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Abstract	Craniomandibular variation characterizes the five species of Asian slow loris ( <i>Nycticebus</i> ), but until now, few ecological studies have been available to understand the factors that underpin it. Here, we review feeding ecology of Asian lorises and African pottos, with emphasis on the importance of exudate feeding, including several new studies. We then present novel data on this behavior based on a 10-week study of <i>N. coucang</i> at Pusat Penyelamatan Satwa Rescue Center, Lampung, Sumatra, Indonesia. Lorises and pottos range in body size from 100 g ( <i>Loris tardigradus</i> ) to more than 2 kg ( <i>N. bengalensis</i> ). Three of the smallest species ( <i>Arctocebus calabarensis</i> , <i>A. aureus</i> , <i>L. tardigradus</i> ) rely mainly on insects and small invertebrates as dietary staples. Although <i>Perodicticus</i> is known to eat gum only from already open wounds, active gouging of bark to extract exudates or consumption of plant sap has now been observed in all other lorises. Five species ( <i>P. potto</i> , <i>N. coucang</i> , <i>N. bengalensis</i> , <i>N. javanicus</i> , <i>N. pygmaeus</i> ) rely
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on exudates as a key food source. Although at all field sites, exudates are eaten all year round, at some, they become a key resource in times of food scarcity. Exudates have been extracted from 14 different plant families; Fabaceae is possibly the most important, currently consumed by all exudativorous species. Despite the lack of keeled nails, gouging behavior of lorises closely resembles that of marmosets and fork-marked lemurs, and involves active breaking of the plant surface; the audible nature of this behavior, as well as the characteristic marks left behind, makes it useful for determining the presence of *Nycticebus* in a forest. The captive lorises in our study also gouged regularly, recorded 2.9 times per hour for both adults and juveniles. Urine and facial markings accompanied the majority of gouges, a behavior recorded before only for marmosets. The functions of this behavior as a resource sharing strategy are explored. The importance of providing opportunity for gouging for captive lorises is also discussed, as a way to mitigate the periodontal diseases, which plague *Nycticebus* in captivity. We conclude by discussing the importance of a better understanding of this relatively unique behavior to improve our knowledge of morphological correlates to loris taxonomy and ecology, and captive management via dietary changes and enrichment.

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Chapter 8  
Comparative Ecology of Exudate Feeding  
by Lorises (*Nycticebus*, *Loris*) and Pottos  
(*Perodicticus*, *Arctocebus*)

K.A.I. Nekaris, C.R. Starr, R.L. Collins, and A. Navarro-Montes

**Abstract** Craniomandibular variation characterizes the five species of Asian slow loris (*Nycticebus*), but until now, few ecological studies have been available to understand the factors that underpin it. Here, we review feeding ecology of Asian lorises and African pottos, with emphasis on the importance of exudate feeding, including several new studies. We then present novel data on this behavior based on a 10-week study of *N. coucang* at Pusat Penyelamatan Satwa Rescue Center, Lampung, Sumatra, Indonesia. Lorises and pottos range in body size from 100 g (*Loris tardigradus*) to more than 2 kg (*N. bengalensis*). Three of the smallest species (*Arctocebus calabarensis*, *A. aureus*, *L. tardigradus*) rely mainly on insects and small invertebrates as dietary staples. Although *Perodicticus* is known to eat gum only from already open wounds, active gouging of bark to extract exudates or consumption of plant sap has now been observed in all other lorises. Five species (*P. potto*, *N. coucang*, *N. bengalensis*, *N. javanicus*, *N. pygmaeus*) rely on exudates as a key food source. Although at all field sites, exudates are eaten all year round, at some, they become a key resource in times of food scarcity. Exudates have been extracted from 14 different plant families; Fabaceae is possibly the most important, currently consumed by all exudativorous species. Despite the lack of keeled nails, gouging behavior of lorises closely resembles that of marmosets and fork-marked lemurs, and involves active breaking of the plant surface; the audible nature of this behavior, as well as the characteristic marks left behind, makes it useful for determining the presence of *Nycticebus* in a forest. The captive lorises in our study also gouged regularly, recorded 2.9 times per hour for both adults and juveniles. Urine and facial markings accompanied the majority of gouges, a behavior recorded before only for marmosets. The functions of this behavior as a resource sharing strategy are explored. The importance of providing opportunity for gouging for

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captive lorises is also discussed, as a way to mitigate the periodontal diseases, which plague *Nycticebus* in captivity. We conclude by discussing the importance of a better understanding of this relatively unique behavior to improve our knowledge of morphological correlates to loris taxonomy and ecology, and captive management via dietary changes and enrichment.

## Introduction

Asian slow lorises (Lorisidae: *Nycticebus*) range from Northern India to the Philippines, occurring in a multitude of habitat types from 0 to 4,000 m above sea level. With a basal metabolic rate lower than 60% of the predicted value (Müller et al. 1985), cryptic behavior of these nocturnal primates has precluded their study. Until recently, large variance in body size (265–2,200 g) (Table 8.1) was explained because of clinal variation (Osman Hill 1953; Ravosa 1998). However, several characters of the craniomandibular complex indicated ecological or genetic explanations for variation within *Nycticebus* (Schwartz and Beutel 1995; Ravosa 1998). Diet, in particular, is predicted to vary, with large Bengal slow lorises having a tougher diet requiring more repetitive loading (i.e., more folivorous), and smaller pygmy and Bornean lorises consuming more insects (Ravosa 1998). Genetic and gross morphological studies have now shown that *Nycticebus* comprises at least five species (Roos 2003; Nekaris and Jaffe 2007). Several characteristics with a genetic basis, such as the persistent absence of P in *N. menagensis*, further support these divisions (Schwartz and Beutel 1995; Groves and Maryanto 2008).

Until now, however, field studies have been lacking that could shed light on how dietary adaptations among *Nycticebus* might affect the masticatory complex. Slow loris diet has been said to resemble that of the mainly frugivorous African pottos (*Perodicticus*) (Charles-Dominique 1977; Fitch-Snyder et al. 2001), a genus that ranges in size from 800 g, larger than the largest slow loris species, to 1,500 g, larger than the smallest *Nycticebus* (Nekaris and Bearder 2007). This suggestion has been in part substantiated by limited field observations of *N. coucang* by Barrett (1984), who found the slow loris to be relatively omnivorous, consuming fruits, flowers, invertebrates, and gum. The key role of this latter food item to *Nycticebus* is becoming evident (Tan and Drake 2001; Wiens et al. 2006; Streicher et al. in review). Indeed, Wiens et al. (2006) mention that toxic and/or digestion inhibiting secondary compounds found in exudates might be related to the evolution of slow life history in lorises.

Here, we review the use of exudates by slow lorises as revealed by several new field studies, and compare these data to studies of the closely related slender lorises, angwantibos, and pottos. We address several questions. Is there a relationship between body size and exudativeness? Is any single exudate source important across sites? Is there any pattern in what species of exudates are processed and how? We then present novel data on exudativeness from a captive study of wild slow lorises (*N. coucang*) recently confiscated from the wildlife trade. We assimilate these data to ascertain the importance of exudativeness to the comparative ecology, morphology, and captive management of slow lorises.

**Table 8.1** This table lists the seven species of Asian loris and three species of African potto, and whether or not exudate eating has been observed in the wild, based on information from available field reports until 2009, and trees from which exudates are eaten

	Species	Weight (g)	Wild		Tree family (genus)	References
			exudatory	No		
t1.1	<i>Arctocebus</i>	150–270	No	–	–	Ambrose (1999), Schein (2008)
t1.2	<i>calabarensis</i>					
t1.3						
t1.4	<i>Arctocebus aureus</i>	270–325	No	–	–	Charles-Dominique (1977)
t1.5	<i>Perodicticus potto</i>	900–1,900	Yes		Fabaceae ( <i>Albizia entada</i> , <i>Albizia sassa</i> )	Rahm (1960), Kingdon (1974), Charles-Dominique (1977), Oates (1984)
t1.6					<i>Piptadenastrum</i> , <i>Pentacletra</i> ; Sterculiaceae	
t1.7					<i>Sterculia tragacantha</i>	
t1.8					–	Nekaris and Jayewardene (2003)
t1.9	<i>Loris tardigradus</i>	120–175	No		–	Rhadakrishna (2001), Nekaris and Rasmussen (2003)
t1.10	<i>Loris lydekkerianus</i>	200–330	Yes		Fabaceae ( <i>Acacia</i> , <i>Prosopis</i> ), Meliaceae ( <i>Azadirachta</i> )	
t1.11					–	Nekaris, personal observation, Pliosoengeon and Savini, (2008), Das (2008)
t1.12	<i>Nycticebus bengalensis</i>	1,000–2,100	Yes		Combretaceae ( <i>Terminalia</i> ), Moraceae ( <i>Artocarpus</i> ); Magnoliaceae ( <i>Manglietia</i> ); Fabaceae ( <i>Acacia</i> , <i>Bauhinia</i> ); Lecythidaceae ( <i>Careya arborea</i> ); Sterculiaceae ( <i>Pterospermum</i> )	
t1.13					–	Tan and Drake (2001), Streicher (2004), Starr and Nekaris, personal observation
t1.14	<i>Nycticebus pygmaeus</i>	360–580	Yes		Sapindaceae ( <i>Sapindus</i> ), Euphorbiaceae ( <i>Vernicia</i> ), Fabaceae ( <i>Saraca</i> ), Anacardiaceae ( <i>Spondias</i> ); Bursaceae	
t1.15					–	Winarti (2008), Nekaris et al., personal observation
t1.16	<i>Nycticebus javanicus</i>	565–1,000	Yes		Fabaceae ( <i>Albizia</i> ), Arecaceae ( <i>Arenga</i> )	
t1.17					–	Barrett (1984), Wiens (2002), Nekaris and Nijman (2007)
t1.18	<i>Nycticebus coucang</i>	590–700	Yes		Fabaceae ( <i>Parsarianthes</i> , <i>Albizia</i> ), Anacardiaceae ( <i>Anacardium</i> , <i>Gluta</i> )	
t1.19					–	Nekaris and Munds, personal observation
t1.20	<i>Nycticebus menagensis</i>	265–700	Yes		Unidentified liana	
t1.21					–	Exudatory is absent only from the three smallest species. Note also the importance of gums from the family Fabaceae for all exudatiferous taxa
t1.22					–	
t1.23					–	
t1.24					–	
t1.25					–	
t1.26					–	

## Methods

We follow the taxonomy of Nekaris and Bearder (2007), and explanatory references therein, throughout this study. For the overview of exudativory, we compiled data from all available reports on loris and potto behavior in the wild and through personal communication with individuals actively engaged in field studies. Gums and saps are included in our definition of exudates. Gums are a group of amorphous, water soluble, acidic polysaccharides that usually form a hard substance over the wounds in plants. Gums are typically obtainable from the surface of a plant, but excavation may be required to induce gum flow. Saps are juices and circulating fluids in plants; although excavation may be necessary to reach saps, they do not form a hard surface (Bearder and Martin 1980).

For the captive study, we collected data from 2 April to 17 June 2007 at Pusat Penyelamatan Satwa (PPS) Rescue Center, Lampung, Sumatra. Included in the study were 12 *N. coucang* (two lactating adult females, ten unweaned juveniles), all recently rescued from the pet trade. The lorises were all from Sumatra, and were confiscated as a group from a village just outside a forest near Lampung; the hunters claimed that the lorises were all from the same forest. The lorises had been in captivity at the center for 2 weeks. Animals were socially housed in an outdoor enclosure measuring 2 × 2 × 2 m. We were required to adhere to caging structure implemented by PPS. Social housing also gave a chance for the unweaned juveniles to suckle on the two lactating females (see Collins and Nekaris 2008 for further details). The enclosure contained an open floor with natural ground and foliage, and was thickly furnished with natural branches at all levels. Observations were recorded nightly from 19:00 to 05:00 h, yielding a total of 153 h of behavioral observation. In the course of constructing a general activity budget (Collins 2007), we collected all occurrences data on diet, with continuous sequence sampling used for gouging behavior (Altmann 1974). Data were entered and analyzed using SPSS 14.0. Results were analyzed using nonparametric statistical tests with significance set at  $p \leq 0.05$  (Lehner 1996).

## Results

### *Review of Exudativory in Wild Lorises and Pottos*

We had access to data from 12 field studies of slow lorises, three on the closely related slender loris, and five on pottos and angwantibos yielding a total of ten lorisid species (Table 8.1). Only three species have not yet been observed to consume exudates – the smallest of the slender lorises *Loris tardigradus tardigradus* and both species of *Arctocebus*. These smaller taxa seem to be primarily insectivorous (Charles-Dominique 1977; Ambrose 1999; Nekaris and Jayewardene 2003). In the case of the potto, old gums found in its stomach form a major basis for our

knowledge of its exudate consumption (Kingdon 1974; Charles-Dominique 1977). Indeed, in Uganda, 19 stomachs obtained during 7 months held ca. 60% gum and ca. 30% insects. Kingdon (1974) suggested that gum is the main food during drier periods. Oates (1984) observed a potto licking gum, and on several occasions, noted focused searching behavior by pottos on gum bearing trees. No researcher to date, however, has observed pottos gouging to stimulate gum flow (Bearder and Martin 1980).

Lorises and pottos consume exudates from 14 different families, with gum from Fabaceae, the pea family, important for all taxa. Exudate consumption by *N. coucang* in Malaysia (Wiens et al. 2006) was a-seasonal, contrary to its seasonal use by *N. pygmaeus* in both Vietnam (Streicher et al. in review) and Cambodia (Starr, personal observation). Studies of *N. menagensis* in Sabah, Borneo (Nekaris and Munds, in press), *N. bengalensis* in Assam, India (Das 2008) and Thailand (Pliosoengeon and Savini 2008), and *N. javanicus* in Java, Indonesia (Winarti 2008) have not yet been conducted over a whole year, although exudate consumption has been observed. Gum represented only a small proportion of the diet for *L. lydekkerianus lydekkerianus* (Nekaris and Rasmussen 2003) and for *L. l. nordicus* (Nekaris, personal observation), but no seasonal pattern was evident.

Consumption of saps and gums by lorises shows a similar pattern (Tan and Drake 2001; Wiens 2002; Das 2008; Pliosoengeon and Savini 2008; Winarti 2008; Nekaris and Starr, personal observation). Lorises consume sap and gum from as low as 1 m to as high as 12 m off the ground. When consuming sap, all lorises observed perforate the superficial layer of the cambium of trees or lianas by scraping with their toothcomb. Lapping of the exposed sap with the tongue lasts from a few seconds to about 4 min, with intermittent additional breaking of the hard surface. Gum is consumed for a longer period, from 2 to 20 min, and involves active gouging with the anterior teeth. In most cases, trees already bore wounds (due to larval infestation, prior injury, or fire), although lorises can also gouge into the wood to induce gum flow (Streicher 2004; Starr and Nekaris, personal observation). By anchoring their upper incisors into the bark or into the solidified gum, lorises then scoop up the gum. By this manner, *N. pygmaeus* can also gouge into bamboo to reveal insects, which it then consumes; they also appear to scrape lichens and fungus off the surface of old bamboo with their toothcomb (Starr et al. 2008; Starr, personal observation). Until now, no loris has been observed to gouge gum with its molar teeth. Pygmy lorises in Cambodia, however, remove “icicles” of gum from open wounds, and while holding them in one hand, alternately chew on them with the posterior teeth and lick them (Starr and Nekaris, personal observation).

Lorises actively search for their gum sources. Head down searching may accompany investigating for sap on branches, or searching along bamboo to find a location to gouge for insects. Visible and audible sniffing sometimes accompanies these searches. On gum trees without active wounds, pygmy lorises race up and down a single trunk, making up to 20 trial holes before feeding (Starr and Nekaris, personal observation). Trees with active wounds seem to be known to the animals, which will make rapid and directed movement to a feeding site (Starr and Nekaris, personal observation). When gouging begins, bark breaking can be audible even from

[AU3]

a distance of 10 m (Streicher et al. in review). The loris may turn its head from side-to-side spitting out bits of bark; this side-to-side movement is often accompanied by scent marking the wound with facial glands. Bits of bark may be consumed in this process (Wiens et al. 2006). The even more noisy process of gouging bamboo involves a loris anchoring its rear feet against the bamboo and bashing its toothcomb into the incredibly hard surface; this behavior also results in shaking of the bamboo stand, making it audible for up to 100 m away.

Lorises consume exudates in an orthograde posture (the head can face up or down) when they are located on a vertical substrate, but also can stand quadrupedally over an exudate source (Wiens 2002; Nekaris and Rasmussen 2003; Streicher 2004; Starr and Nekaris, personal observation). When licking, the loris does it with gusto; its long tongue is easily visible, and licking of the nose and face is intermittent with licking the exudate source. Lorises regularly return to the same gouging site over 10 days and weeks, and multiple members of a social group may use the same gouging locality (Nekaris and Rasmussen 2003; Streicher 2004; Wiens et al. 2006). Indeed, in Cambodia, a single gum lick occurred in an area of range overlap of two groups of pygmy lorises; up to four lorises were seen at one time using this lick (Starr and Nekaris, personal observation). Overall, gouging is a very vigorous repetitive action and is unmistakable. The marks left on branches, too, are characteristic and may aid field workers in determining loris presence in an area (Tan and Drake 2001) (Figs. 8.1 and 8.2). Indeed, there is no relationship between the study duration and whether or not gouging has been observed in lorises and pottos, with two out of four short studies (less than a year) and three out of six long studies reporting gouging (Fisher Exact Probability Test,  $p < 1.0$ ), suggesting that it is a behavior relatively easy to observe.

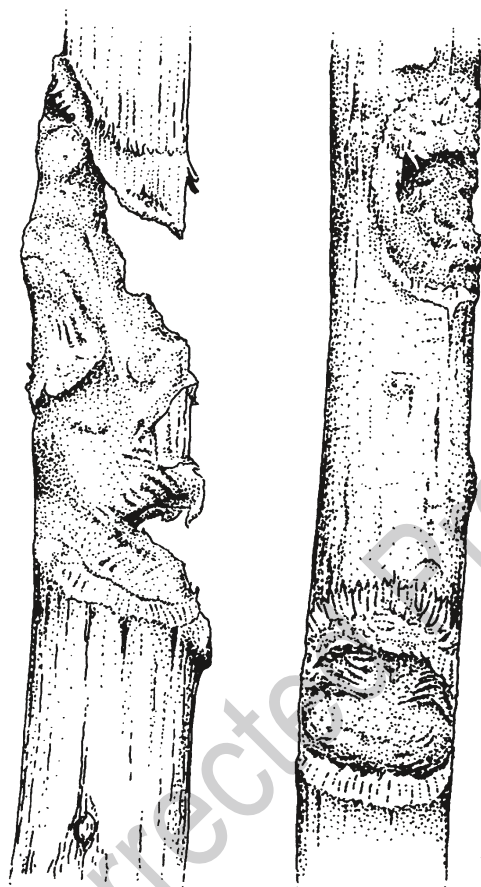
### Captive Sumatran Study

During the first 3 weeks of the study, juvenile *N. coucang* commonly chewed and gouged the timber beams of their enclosure and nest boxes, although no exudates could be obtained. We identified the timber as “sengon” (Fabaceae: *Paraserianthes falcata*), and placed branches of this species throughout the enclosure. At this stage, adult females also began to gouge. The leafy branches added also contained flower buds, as *P. falcata* flowers throughout the year (Gutteridge and Shelton 1998). The flowers and leaves were licked or eaten by both age classes.

By the end of the study, 441 visual and auditory gouging events had occurred (adults=44, juveniles=397), with 23 that were auditory only, resulting in a gouging rate of 2.9 times per hour. Lorises gouged the timber beams (71%), nest boxes (13%), and sengon branches (16%) (Figs. 8.2 and 8.3). Clearly juveniles gouged more than adults but interestingly, adults gouged sengon branches significantly more than juveniles did ( $0.2 = 19.98$ ,  $df = 2$ ,  $p < 0.001$ ). Gouging episodes ranged from a few seconds in duration to 2 min, but median gouging periods were short lasting 11–15 s.

[AU4]





**Fig. 8.1** Examples of branches gouged by *N. coucang*, showing the typical gnawing pattern for this genus (drawing: H. Schulze)

Gouging behavior consisted of anchoring the upper incisors into the wood, while deeply gouging with the lower anterior teeth. Gouging was audible, and longer sessions left impressions in the wood of about 2.5 cm diameter, and about 0.6 cm deep. The average height at which animals gouged was 1.6 m+sd 0.35.

An unexpected behavior of note was that the majority of gouges (52%) were also scent marked by an individual while it chewed, either in the form of facial rubbing or urine marking, via depositing urine directly into the gouge. Of 228 observations of scent marking while gouging, urine marking accompanied 83%, significantly more than facial rubbing ( $\chi^2=98.68$ ,  $df=1$ ,  $p<0.001$ ). Although scent marking occurred for both age classes during daily interactions, the majority of marking occurred while gouging the enclosure timber and sengon branches. The adults scent marked more than juveniles (66 vs. 57% of observations) when gouging, but this difference only showed a trend toward significance.



**Fig. 8.2** Gouge mark (indicated by *arrows*) from which exudates have been consumed by *N. pygmaeus* from a tree in Seima Biodiversity Conservation Area, Cambodia. An adult female spent only 30 s producing this 5 × 12 mm hole. Photo: C.R. Starr



**Fig. 8.3** Juvenile *N. coucang* at PPS Rescue Center, Sumatra, standing on a sengon branch (*P. falcataria*) exhibiting several small gouge marks. Photo: A. Navarro-Montes

## Discussion

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Tan and Drake (2001) were the first to provide strong evidence that slow lorises exhibit gouging behavior specialized to elicit sap or gum flow, and suggested that they rely on gum as an important source of nutrients. The specialized behavior of using the lower anterior teeth to gouge a hole in bark is rare among primates and occurs in only three other genera: *Callithrix*, *Cebuella* (Callitrichidae) and *Phaner* (Cheirogaleidae) (Coimbra-Filho and Mittermeier 1978; Petter et al. 1971). Wiens (2002) too concluded that *Nycticebus* belongs to a specialized exudate-feeding guild (Nash 1986). The data presented in this paper solidify this view, showing that all five species of *Nycticebus* and one of the two *Loris* species utilize this resource, with some of the taxa relying on exudates as a major food source.

When the soft anatomy of lorises is examined, it is perhaps no surprise that gum should play an important role in their diets. As is the case with other exudativorous primates, both *Nycticebus* and *Loris* are characterized by a long relatively narrow tongue, large caecum, and a short duodenum (Kubota and Iwamoto 1966; Osman Hill 1953). With all species also showing a propensity to eat insects, this anatomical arrangement may be useful in breaking down “structural carbohydrates present in both gum and the chitinous exoskeletons of invertebrates (Fleagle 1999, p. 296).” A simple stomach complements this arrangement, and may aid in digestion of fruits and flowers (Chivers and Hladik 1980). All species of lorises so far lack keeled nails. A strong grip when on vertical surfaces combined with consuming exudates on more oblique and horizontal branches may reduce the need for this adaptation.

On the basis of field studies conducted so far of African and Asian lorises, exudate consumption tends to be more important for the larger-bodied taxa. The potto seems to differ from Asian lorises, in that, although it seems to eat appreciable quantities of gum, it has never been observed to gouge actively but seems to extract gum from already opened wounds (Charles-Dominique 1977; Oates 1984). In a more recent study of *P. potto edwardsi*, it was not seen to eat gum at all, although it did extract snails from their shells with its long pointed tongue (Pimley 2002). Its exudativory seems to more closely resemble that of *Galago*, *Saguinus*, *Papio*, *Cercopithecus*, and *Erythrocebus* (Nash 1986). Active gouging is conducted by all species of *Nycticebus* and *Loris* seen eating gum thus far. In a study of *N. coucang* (probably a mixed sample of *N. coucang* and *N. bengalensis*) and *N. pygmaeus*, Schwartz and Beutel (1995) demonstrated that *Nycticebus* has the deepest mandible with the most developed gonial region and the most robust upper canine roots of the lorises and pottos. Biting forces that produce a greater magnitude of stress are thought to be important for shaping the primate masticatory complex. A deep mandible has been implicated in countering bending during heavy incisal biting in some primates (Hylander 1985), and may explain this condition in *Nycticebus*. Williams et al. (2001) and Vinyard et al. (2003) arrived at different results, noting that gouging primates have a masticatory complex that permits the mandibular incisors to move more vertically when the jaw gapes. The vigorous open-mouthed gouging by *Nycticebus*, creating large holes in a few seconds, accords well with this suggestion. Ravosa (1998) described variability of the masticatory complex of *Nycticebus* and

suggested that it was clinal, predicting a variety of different diets for the species. Examination of the biomechanical force required by slow lorises to engage in gouging behavior, and comparing this with the extent to which each species relies on exudates may lend further scope to the morphological adaptations of the different species.

All exudativorous taxa in our study consume exudates from the family Fabaceae, although not yet at all sites. For example, although *N. bengalensis* in both Thailand and Assam consume exudates of Combretaceae, Fabaceae consumption has so far only been observed for Thai *N. bengalensis*. We also found a tendency for seasonal use of exudates at several of the sites where long-term studies were conducted. Fabaceae, the pea family, is widely dispersed throughout Asia; species of this family often colonize edges and tree fall zones (Gutteridge and Shelton 1998), a habitat said to be preferred by some loris species (Nekaris et al. 2008). Both gum and sap from this family may provide a year-round energy source for lorises or an important readily-available fallback food source in times of food scarcity (Hladik 1979). The exudates consumed by lorises probably contain high amounts of easily digestible mono and disaccharides (high concentrations of carbohydrate) and lipids (Bearder and Martin 1980; Nash 1986). Gums from Fabaceae also are an important part of the diet of other nocturnal primates. *Galago senegalensis braccatus* preferred *Acacia* gum to other types, particularly to those containing extra tannins (Nash 1989), and both *G. moholi* and *Otolemur crassicaudatus*, whose highly seasonal environment resembles that of *N. pygmaeus* and *N. bengalensis*, relied almost wholly or extensively (respectively) on gum during some periods of the year.

The process by which exudates are consumed is remarkably similar across taxa. Although slow lorises lack specialized keeled nails, they are nonetheless capable of clinging to a vertical substrate while engaged in gouging for up to 20 min. Like marmosets and fork-marked lemurs, lorises remain focused on gouging, which might leave them vulnerable to predation. This could explain the presence of a dorsal stripe in all *Nycticebus* (Nekaris and Jaffe 2007), and might even explain the seasonal appearance of this stripe in Vietnamese *N. pygmaeus* (Streicher 2004), which is only present during the harsh winter months when exudativory seems to increase. Although the closely-related African galagos are known to scrape gum from the tree surface and to extend existing wounds to get at gum, they do this with specialized cheek teeth rather than with the anterior teeth (Bearder and Martin 1980). There is still debate over whether or not pottos are more closely related to galagos or to Asian lorises (Schwartz and Beutel 1995; Nekaris and Bearder 2007). More observations of pottos are needed to see how they extract exudates, and to which of these two groups this behavior more closely resembles.

A novel finding in our captive study was that urine marking or facial rubbing often accompanied gouging episodes by both adult and juvenile slow lorises. Gouging behavior has been observed among Bengal slow loris infants between 2 and 4 weeks of age, although scent marking was not reported (Zimmermann 1989). However, vigorous circumgenital scent marking the context of gouge holes is an important part of the behavioral repertoire of South American marmosets (Rylands 1984, 1985). Indeed, this behavior is used infrequently in any other context. Several explanations

for scent marking gouges have been proposed, including territory marking, regulation of group movement, intra-group sexual dominance, deterring other groups from using a hole, or indicating the profitability of a certain hole (Rylands 1990). As gouging is essentially a risky business in terms of predation susceptibility and in terms of potential tooth damage (Bearder and Martin 1980), all of these hypotheses may be relevant to and interesting to test in the case of *Nycticebus*. Here we propose an additional role for marking gouges. Wiens and Zitzmann (2003) describe that young slow lorises clearly learn to eat items consumed by their parents, but did not witness any evidence of direct social learning. They suggested that information about food resources might be transferred chemically. Our observations that adult *N. coucang* did not begin to scent mark their gouges until presented with fresh branches that provided a better chance of producing exudates suggests that they may have been submitting information about food sources to their offspring. Because scent marking is a common part of loris behavior, it is therefore difficult to quantify (Nekaris and Jayewardene 2003, see also Rylands 1990 for marmosets), and the studies reviewed here may have overlooked scent marking of gouges in the wild. Future researchers should be alert to this possibility, and attempt to interpret its function.

Our results carry implications for captive management. Captive lorises suffer from obesity (Ratajszczak 1998) and dental diseases, including abscesses, recurrent periodontal disease, facial swelling, and osteomyelitis of the zygomatic arch (Fitch-Snyder et al. 2001). A diet too rich in sugar, and lack of substrates on which to gouge have been implicated for both conditions (Streicher 2004). Streicher (2004) noted a high standard of dental hygiene when wild-caught *N. pygmaeus* were given the opportunity to gouge fresh branches regularly. Craig and Reed (2003) presented puzzle feeders to *N. pygmaeus* that necessitated gouging and thereby increased activity, an aid to reducing obesity. Fitch-Snyder et al. (2001) used gum arabic placed into a treat log to stimulate activity; both *N. bengalensis* and *N. pygmaeus* gouged into the log far beyond the original diameter of the initial drill holes. In marmosets, too, the full suite of wild behaviors, including urine marking, can be stimulated by providing gum enrichment (McGrew et al. 1986). In our study, the *N. coucang* were ultimately released to the wild; the resident veterinarian particularly commented on the healthy state of the animals, including their dentition (Collins and Nekaris 2008). Animals were also fed on plenty of live prey, including birds, and local uncultivated fruits that were more likely to be lower in sugar (Streicher et al. in review). The health of captive populations of lorises may be greatly enhanced by providing regular opportunities for gouging, and further studies should investigate this.

In previous reviews of gouging behavior of primates, Asian lorises were an unstudied enigma (Bearder and Martin 1980; Nash 1986). Unique in many aspects of their behavior and anatomy, we show here that they are one of the few primate genera to engage in specialized extractive gouging of plant exudates. This specialization is reflected to some extent in their pelage, life history, masticatory complex, and social behavior. These data we present here are mainly from field studies of slow lorises still in their early stages. We hope we present many challenges to this new generation of researchers to further our knowledge of the role of exudativory in loris



ecology and evolution, and to the improvement of the welfare and health of captive lorises through the promotion of this natural behavior in zoos and sanctuaries.

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## References

- Altmann J (1974) Observational study of behaviour: sampling methods. *Behavior* 49: 227–267
- Ambrose L (1999) Species diversity in West and Central African galagos (Primates, Galagonidae): the use of acoustic analysis. PhD thesis, Oxford Brookes University, Oxford
- Barrett E (1984) The ecology of some nocturnal, arboreal mammals in the rainforests of peninsular Malaysia. Unpub. Ph.D. dissertation, University of Cambridge, Cambridge
- Bearder S, Martin RD (1980) Acacia gum and its use by bushbabies, *Galago senegalensis* (Primates: Lorisidae). *Int J Primatol* 1:103–128
- Charles-Dominique P (1977) Ecology and Behaviour of the Nocturnal Primates. Prosimians of Equatorial West Africa. Duckworth, London
- Chivers DL, Hladik CM (1980) Morphology of the gastrointestinal tracts in primates: comparisons with other animals in relation to diet. *J Morphol* 166:337–386
- Coimbra-Filho AF, Mittermeier RA (1978) Tree-gouging, exudate-eating and the “short-tusked” condition in *Callithrix* and *Cebuella*. In: Kleimann DG (ed) *The Behaviour and Conservation of the Callithrichidae*. Smithsonian Institution Press, Washington
- Collins RL (2007) Behavioural data of captive greater slow loris (*Nycticebus coucang*) & Javan slow loris (*N. javanicus*), and a survey of Javan slow loris in Mt. Salak, West Java, Java. Unpub. MSc dissertation, Oxford Brookes University, Oxford
- Collins R, Nekaris KAI (2008) Release of greater slow lorises (*Nycticebus coucang*), confiscated from the pet trade, to Batutegi Protected Forest, Sumatra, Indonesia. In Soorae PS (ed) *IUCN Global Re-introduction Perspectives: Re-introduction Case Studies from Around the Globe*. IUCN/SSC Reintroduction Specialist Group, Abu Dhabi, UAE
- Craig J, Reed C (2003) Diet-based enrichment ideas for small primates. *Int Zoo News* 50(1):16–20
- Das N (2008) Comments on the feeding ecology of *Nycticebus bengalensis* in Gibbon Wildlife Sanctuary, Assam, India. Report submitted to the Nocturnal Primate Research Group, Oxford, UK, p. 1
- Duckworth JW (1994) Field sightings of the pygmy loris (*Nycticebus pygmaeus*) in Laos. *Folia Primatol* 63:99–101
- Fitch-Snyder H, Schulze H, Larson L (eds) (2001) Management of lorises in captivity. A husbandry manual for Asian lorises (*Nycticebus* & *Loris* spp.). Center for Reproduction in Endangered Species (CRES), Zoological Society of San Diego, San Diego
- Fleagle J (1999) *Primate Adaptation and Evolution*. Academic Press, San Diego
- Ford and Davis, this volume
- Groves C, Maryanto I (2008) Craniometry of slow lorises (genus *Nycticebus*) of insular Southeast Asia. In: Shekelle M (ed) *Primates of the Oriental Night*. Treubia, Jakarta

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[AU6]

- Gutteridge RC, Shelton HM (1998) Forage tree legumes in tropical agriculture with case studies from Australia and Southeast Asia. CABI Publishing, Australia 390
- Hladik CM (1979) Diet and ecology of prosimians. In: Doyle GA, Martin RD (eds) The Study of Prosimian Behaviour. Academic Press, New York 391
- Hylander WL (1985) Mandibular function and biomechanical stress and scaling. Am Zool 25:315–330 392
- Kingdon J (1974) East African Mammals. An Atlas of Evolution in Africa, Vol. 1. Academic Press, London 393
- Kubota K, Iwamoto M (1966) Comparative anatomical and neurohistological observations on the tongue of slow loris (*Nycticebus coucang*). Anat Rec 158:163–176 394
- Lehner PN (1996) Handbook of Ethological Methods. University Press, Cambridge 395
- McGrew WC, Brennan JA, Russell J (1986) An artificial “gum-tree” for marmosets (*Callithrix j. jacchus*). Zoo Biol 5(1):45–50 396
- Müller EF, Nieschalk U, Meier B (1985) Thermoregulation in the slender loris (*Loris tardigradus*). Folia Primatol 44:216–226 397
- Nash L (1986) Dietary, behavioural, and morphological aspects of gummivory in primates. Yearb Phys Anthropol 29:113–137 398
- Nash L (1989) Galagos and gummivory. Hum Evol 4(2–3):199–206 399
- Nash LT, Whitten PL (1998) Preliminary observations on the role of *Acacia* gum chemistry in *Acacia* utilization by *Galago senegalensis* in Kenya. Am J Primatol 17(1):27–39 400
- Nekaris KAI, Bearder SK (2007) The strepsirrhine primates of Asia and Mainland Africa: diversity shrouded in darkness. In: Campbell C, Fuentes A, MacKinnon K, Panger M, Bearder SK (eds) Primates in Perspective. Oxford University Press, Oxford 401
- Nekaris KAI, Jaffe S (2007) Unexpected diversity within the Javan slow loris trade: implications for slow loris taxonomy. Contrib Zool 76:187–196 402
- Nekaris KAI, Jayawardene J (2003) Pilot study and conservation status of the slender loris (*Loris tardigradus* and *Loris lydekkerianus*) in Sri Lanka. Primate Conserv 19:83–90 403
- Nekaris KAI, Nijman V (2007) Survey on the abundance and conservation of Sumatran slow lorises (*Nycticebus coucang hilleri*) in Aceh, Northern Sumatra. Proceedings of the European Federation of Primatology, Charles University, Prague, p. 47 404
- Nekaris KAI, Rasmussen DT (2003) Diet and feeding behaviour of the Mysore slender loris. Int J Primatol 24(1):33–46 405
- Nekaris KAI, Blackham GV, Nijman V (2008) Implications of low encounter rates in five nocturnal species (*Nycticebus* spp.). Biodivers Conserv 17(4):733–747 406
- Oates JF (1984) The niche of the potto, *Perodicticus potto*. Int J Primatol 5(1):51–61 407
- Osman Hill, WC (1953) Primates. Comparative Anatomy and Taxonomy. I. Strepsirhini. Edinburgh University Press, Edinburgh 408
- Petter JJ, Schilling A, Pariente G (1971) Observations eco-ethologiques sur deux lemuriens malgaches nocturnes: *Phaner furcifer* et *Microcebus coquereli*. Terre Vie 118:287–327 409
- Pimley ER (2002) The behavioural ecology and genetics of the potto (*Perodicticus potto edwardsi*) and Allen’s bushbaby (*Schiurocheirus alleni cameronensis*). Unpub. Ph.D. thesis, University of Cambridge, Cambridge 410
- Pliosoengeon M, Savini T (2008) Spatial and feeding behavior of the endangered Bengal slow loris, *Nycticebus bengalensis* in Khao Angrunai Wildlife Sanctuary, Thailand. Unpublished report to the Primate Society of Great Britain, p. 8 411
- Rahm U (1960) Quelques notes sur le potto de Bosman. Bull Inst Fr d’Afr Noire, Ser A 22:331–341 412
- Ratajszczak R (1998) Taxonomy, distribution and status of the lesser slow loris *Nycticebus pygmaeus* and their implications for captive management. Folia Primatol 69(1):171–174 413
- Ravosa MJ (1998) Cranial allometry and geographic variation in slow lorises (*Nycticebus*). Am J Primatol 45:225–243 414
- Rhadakrishna S (2001) The Social Behavior of the Mysore Slender Loris (*Loris tardigradus lydekkerianus*). Unpub. Ph.D. thesis, University of Mysore, Manasagangotri 415

- 443 Roos C (2003) Molekulare Phylogenie der Halbaffen, Schlankaffen, und Gibbons. Unpub. Ph.D.  
444 thesis, Technische Universität München
- 445 Rylands AB (1984) Exudate-eating and tree-gouging by marmosets (Callitrichidae, Primates). In:  
446 Chadwick AC, Sutton SL (eds) Tropical Rain Forest. The Leeds Symposium. Leeds  
447 Philosophical and Literary Society, Leeds
- 448 Rylands AB (1985) Tree-gouging and scent-marking by marmosets. Anim Behav  
449 33(4):1365–1367
- 450 Rylands AB (1990) Scent-marking behaviour of wild marmosets, *Callithrix humeralifer*  
451 (Callitrichidae, Primates). In: Macdonald DW, Müller-Schwarze D, Natynczuk SE (eds)  
452 Chemical Signals in Vertebrates 5. Oxford University Press, Oxford
- 453 Schwartz JH, Beutel JC (1995) Species diversity in lorises: a preliminary analysis of *Arctocebus*,  
454 *Perodicticus* and *Nycticebus*. In: Alterman L, Doyle GA, Izard MK (eds) Creatures of the  
455 Dark: The Nocturnal Prosimians. Plenum Press, New York
- 456 Starr CR, Streicher U, Nekaris KAI (2008) The distribution and conservation of the pygmy loris  
457 (*Nycticebus pygmaeus*) in Eastern Cambodia. XXIIIth Congress International Primatological  
458 Society Abstracts, Primate Eye:116
- 459 Streicher, U (2004) Aspects of the ecology and conservation of the pygmy loris *Nycticebus pyg-*  
460 *maeus* in Vietnam. Dissertation. Ludwig-Maximilians Universität, Germany
- 461 Streicher U, Collins R, Navarro-Montes A, Nekaris KAI (in review) Observations on the feeding [AU7]  
462 preferences of slow lorises (*N. pygmaeus*, *N. javanicus*, *N. coucang*) confiscated from the  
463 trade. In: Masters J, Crompton R, Genin F (eds) Prosimians. Springer, New York
- 464 Tan CL, Drake JH (2001) Evidence of tree gouging and exudate eating in pygmy slow lorises  
465 (*Nycticebus pygmaeus*). Folia Primatol 72:37–39
- 466 Vinyard CJ, Wall CE, Williams SH, Hylander WL (2003). Comparative functional analysis of  
467 skull morphology of tree-gouging in primates. Am J Phys Anthropol 120:153–170
- 468 Waterman PG (1984) Food acquisition and processing as a function of plant chemistry. In: Chivers  
469 DJ, Wood BA, Bilsborough A (eds) Food Acquisition and Processing in Primates. Plenum  
470 Press, New York
- 471 Wiens F (2002) Behaviour and ecology of wild slow lorises (*Nycticebus coucang*): social organi-  
472 sation, infant care system, and diet. Dissertation. Faculty of Biology, Chemistry and  
473 Geosciences, Bayreuth University, Germany
- 474 Wiens F, Zitzmann A (2003) Social dependence of infant slow lorises to learn diet. Int J Primatol  
475 24(5):1008–1021
- 476 Wiens F, Zitzmann A, Hussein NA (2006) Fast food for slow lorises: is low metabolism related to  
477 secondary 5 compounds in high-energy plant diet? J Mammal 87(4):790–798
- 478 Williams SH, Wall CE, Vinyard CJ, Hylander WL (2001) A biomechanical analysis of skull form  
479 in gum-harvesting galagids. Folia Primatol 73:197–109
- 480 Winarti I (2008) Field research on Javan slow loris' population in Sukakarta Ciamis and  
481 Kawungsari Tasikmalaya, West Java, Indonesia. Report to IAR Indonesia, Ciapus, Bogor,  
482 Indonesia, p. 7
- 483 Zimmermann E (1989) Reproduction, physical growth and behavioural development in slow loris  
484 (*Nycticebus coucang*, Lorisidae). Hum Evol 4(2–3):171–179



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