



# Foraging behaviour of the slender loris (*Loris lydekkerianus lydekkerianus*): implications for theories of primate origins

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Received 3 May 2004; accepted 18 April 2005

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## Abstract

Members of the Order Primates are characterised by a wide overlap of visual fields or optic convergence. It has been proposed that exploitation of either insects or angiosperm products in the terminal branches of trees, and the corresponding complex, three-dimensional environment associated with these foraging strategies, account for visual convergence. Although slender lorises (*Loris sp.*) are the most visually convergent of all the primates, very little is known about their feeding ecology. This study, carried out over 10 ½ months in South India, examines the feeding behaviour of *L. lydekkerianus lydekkerianus* in relation to hypotheses regarding visual predation of insects. Of 1238 feeding observations, 96% were of animal prey. Lorises showed an equal and overwhelming preference for terminal and middle branch feeding, using the undergrowth and trunk rarely. The type of prey caught on terminal branches (Lepidoptera, Odonata, Homoptera) differed significantly from those caught on middle branches (Hymenoptera, Coleoptera). A two-handed catch accompanied by bipedal postures was used almost exclusively on terminal branches where mobile prey was caught, whereas the more common capture technique of one-handed grab was used more often on sturdy middle branches to obtain slow moving prey. Although prey was detected with senses other than vision, vision was the key sense used upon the final strike. This study strongly supports the notion that hunting for animal prey was a key ecological determinant in selecting for visual convergence early on in primate evolution. The extreme specialisations of slender lorises, however, suggest that early primates were not dedicated faunivores and lend further support to the emerging view that both insects and fruits were probably important components of the diet of basal primates, and that exploitation of fruits may account for other key primate traits.

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*Keywords:* Primates; Lorisiformes; Strepsirrhini; Visual predation; Insectivory; Primate evolution

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## Introduction

Optic convergence and the presence of a post-orbital bar delineate the earliest known fossil primates from their forebears. These traits are crucial in distinguishing euprimates from other basal mammals, and their ecological function has been the question of lively debate (i.e. Wood Jones, 1916; Smith, 1924; Cartmill, 1972, 1974a; Sussman, 1991; Crompton, 1995; Kay et al., 1997).

One of the principal contending hypotheses regarding the evolution of convergent optic axes in primates is the Visual Predation Hypothesis (Cartmill, 1972, 1974b, 1980, 1992). Cartmill argued that marked optic convergence tends to be a trait of animals that rely on vision to track and capture prey items, i.e. visual predators. Furthermore, he contended that increased stereoscopy reduces parallax, diminishing depth perception at a distance, but is useful for hunting at close range. Amongst primates, these features in combination with stealthy locomotion and grasping extremities, used during hunting in the terminal branches of the canopy understory or shrub layers, would favour the evolution of those traits exhibited by the earliest primates (euprimates). In addition to convergent eyes, reduced incisors would be selected for as prey acquisition functions transferred to the hands, as would a reduced snout as eye/hand replaced nose/mouth coordination. Cartmill pointed out that these trends culminated in *Loris*, an Asian strepsirrhine primate belonging to the subfamily Lorisinae. He suggested that members of this genus “are more highly specialised than any other living strepsirrhine for the mode of life whose adoption led to the differentiation of the order Primates from the other placentals (p. 120, 1972).”

Aspects of Cartmill’s hypothesis have been tested in the laboratory (Lemelin and Grafton, 1998; Lemelin, 1999), in the field (Garber, 1980, 1991; Rasmussen, 1990) and against the fossil record (Hamrick, 2001; Bloch and Boyer, 2002). These experiments have provided evidence for and against the Visual Predation hypothesis, which is not without contention (Sussman and Raven, 1978; Sussman, 1991, 1995; Bloch and Boyer, 2002). Although all authors concur that transition

to an arboreal mode of life was essential for the evolution of primate traits such as grasping hands and feet characterised by nails (Wood Jones, 1916; Rasmussen, 1990; Crompton, 1995), some authors suggest that acquisition of inconspicuous angiosperm products (fruits, flowers, nectar) in the terminal branches of trees was the essential selective pressure for the evolution of forward facing eyes (Sussman, 1991; Bloch and Boyer, 2002). Evidence for this point of view is drawn from parallels with fruit-eating megachiropteran bats, and phalangerid marsupials, which also have relatively convergent eyes, yet rely mainly on fruit (Sussman, 1995). Sussman also pointed out that African pottos (Perodicticinae, formerly classified as Lorisinae) rely extensively on repugnant prey that may be detected by scent rather than vision (Sussman, 1991).

Despite the acknowledged importance of the Lorisinae in this debate (Cartmill, 1972; Ross, 1995; Gebo, 2004), no studies have clarified the extent to which lorises are ‘visual predators,’ although they have been described as thus in the absence of field data (Cartmill, 1974a; Ross, 1996). Even the widely cited dietary study of African perodicticines relied on stomach contents analyses and observations of wild animals under experimental conditions, as field conditions were too difficult to observe hunting behaviour in detail (Charles-Dominique, 1977).

If visual predation as described by Cartmill was indeed crucial to the selection of modern lorisine traits, one would expect them to include at least 50% animal material in their diet, to catch animal prey with stealth, to procure this prey from small fine branches, and to use their hands whilst eating it. Two field studies have now shown that slender lorises are almost exclusively faunivorous, with 96% (*Loris lydekkerianus lydekkerianus*) to 100% (*Loris tardigradus*) of their diet consisting of animal prey (Nekaris, 2002; Nekaris and Rasmussen, 2003; Nekaris and Jayewardene, 2003). The diet of lorises is characterised by insects of small size that can be easily snatched, and taxa containing high amounts of toxic secondary compounds, but also includes high energy animals like lizards. Slender lorises are capable of moving at high speed, (Nekaris, 2001; Nekaris and Stevens, 2005),

and move swiftly and fluidly until within range of an evasive prey item, at which point they move with more stealth, fix on it with their eyes and then pounce on it rapidly. *Loris* catches most prey on branches smaller than 5 cm in diameter almost exclusively manually removing prey from a substrate. Hands are also used to dismember prey, or to hold prey whilst the teeth remove undesirable elements (e.g. wings of cicadas).

Although characterising the diet, these studies did not address *where* lorises acquired their prey and did not attempt to quantify *how* they obtained their prey beyond the qualitative level. In this paper, I consider prey detection method, prey acquisition strategy, and positional behaviour of slender lorises whilst foraging in relation to locality within the arboreal environment. I address how factors of the arboreal environment relate to foraging behaviour of *Loris* as regards visual predation. In particular, is visual predation the preferred hunting tactic of slender lorises? If so, when, where and on what type of prey do they engage in this mode of food acquisition? Finally, what is the relevance of these observations in understanding the environmental and ecological variables that may have influenced the evolution of primate traits?

## Methods

From 1997–1998, I conducted a socio-ecological study of the Mysore slender loris (*Loris lydekkerianus lydekkerianus*) over 10 ½ months in the Beerangi Karadu hill range of Ayyalur Interface Forestry Division, Dindigul District, Tamil Nadu, South India. I describe this dry scrub forest in detail elsewhere (Nekaris, 2001).

Feeding observations were recorded with all occurrences sampling (Nekaris and Rasmussen, 2003). As lorises hunted in dry scrub vegetation replete with bushes and short trees (Nekaris, 2001), foraging locations were divided into four categories: fine terminal branches, sturdy middle branches, the trunk, and the ground.

Food items were classified according to type (defined to Order for prey items whenever possible), and size relative to the size of a loris'

hand (small, covered by hand; medium, prey overlaps the hand on the edges; large, several orders larger than a loris' hand). Prey capture technique included swiftly catching the prey with one hand ('grab'), catching it with two hands ('catch'), tugging it forcibly from a substrate ('pull'), and removing it from the substrate with the mouth alone ('mouth'). Method of prey detection, using vision, scent or hearing, was recorded qualitatively based on the behaviour of the loris. Visual detection included fixing the eyes on a prey item, often from a distance of 2 m or gently head cocking while gazing at a prey item; auditory detection involved twitching the ears; and olfactory detection involved pronounced sniffing, sometimes accompanied by drooling.

Non-parametric Mann Whitney U and  $\chi^2$  analyses were conducted with SPSS V11.0 with probability set at the 0.05 level. Figures were drawn by A. Brady from video sequences taken by Nekaris with a Hi8 Sony Video Camera with Nightshot<sup>®</sup>.

## Results

A total of 1240 food acquisition events were recorded, 1189 of which involved capture and consumption of animal prey. Of prey items, 605 could be identified to ordinal level (Nekaris and Rasmussen, 2003). When all feeding events are considered, the one-handed grab was the preferred acquisition technique for all observations ( $\chi^2 = 2401.57$ ,  $df = 3$ ,  $p \leq 0.0001$ ), as well as for identifiable food items ( $\chi^2 = 1066.67$ ,  $df = 3$ ,  $p \leq 0.0001$ ). Slender lorises, when all items are considered, acquired food in the following way: one-handed catch (85%), two-handed catch (8%), by mouth (5%), and by pulling (2%).

When identifiable items are considered, some food items were obtained with a specific acquisition technique. A  $\chi^2$  cross tabulation revealed that the mouth was used for consuming gum, grabbing with one hand was the preferred technique for Hymenoptera, whereas catching with two hands was used significantly more for larvae, Orthoptera and Lepidoptera ( $\chi^2 = 1002.54$ ,  $df = 24$ ,  $p < 0.0001$ ) (Table 1).

Table 1

Proportion of observations that slender lorises used various acquisition methods for food items procured five times or more

	Catch	Grab	Mouth	Pull
Hymenoptera (n = 368)	0.01	0.96*** <sup>1</sup>	0.03	0
Coleoptera (n = 69)	0.04	0.92	0.03	0.01
Larvae (n = 33)	0.333	0.583		0.083
Orthoptera (n = 74)	0.18	0.82		
Lepidoptera (n = 34)	0.62*** <sup>1</sup>	0.38		
Mollusca (n = 16)		0.25		0.75*** <sup>1</sup>
Odonata (n = 6)		1.0		
Homoptera (n = 21)	0.19	0.81		
Gum (n = 35)			1.0*** <sup>1</sup>	

<sup>1</sup> Four capture techniques were associated with food types significantly more than would be expected by chance at the  $p \leq 0.0001$  level.

Only 1% (n = 14) of observations involved slender lorises acquiring food from the undergrowth. In all cases, the animal hung bipedally from a low-hanging branch, listened for insects moving in the leaf litter, visually located the prey, and caught it with one hand. Although one slug, one larva, and two hymenopterans were procured from the undergrowth, most prey items caught in this area were from the Family Blattidae of the Order Orthoptera (n = 9) ( $\chi^2 = 17.43$ , df = 4,  $p = 0.002$ ). Most items were of a large size class (n = 10) ( $\chi^2 = 9.14$ , df = 2,  $p < 0.01$ ).

Trunk foraging comprised 3.3% (n = 42) of food acquisition episodes. Although four ants and three beetles were procured from the trunk, most (n = 35) of these incidences were of gum eating ( $\chi^2 = 47.29$ , df = 2,  $p < 0.0001$ ). This type of feeding was accompanied by olfactory and visual detection, oral consumption (no use of hands to extract food except to hold onto the trunk) ( $\chi^2 = 27.524$ , df = 1,  $p < 0.0001$ ), and clinging to the substrate (Schulze and Meier, 1995).

Foraging in the more sturdy middle branches comprised 46% (n = 571) of all observations. In general detection was visual with the animal fixing its eyes on the branch as it walked, plucking prey items with a one-handed grab, keeping the other three limbs firmly attached to the substrate ( $\chi^2 = 1444.59$ , df = 3,  $p < 0.0001$ ) (Fig. 1). On four occasions olfactory detection was used whereby the animal raised its chin and pronouncedly sniffed the air; this was used for slugs and tenebrionid beetles, which emit a strong smelling chemical compound. Quadrupedal

walking, standing and climbing accompanied middle branch foraging. Of prey consumed on the middle branches, Hymenoptera and Coleoptera were consumed the most ( $\chi^2 = 648.09$ , df = 5,  $p < 0.0001$ ), and were also consumed significantly more in the middle branches than in the terminal branches ( $\chi^2 = 70.93$ , df = 7,  $p < 0.0001$ ). Small prey, due to the predominance of ants consumed in this microhabitat, were consumed more than other prey sizes ( $\chi^2 = 292.36$ , df = 3,  $p < 0.0001$ ). Lorises consumed insects in bouts of up to 36 individuals (Nekaris and Rasmussen, 2003). Insects were consumed in bouts more on middle branches than on terminal branches ( $U = 35928.0$ ,  $Z = -3.30$ ,  $p = 0.001$ ) (Table 2).

Terminal branch foraging in the mobile fine branches occurred 49% of the time (n = 612). Detection mode was usually visual, with the animal fixing on a prey item from the sturdy middle branches, and then fluidly venturing out to the terminal branches to catch the prey item (Fig. 2). On only two occasions did a loris catch a prey item in the terminal branches and move with it back to the middle branches; both of these were large prey that required 3–5 minutes to eat. Other food items were eaten *in situ*. Flying insects, particularly of small size class, sometimes caught a loris' attention auditorily, after which it would visually fix on the insect for the final strike. Several prey types were caught more on the terminal branches than anywhere else and included Lepidoptera, Orthoptera, and unidentified larvae ( $\chi^2 = 427.72$ , df = 7,  $p < 0.0001$ ). Insects of the orders Odonata, Homoptera, and Diptera, as well

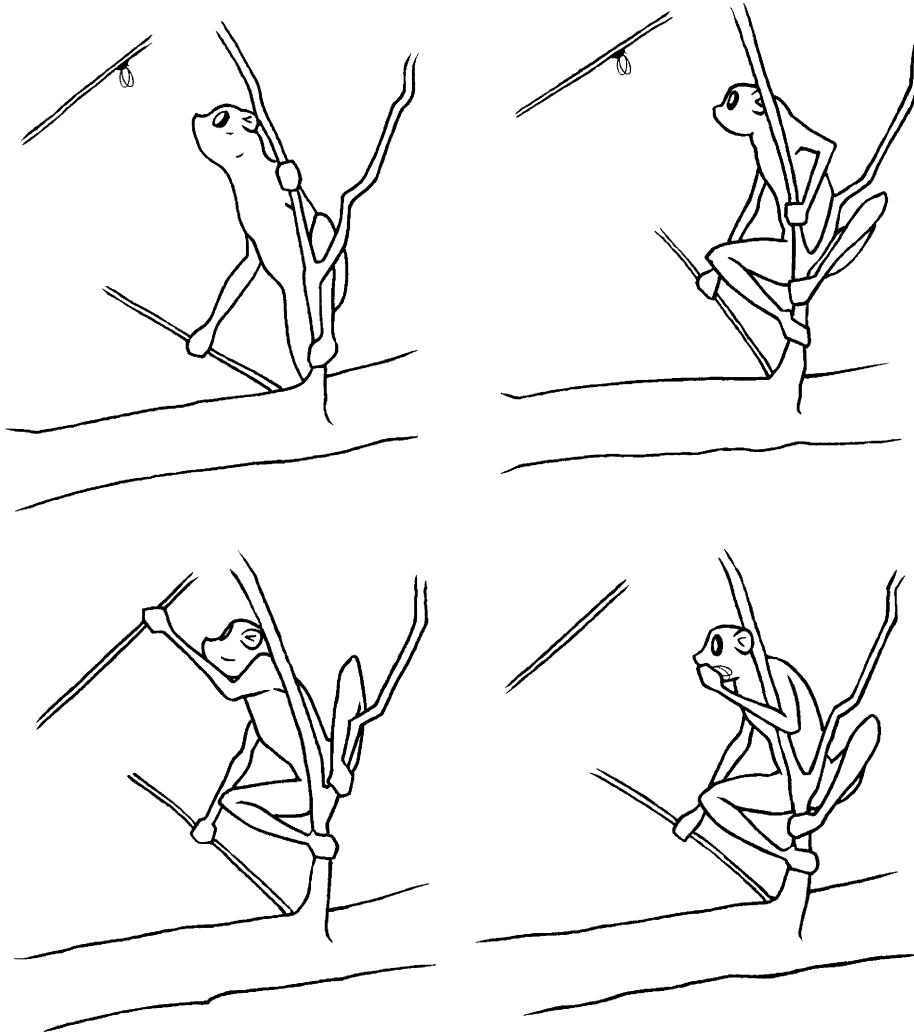


Fig. 1. Shows a slender loris visually detecting a prey item on the sturdy middle branches, and procuring it with a one-handed grab, whilst keeping all other limbs on the substrate.

as a lizard, were caught more on the terminal branches, but sample sizes were not enough to test significance. Some of these prey items (dragonflies in particular) were removed from their sleeping sites, and were caught with such stealth that they were not awoken. Ants comprised a large portion of the terminal branch foraging regime, and the overall predominant size class chosen on terminal branches was small ( $\chi^2 = 117.23$ ,  $df = 3$ ,  $p < 0.0001$ ). Still, large and medium-sized prey were caught more on terminal branches than on

middle branches ( $U = 170853.50$ ,  $Z = -2.388$ ,  $p = 0.017$ ). Other than grabbing, the most common type of prey acquisition was the two-handed catch, in general accompanied by the more acrobatic cantilever, bipedal hang or bipedal stand ( $\chi^2 = 718.26$ ,  $df = 3$ ,  $p < 0.0001$ ) (Table 2).

### Discussion

Slender lorises were almost exclusively arboreal hunters, specialising in the small branch milieu.

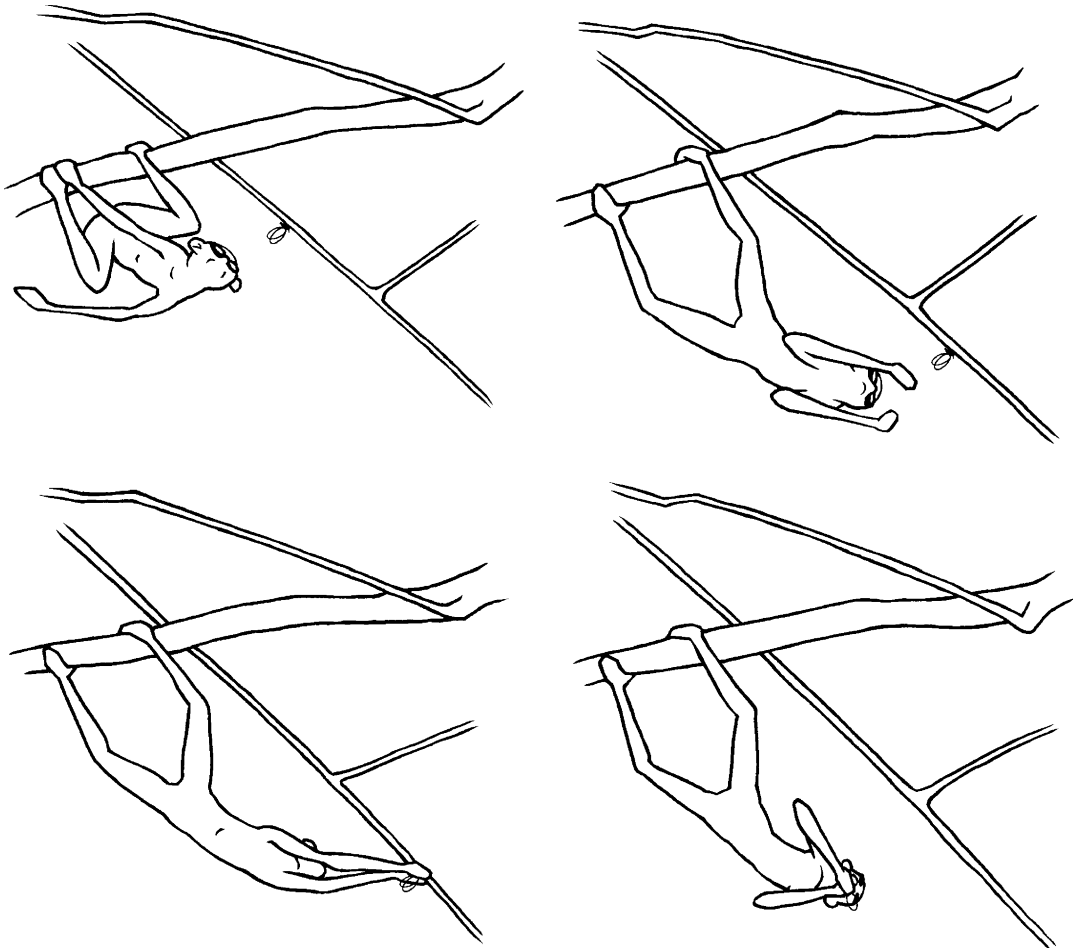


Fig. 2. Shows a slender loris visually detecting a prey item in the flexible terminal branches, and procuring it with a two-handed grab, whilst maintaining hold on a branch with a cantilever stance.

Even when selecting prey items from the undergrowth, at least two limbs remained in contact with a branch. This is unlike some other predatory nocturnal prosimians (e.g. *Tarsius spectrum*, *Sciurocheirus alleni cameronsis*) which descend to the ground for hunting up to 10% of observations (Gursky, 2000; Pimley, 2002).

In general, clear visual tracking of prey was followed by a ballistic single or two-handed strike of prey items. A similar technique has also been observed in some pottos (*Perodicticus potto edwardsi*) (Pimley, 2002) and chameleons (Schwenk, 2000). Although the primary technique,

vision was not the only sense used by lorises to perceive prey. Olfactory and auditory prey detection played a limited role. Auditory localisation of flying insects was not as marked as in galagos (Charles-Dominique, 1977). Olfactory inspection, used to search for slugs and repellent beetles, was not as common as interpreted for some pottos (*P. p. juju*, *P. p. potto*) (Oates, 1984). It should be emphasised, however, that even when another detection technique was used, as soon lorises came within close range, they fixed on an item visually in order to snatch it. Galagos, too, although often using auditory means to detect prey, rely chiefly on

Table 2

This table shows the proportion of prey items (selected more than five times) making up dietary choices on the middle and terminal branches (n = 577). A + shows prey types that were potentially evasive

Food eaten	Location	
	middle	terminal
Formicidae/Isoptera (ants and termites)	75.2% (n = 188) <sup>***1</sup>	53.5% (n = 175)
Coleoptera (beetles and weevils)	15.2% (n = 38) <sup>***1</sup>	8.9% (n = 29)
+ Orthoptera (crickets, mantids, cockroaches, etc.)	6.0% (n = 3)	9.2% (n = 12) <sup>***1</sup>
+ Homoptera (cicadas and relatives)	2.0% (n = 5)	4.9% (n = 16)
Mollusca (slugs)	1.2% (n = 3)	3.7% (n = 12)
+ Lepidoptera (moths and butterflies)		7.3% (n = 24) <sup>***1</sup>
+ Odonata (dragonflies and damselflies)		1.8% (n = 6)
unidentified larvae	0.4% (n = 1)	10.7% (n = 35) <sup>***1</sup>

<sup>\*\*\*1</sup> indicates that these prey types were chosen more at their respective localities more than would be expected by chance at the 0.0001 level.

vision when it comes to the catch (Bearder et al., in press; Bearder, pers. comm.).

Slender lorises were not terminal branch specialists, but spent an almost equal proportion of observations foraging on more stable middle branches and slender mobile terminal branches. It should be noted that in this scrub environment, the 'more stable' middle branches were still of a size class between 5–10 cm, and generally fell at the lower end of the size spectrum (Nekaris, 2001). The primary identifiable food items consumed by lorises were ants, and these were caught in both the middle and terminal branches.

When analysing locality of prey items, intriguing patterns emerge. The middle branches provided lorises with a venue on which to move steadily whilst actively visually scanning and smelling their environment (Oates, 1984). Animals hunted with three limbs securely attached to a substrate, and easily obtained small prey consumed in bouts. On only four occasions lorises lapped up ants or termites directly with the mouth, as has also been exhibited by thick-tailed bushbabies (*Otolemur crassicaudatus*), Allen's bushbabies (*S. a. cameronensis*), and pottos (*P. p. juju*, *P. p. potto*) (Oates, 1984; Happold and Happold, 1992; Pimley, 2002). Ants were usually picked up one after the next with the hand and placed in the mouth.

A marked difference in foraging strategy occurred in the terminal branches. Although hunting in bouts decreased, acquisition of high energy larger prey increased. These included

evasive prey (cicadas, cricket-like orthopterans, moths), as well as potentially evasive sleeping insects, which were rarely seen to be awakened by the stealthy loris. Disturbance of such prey could result in a considerable energetic loss, making fluid, non-leaping locomotion beneficial. A similar strategy has been suggested for chameleons, which are renowned for their keen visual predation (Herrel et al., 2001). Evasive prey items were detected from a distance of approximately two meters or less, stalked, and then snatched from a branch or from the air whilst the loris was engaged in a more acrobatic posture, usually accompanied by grasping of branches with only two limbs. Often before seizing a prey item, the loris noiselessly coiled up its rear limbs, compressed its ears, and visually focussed on the prey item (not unlike a house cat catching a mouse), and almost always caught the insect. Lorises were also adept at catching prey on the wing, but did this by detecting insects already flying, rather than those it disturbed by moving through a tree (c.f. *Galagoideis demidovii*, Charles-Dominique, 1977).

On-going studies of Sri Lankan slender lorises (*L. l. nordicus* and *Loris tardigradus tardigradus*) corroborate the view that *Loris* is a visual predator (Nekaris, 2002). *Loris t. tardigradus* relies on more vertebrate prey than *L. lydekkerianus*, stalking nocturnal geckoes, and relishing sleeping lizards, which camouflage themselves splayed amongst the terminal branches; good vision with an efficient strike is important, as these lizards awaken easily (Nekaris and Jayewardene, 2003). A pattern is

beginning to emerge that the middle and terminal branches offer distinct feeding niches for slender lorises. Further studies should consider the relative nutrient intake of terminal versus middle branch prey not only amongst slender lorises, but also amongst primates in general.

The slender loris, with its marked optic convergence, appears to be the ultimate visual predator, but do the data presented here corroborate the visual predation hypothesis? This depends on one's view of another major scenario, which has been invoked to explain the origin of primate traits. The 'Angiosperm Co-evolution' hypothesis proposes that the origin and expansion of euprimates took place alongside an adaptive radiation of angiosperms and tropical forests, and that sophisticated exploitation of angiosperm products in the terminal branch niche selected for primate traits (Sussman and Raven, 1978; Sussman, 1991, 1995). Many primates are indeed keystone pollinators of tropical forest species; these co-evolutionary relationships are clearly deep rooted. Sussman argues that primates would have required grasping hands and feed and convergent vision in order to effectively manoeuvre through the complex three dimensional environment of the terminal branches, while at the same time collecting fruits, many of which might be small and cryptically coloured.

Sussman's view has recently been potentially substantiated with a new important fossil find – a relatively complete fossil of *Carpolestes simpsoni* (Bloch and Boyer, 2002). This animal belongs to a group of archaic mammals called plesiadapiforms, which some authors suggest is the sister group to primates, and thus should share primitive traits with the first euprimates (Fox, 1993; Bloch and Silcox, 2001). The new specimen, which could be a basal primate, is replete with a grasping toe with a nail, as well as hands with grasping capabilities not unlike that of a tree shrew (Sargis, 2001), but lacks orbital convergence. The authors suggest that their evidence that grasping developed independently of other traits would be adaptive for angiosperm product exploitation, but not for visual predation. Indeed, Cartmill (1992) has stated that discovering the order in which primate traits evolved would be vital for understanding the

decisive selective factors of the ancestral primate niche. Sussman's elegant hypothesis, combined with the new data on *Carpolestes*, leaves little room for a highly predatory loris to be of any relevance to the evolution of primate traits – or does it?

Not all authors agree that *Carpolestes* is relevant to the question of primate origins. Firstly, it has been strongly argued that the plesiadapiforms have closer affiliations to the order Dermoptera and are not a sister group to primates (Beard, 1993). Even if this interpretation is rejected, other analyses of the material suggest that *C. simpsoni* resembles other plesiadapiforms in all skeletal features but the feet (Kirk et al., 2003). Gebo (2004) posited that including carpolesitids as a euprimate sister group would create taxonomic havoc, and that at best one might be able to consider *C. simpsoni* a 'protoprimate' with little bearing on the question of primate origins.

Prehensility in the hands and feet not unlike that exhibited by *C. simpsoni* has evolved in numerous other mammals, including a number of carnivores, rodents and marsupials (Cartmill, 1972; Soligo and Müller, 1999; Hamrick, 2001). Lemelin (1999), in a comparative study of didelphids, found that prehensility of the hands increased in animals that rely more on smaller gauged substrates, such as vines and terminal branches. His study supported the potential importance of the terminal branch niche, but could not address whether dietary choice was related to the evolution of cheiridial prehensility, especially considering that didelphids tend to consume a combination of fruits and insects (Charles-Dominique, 1983). In a related study of nocturnal primates, however, he did find that catching and moving live prey with the hands were related to digit length, and subsequently with locomotor pattern in fine branches (Lemelin, 1996). These results suggest that Bloch and Boyer's grasping plesiadapiform need not have been wholly frugivorous; Bloch and Boyer themselves suggest that all carpolesitids were probably omnivores (2002).

The only other field study that has directly tested the Visual Predation hypothesis was again conducted on a primate-like marsupial, *Caluromys derbianus* (Rasmussen, 1990). Based on convergent



similarities with primates, Rasmussen studied substrate choice, diet and degree of arboreality of *Caluromys* in relation to hypotheses regarding primate origins. He found that *Caluromys*, which visually foraged for insects in the terminal branch milieu, provided ‘a perfect living illustration of an ancestral primate as envisioned by Cartmill’ (Rasmussen, 1990, p. 272). Unlike *Loris*, however, *Caluromys* was not a dedicated visual predator, but took advantage of resources available in the fine branch niche almost wholly ignored by *Loris* – fruits and flowers.

The complex terminal branch feeding strategy led Rasmussen (1990) to synthesise the Visual Predation hypothesis with the Angiosperm Co-evolution hypothesis. Rasmussen argues these hypotheses are not mutually exclusive, and suggested that early primates may have been lured to the terminal branches to first exploit fruits, flowers and nectar obtained by dexterity and co-ordination, complying with the view of Sussman, and also with the interpretation of *C. simpsoni* of Bloch and Boyer. Once in this environment, those who could also effectively exploit associated insect assemblages, procured by visual predation and facilitated by their grasping hands, would have an advantage, thus accounting for primate visual convergence. The innovative aspect of this synthesis was not suggesting that euprimates may have been omnivores, but in acknowledging that the environmental stage set by Sussman could be occupied by a fruit eater that would ultimately also engage in visual predation. Indeed, Cartmill (1972) himself suggested that ancestral primates formed part of a shrub layer insectivore guild, taking advantage of insect resources *in combination* with varying amounts of fruit. Crompton (1995) invoked a similar ‘fruit first’ combined with opportunistic insectivory to explain extreme convergence in *Tarsius*.

A comparison of slender loris feeding ecology with that of other lorisiforms provides further evidence that visual convergence is an important adaptation for insect feeding, at least amongst this infraorder. Insects are a key dietary component to most species of lorisiform primates (galagos, pottos and lorises). Out of 17 species of lorisiforms where diet has been studied in some detail, animal

matter makes up from 50–100% in nine taxa (Nekaris and Bearder, in press). *Galago moholi*, like *L. lydekkerianus*, subsists exclusively on insects and gum (Bearder, 1987), and vision has been shown to be the most important sense in this species (Bearder et al., in press). *Galagoideis rondoensis* is almost exclusively insectivorous, acquiring insects from the fine branches and undergrowth by visually scanning these areas, and leaping rapidly to acquire prey (Perkin, 2001). In general, larger galagos which rely more on fruit have increasingly less convergent vision than their smaller more insectivorous relatives (Cartmill, 1974b; Ross, 1995). Further studies of the degree of convergence of new galago taxa in relation to dietary preference will be of interest.

As mentioned at the outset of this article, the Lorinae and Perodicticinae are posited in the literature as being the most specialised primate visual predators (e.g. Cartmill, 1972). Available evidence corroborates this view to a limited extent. Olfaction and hearing may be of greater importance for the African lorises, with their galago-like interorbital breadths (Charles-Dominique, 1974, 1977; Oates, 1984; Ross, 1995). Pottos do catch prey visually, but the genus as a whole appears to rely mainly on fruits (Charles-Dominique, 1977; Oates, 1984; Pimley, 2002). Recent observations of pottos in Cameroon lend support to Rasmussen’s synthesised view, in that pottos were seen to bipedally hang over nectaries, consuming both nectar and associated insects (Pimley, 2002). On the other hand, Walker (1969) suggested that careful hunting of prey, including birds, probably accounts for the locomotor anatomy of the potto. The angwantibo, a shrub layer insectivore, relies on slow moving pungent prey, perhaps with greater reliance on olfaction (Charles-Dominique, 1977). It relishes high energy prey in the captive setting, and may exploit these resources in areas of its range where it is in less competition with other lorisiforms.

Amongst the Asian lorises, *Nycticebus pygmaeus* has been shown to exhibit hunting adaptations not unlike that of *Loris*, consuming birds, flying insects, and ants; gum forms an important addition to its diet (Tan and Drake, 2001; Streicher, 2004). Although consuming some insects, limited

observation of *N. coucang* at a study site in Malaysia suggest that they specialised on gum and nectar (Wiens, 2002). Furthermore, unlike their 'slender' counterparts, slow lorises in captivity preferred larger and more stable supports, rather than flexible small gauged branches (Dykyj, 1980). Still, slow lorises are known to relish birds, rodents and other animal prey in both captivity and semi-free ranging environments suggesting that these probably play an important part in their diet in the wild (Fitch-Snyder and Schulze, 2001; pers. obs.).

The Mysore slender loris conforms to Cartmill's image of a small branch visual predatory specialist in numerous respects. Orbital approximation, in combination with stealthy but swift locomotion, allows lorises to catch close range prey upon the first strike, a process not hindered by low degrees of orbital frontation (Cartmill, 1992; Ross, 1995). Tiny hands allow lorises to grasp the smallest of the terminal branches, specialised *retia mirabilia* allow for extended grasping until the moment comes to strike the prey, and vice-like feet allow for acrobatic hunting tactics (Osman Hill, 1953; Cartmill, 1992; Rasmussen and Nekaris, 1998). Slender lorises are so specialised for these small supports, they are rarely seen on any support that they cannot grasp fully (Nekaris, 2001; Nekaris and Jayewardene, 2003).

Clearly the evidence from the lorisiforms lends itself to the Rasmussen synthesised view, with both insects and fruit playing a role. The slender lorises, however, being the most faunivorous of the lorisiforms, demonstrate how selective pressures surrounding visual predation can result in primate adaptations to the extreme.

## Conclusions

Traditionally, most researchers suggest that the stem lineage of primates was probably small, and in accordance with diet being in part a function of body size, they must have been partly insectivorous (Gebo, 2004). With this in mind, a specialised faunivore like the Mysore slender loris can by no means be used as an exact model for the ancestral euprimate. It is, however, highly adapted to life in an arboreal environment, and exhibits the primate

traits of visual convergence and grasping hands and feet to an extreme (Cartmill, 1974b). The ecological parameters related to its divergence from other lorisiforms to such an extent thus may be relevant to reconstructing the ancestral primate niche. As Rasmussen (1990) rightly points out, both the Visual Predation and Angiosperm Co-evolution theories for primate origins are not mutually exclusive, both envisioning an acrobatic grasping euprimate foraging in the fine branch milieu. Even Cartmill concurs that ancestral primates probably consumed fruit to some extent, but that visual predation may be responsible for the trait of orbital convergence (Cartmill, 1972). The present study provides strong evidence that the adaptive advantage of orbital convergence is probably linked to the visual acquisition of prey prior to a precision strike.

## Acknowledgements

I thank C. Southwick, S. M. Heinrichs and C. A. Buzzell for assistance in the field, and D.T. Rasmussen, R. W. Sussman, S.K. Bearder, and S. M. Ford for valuable discussions on this project. Editorial assistance was provided by A. Miehs and L. Birkett, and illustrations were prepared by A. Brady. Three anonymous reviewers improved the quality of this manuscript immensely. This field study was supported by grants from One with Nature of the Philadelphia Zoo, Sophie Danforth Conservation Biology Fund, Primate Conservation Inc., Bruce Wulff, Wenner-Gren Foundation (all to Nekaris), and an NSF dissertation improvement grant to Nekaris and D. T. Rasmussen (SBR-9714870).

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