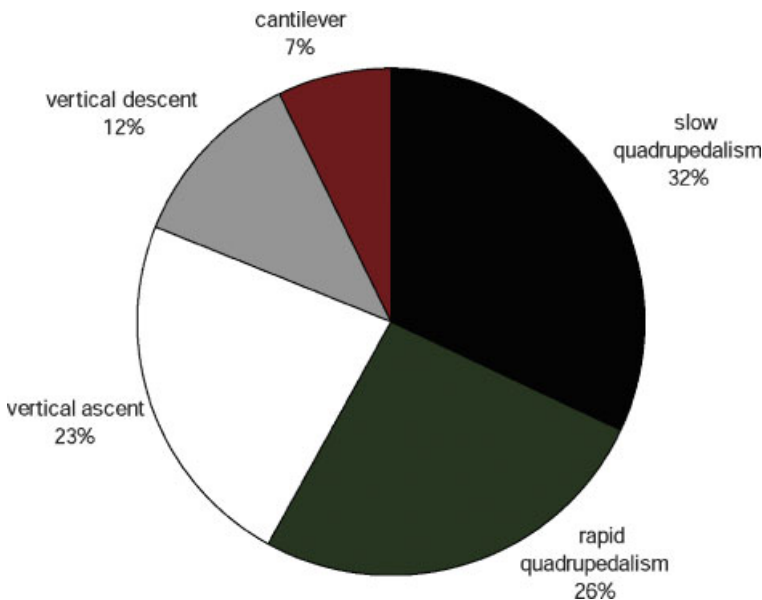


Fig. 2. Use of rapid quadrupedalism as a percentage of all sample points for locomotor activity ( $n = 69$ ). [Color figure can be viewed in the online issue, which is available at [www.interscience.wiley.com](http://www.interscience.wiley.com).]

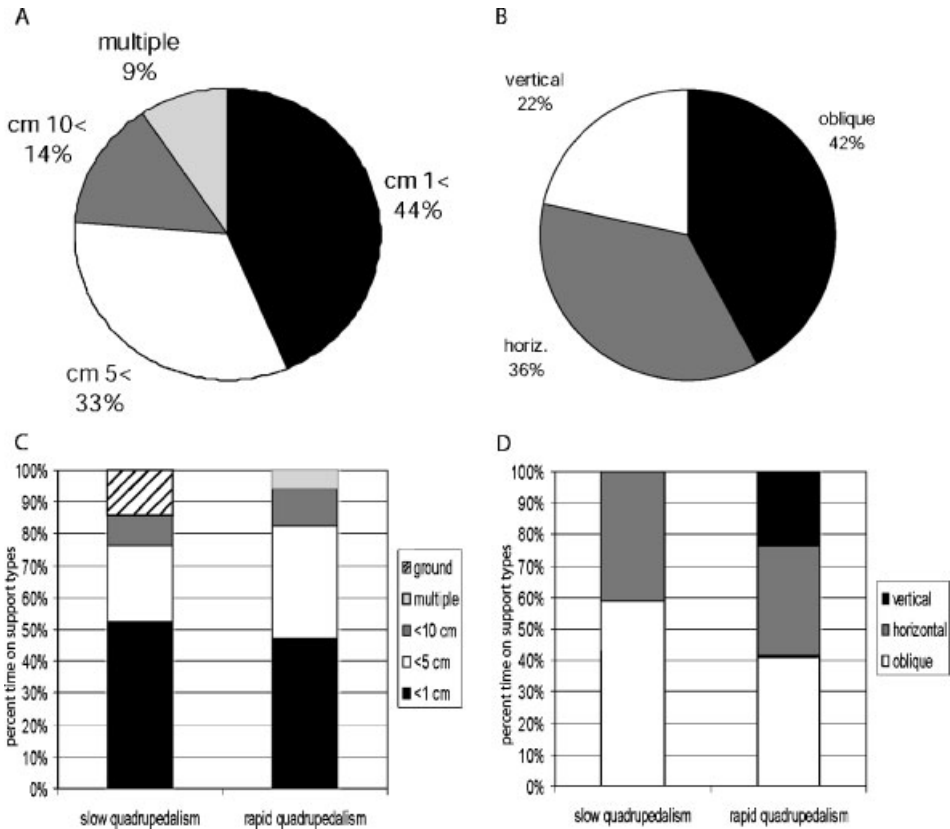


Fig. 3. Substrate types used by red slender lorises. **A:** Proportion of all locomotor activities on substrates of varying sizes (n = 61). **B:** Proportion of all locomotor activities on substrates of varying orientations (n = 61). **C:** Branch diameters used during just slow (n = 21) and rapid (n = 17) quadrupedalism. **D:** Branch orientations used during just slow (n = 21) and rapid (n = 17) quadrupedalism.

**TABLE I. Comparison of Distances Covered by Red (*L. tardigradus*) and Gray (*L. lydekkerianus*) Slender Lorises, Both Collected in the Wild (n = 3 Observations for Each Time Interval for Each Species)\***

|                            | 15 minutes   | 30 minutes  | 60 minutes    | 6 hours       |
|----------------------------|--------------|-------------|---------------|---------------|
| <i>L. l. lydekkerianus</i> | 13 m ± 7.8   | 33 m ± 11.5 | 65 m ± 24.8   | 266 m ± 32.9  |
| <i>L. t. tardigradus</i>   | 104 m ± 68.1 | 274 m ± 182 | 419 m ± 181.5 | 833 m ± 279.3 |

\*Although other ecological factors may contribute to the short distances traveled by the larger-bodied gray slender loris, rapid quadrupedalism in red slender lorises likely facilitates longer travel distances.

**DISCUSSION**

The red slender loris is restricted to Sri Lanka’s wet zone, where arboreal pathways are formed by a rich assemblage of branches, vines, and lianas [Nekaris & Jayewardene, 2003; Nekaris et al., 2005]. In addition to providing enhanced opportunities for acrobatically negotiating a complex arboreal network, this moist habitat offers a greater variety of dietary options to red slender lorises than are

available to lorises living in drier habitats [Gunatilleke & Gunatilleke, 1990]. Rasmussen and Nekaris [1998] suggested that the slow-climbing adaptations that distinguish lorises from the closely-related bushbabies may have emerged as a response to a diet. Unlike the bushbabies, which mainly consume high-energy arthropods and fruits, lorises and pottos tend to specialize on insects and leaves that are either of low quality or toxic [Charles-Dominique, 1977; Nekaris & Rasmussen, 2003; Wiens, 2002]. Like many xenarthans (e.g., anteaters and pangolins), lorises are characterized by low basal metabolic rates and associated “slow” life histories relative to other primates of similar body size [McNab, 1984]. Interestingly, preliminary observations suggest that the red slender loris consumes a larger proportion of higher-quality prey compared to other lorises, with a diet that includes lizards, mollusks, and high-energy arthropods [Nekaris & Jayewardene, 2003; Nekaris, 2005]. Finally, although red slender lorises exhibit morphological adaptations characteristic of other slow-climbing lorises, they are the smallest of the lorises and pottos (having nearly half the body mass of their congeners) and exhibit relatively longer limb proportions [Groves, 1998]. Perhaps small body size and higher dietary quality interact to release these animals from the metabolic constraints that restrict stride frequency [Bundle et al., 1999], while their longer limb proportions enable them to cover relatively greater distances in a given stride [Demes et al., 1990; Nieschalk & Demes, 1992].

Although the regular choice of high-velocity locomotion appears to characterize red slender lorises to the exclusion of their congeners in the wild [Nekaris & Jayewardene, 2003], it is important to recognize that high speeds have been recorded in the laboratory setting in larger gray slender lorises that have been urged to move more rapidly, suggesting that locomotor capabilities of the slender lorises may be fundamentally different from those of the slow loris genus, *Nycticebus* [Demes et al., 1990]. Moreover, a number of differences between the captive and wild settings may also play a role in determining the velocities at which animals typically choose to move. The rarity of the use of rapid locomotion in captive lorises may reflect aspects of enclosure design that discourage animals from achieving high speeds. For example, despite the traditional view that wild lorises typically travel only very short distances [Petter & Hladik, 1970], slender lorises are known to regularly move over several hundred meters in a single night [Nekaris, 2003b; Bearder et al., 2006]. If speed is related to travel distance, then small cage size may suppress rapid quadrupedalism in captive animals. Finally, habituated lorises in the wild generally freeze when exposed to white lights [Nekaris, 2003b]; hence, bright captive conditions may also have an effect on observed velocities in captivity. Emerging techniques for field kinematics promise to assist researchers in discerning the roles played by phylogeny and environmental settings in determining loris travel velocities and limb kinematics [Stevens et al., 2006].

In summary, we have presented the first quantitative report of rapid arboreal quadrupedalism in wild red slender lorises. Regular use of this behavior may be related to a comprehensive use of networks of continuous vines that link the forest canopy and the undergrowth. Several potential catalysts may explain this novel locomotor pattern, all of which are worthy of further research. Lorises and pottos have long been considered a relatively unspicuous and behaviorally uniform group, perhaps as a result of being the most understudied primate clade [Rasmussen, 1997]. As interest in this group grows, new species are being recognized and details are emerging regarding dietary differences [Nekaris & Jayewardene, 2003; Pimley, 2002] and behavioral variation in mating and rearing systems [Fitch-Snyder & Ehrlich, 2003; Nekaris, 2003a]. Our work shows that

even the most fundamental link uniting the lorises and pottos—that of slow, cautious climbing—is also open to new discoveries of unexpected variability.

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