

RESEARCH ARTICLE

Obligate Exudative Characterizes the Diet of the Pygmy Slow Loris
*Nycticebus pygmaeus*CARLY STARR¹ AND K.A.I. NEKARIS^{2*}¹School of Agriculture and Food Science, University of Queensland, Gatton, Queensland, Australia²Oxford Brookes University, Nocturnal Primate Research Group, School of Social Sciences and Law, Oxford, United Kingdom

Few primate species are known to excavate plant sources to procure exudates and other foods via active gouging. It is now apparent that slow lorises belong to this rare guild of obligate exudativorous primates. We investigate the diet of the pygmy loris (*Nycticebus pygmaeus*) in a mixed deciduous forest in the Seima Protection Forest, Eastern Cambodia, and attempted to determine the importance of this resource in their diet. Feeding behaviors of six females and seven males were observed using radio-tracking to facilitate follows, and nine fecal samples were collected in February–May and January–March in 2008 and 2009 respectively. We observed 168 feeding bouts, during which the animals ate exudates (76); fruits (33); arthropods (27); flower parts (21); fungi (3); parts of bamboo culms (7); and reptiles (1). We filmed 19 bouts of exudative, and observed animals consuming exudates in an orthograde posture, or standing quadrupedally over the exudate source. Pygmy lorises also gouged bamboo to collect lichen and fungi, or broke open dead culms to access invertebrates. Feeding occurred on terminal tree branches (24), tree trunks (21), bamboo (13), the middle of branches (7), and the undergrowth (1). The fecal samples contained plant parts, small-sized arthropods (primarily Coleoptera and Lepidoptera), reptile scales, animal bones, and animal hairs. Pygmy slow lorises are morphologically specialized for processing and digesting exudates, displaying small body sizes, specialized dentitions, elongated, and narrow tongues, large caecums, short duodenum, expanded volar pads, and modified hindlimbs. These features, combined with the prevalence of exudates in their diet across seasons, and ill health when exudates are missing from their diet in captivity, points to this species being an obligate exudative. *Am. J. Primatol.* 9999:1–8, 2013. © 2013 Wiley Periodicals, Inc.

Key words: radio-tracking; slow loris; gummivory; fallback foods

INTRODUCTION

Exudates, including gums, and saps, provide a carbohydrate-rich energy source for those primates able to access and digest them [Heymann & Smith, 1999]. Although saps, the circulating fluids in plants, can be reached without excavation, gum consumption often requires active gouging of the surface of a tree [Bearder & Martin, 1980b; Vinyard et al., 2003]. At least 69 primate species are now known to use exudates, but until recently only five genera (*Callithrix*, *Mico*, *Cebuella*, *Phaner*, and *Euoticus*) were known to gouge the surface of trees to obtain exudates [Nash, 1986; Nash & Burrows, 2010; Smith, 2010; Fig. 1]. These taxa are defined as obligate exudativores and exudates comprise 40% or more of their feeding time (hereafter referred to as diet) [Nash & Burrows, 2010]. Morphological specializations characterizing these primates include modified anterior dentition, small body size, a large caecum and/or colon, a long tongue, and keeled nails [Hladik, 1979]. Nekaris et al. [2010a] suggest that

Asian lorises (*Nycticebus*, *Loris*) should be added to this list of exudativores given that they possess all but the last of these adaptations.

Nekaris et al. [2010a] reviewed field studies of lorises and pottos, and showed that nine species are now known to include exudates in their diet. Whereas, pottos are only known to scrape gum, seven species of *Loris* and *Nycticebus* actively gouge for exudates. *Loris* clearly seems to use exudates as

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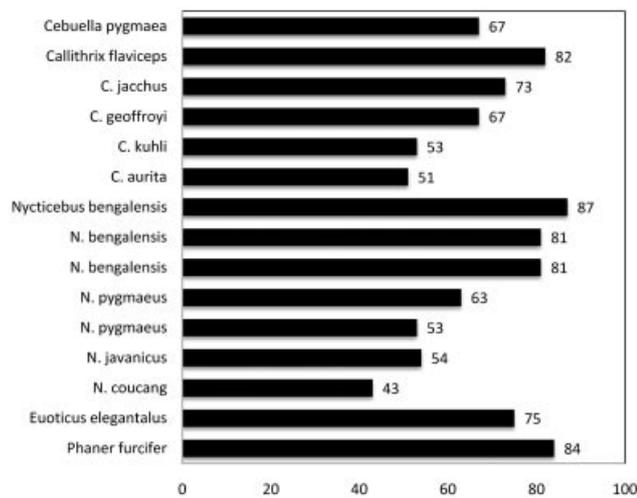


Fig. 1. Selected obligate exudativorous primates for which gum comprised >40% of their total diet showing that slow lorises consume substantial amounts of exudates.

a supplement, with more than 90% of the diet comprising animal prey [Nekaris & Jayewardene, 2003; Nekaris & Rasmussen, 2003]. In *Nycticebus*, the percentage of exudates in the diet differs by site and varies between species. For example, *N. coucang* consumes the least amount of exudates of any slow loris yet documented, accounting for 43% of its diet in Peninsular Malaysia [Wiens et al., 2006]. At the other extreme lies *N. bengalensis* whose exudate consumption reached 94.3% [Swapna et al., 2010]. In two reintroduction studies, exudates formed 63% of the diet of *N. pygmaeus*, whereas, the diet of reintroduced Javan slow lorises *N. javanicus* was only 2% exudates despite regularly gouging in their pre-release enclosures [Moore, 2012]. Wild *N. javanicus*, however, consume exudates nightly, comprising as much as 70% of their diet [Nekaris and Rode, unpublished data]. As a result of these differences between studies, there has been no consensus among researchers as to whether gum comprises a preferred food item [defined as those foods selected disproportionately often relative to their abundance within the population's habitat], or one which is utilized during times when preferred food items are unavailable [fallback food; Marshall & Wrangham, 2007].

Slow lorises show numerous morphological and behavioral adaptations to exudativory [cf. Nash & Burrows, 2010]. All taxa are characterized by a relatively small body size, long narrow tongue, large caecum, short duodenum [Nekaris et al., 2010a], and expanded volar pads for gripping [Wheeler, 2010]. They also have long hind legs, suitable for gripping the trunks of trees and saplings [Rode, pers. comm.]. Their dorsal coloration makes them perfectly suited for background matching the trunk environment on which many exudates occur, including seasonal coat color changes in some taxa that may be related to leaf

loss [Nekaris et al., 2010b]. Both *N. bengalensis* and *N. pygmaeus* clearly “know” the location of exudate sites, visiting the same trees repeatedly [Streicher, 2004; Tan & Drake, 2001]. Streicher et al. [2012] observed “stereotyped” gouging in captive and wild juvenile *N. coucang* and *N. javanicus* as young as 3 months old. Captive adults regularly gouge substrates with no gum [Nekaris et al., 2010a; Streicher, 2004]. Gouging behavior observed in captive animals is likely to be associated with a cranio-dental complex highly adapted for producing large gapes in a substrate [Vinyard et al., 2003].

The first evidence for loris gouging in the wild came from gouge marks produced by the pygmy slow (hereafter pygmy) loris [*N. pygmaeus*; Tan & Drake, 2001], and gouging was confirmed when it was seen in reintroduced radio-collared animals [Streicher et al., 2012]. Here we present the first quantitative data on the diet and feeding behavior of wild pygmy lorises in a mixed deciduous forest in eastern Cambodia during the dry and early wet season. We examined to what extent the pygmy loris used exudates, by examining proportion of the diet (based on feeding time) containing exudates, and how they were procured. We use these data to determine whether the pygmy slow loris can be deemed an obligate exudativore.

METHODS

We conducted this study in the Seima Protection Forest (PF), in southern Monduliri province, Cambodia (Fig. 2). Field conditions were too difficult for tracking animals during the wet season when there was severe signal-bounce during radio tracking, hazardous health conditions, and difficulty accessing, and observing animals in heavy rain. Therefore, we conducted the study over two periods: from February 12 to May 31, 2008, and from January 9 to March 24, 2009. The dry season extends from November to April, and the rainy season from May to October in Monduliri and the mean annual rainfall is 2000–2500 mm [Javier, 1997]. Seima PF encompasses 292,690 ha, and lies between 100 and 700 m asl on the western slopes of the Sen Monorom plateau, and in the south is part of the Annamite range [Evans et al., 2003]. We present the mean, minimum, and maximum nightly temperatures across the study months (Fig. 3).

Seima PF consists of a mosaic of forest types, including semi-evergreen, mixed deciduous, deciduous dipterocarp, and evergreen forests [Walston et al., 2001]. We selected a mixed deciduous forest habitat as our study site as preliminary surveys recorded higher encounter rates in this habitat type [Starr et al., 2011].

We collected behavioral data using focal animal instantaneous sampling at 5-min intervals, recording data at the end of each observation point [Martin & Bateson, 2007; Nekaris & Rasmussen, 2003]. Due to

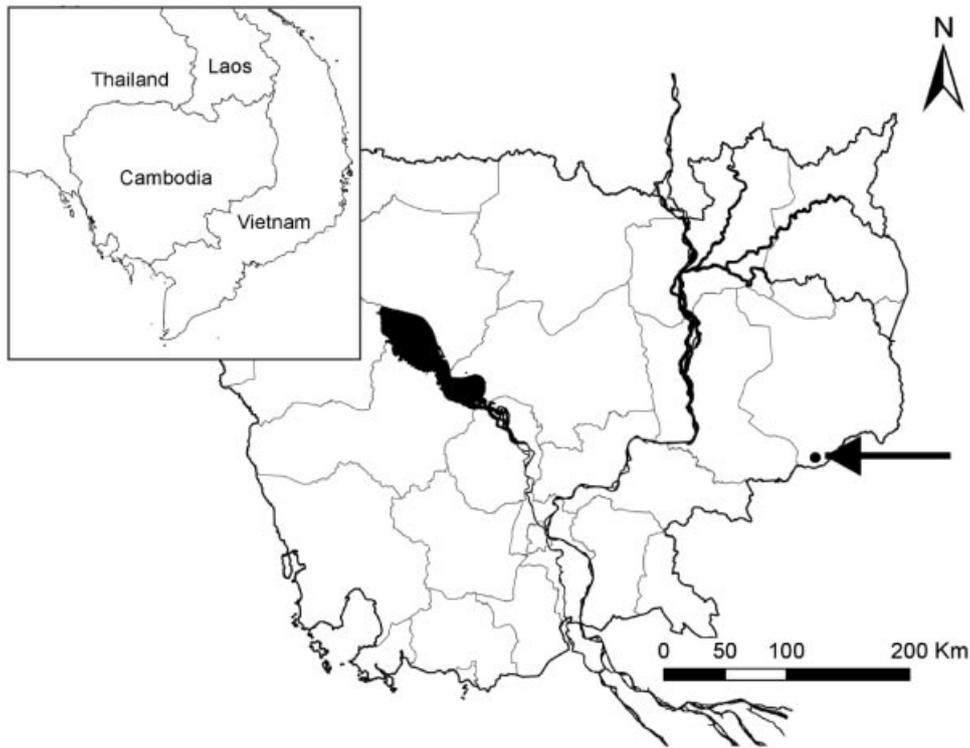


Fig. 2. Location of Seima Protection Forest, Mondul Kiri Province, Cambodia. Dark lines are major rivers and water sources. The study site is indicated with an arrow on the map.

limited visibility, all-occurrence sampling [Altmann, 1974; Martin & Bateson, 2007] was used [n = 168] to collect feeding observations following Nekaris and Rasmussen [2003]. We recorded the following information during observations: (1) type of food item (exudate, nectar, plant, animal prey); (2) size of prey (small = smaller than hand of loris; medium = up to twice the size of hand of loris; large = more than twice the size of the loris' hand—mean hand span of the study animals was 47.18 ± 3.4 mm); and (3) method of capture (one-hand grab, two-handed catch, pulling object manually, or removing it from the substrate orally); the substrate the loris fed from (terminal branch, middle of branch, trunk, undergrowth, bamboo) [Nekaris & Rasmussen,

2003]. When animals were high in the canopy and not clearly visible, we discarded the observation. Thus, the data may be biased towards bouts, and events of animal prey feeding were missed. We collected feeding observations in the cool season (from January to mid-February), and the warm season (from mid-February to May). We used a Sony Handy cam with night shot and 25× optical zoom (Sony®, Minato, Tokyo, Japan) to film exudate feeding; clips were filmed when animals were visible and thus we did not always represent entire bouts. We analyzed clips using Adobe Premier Software (Adobe®, United States). We distinguished tree gouging to elicit exudate flow from scraping of hardened exudates that accumulate due to insect damage to the tree following Williams et al. [2002]. Our research adhered to the American Society of Primatologists Principles for the Ethical Treatment of nonhuman Primates; ethics approval for this project was approved by the University of Queensland Behavioral and Social Sciences Ethical Review Committee.

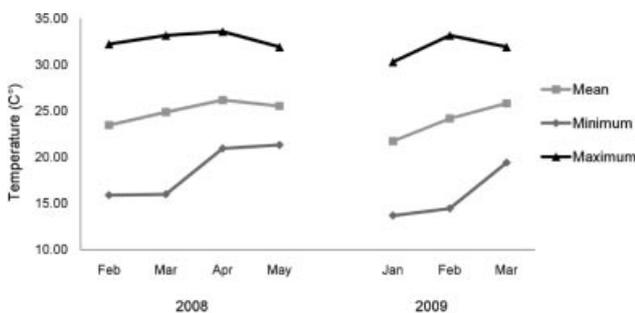


Fig. 3. Mean, minimum, and maximum nightly temperatures in the Seima Protection Forest during the study period.

We collected nine fecal samples from animals that we captured for radio-collaring. Feces were stored in 70% ethanol before analysis in the laboratory. We softened feces by soaking them in water, and then used tweezers to pull them apart in a petri dish under a binocular microscope (10–40×). We took 21 subsamples of each fecal sample; all items

were counted and visually assigned to one of the following categories: plant part; arthropod; bone; animal hair; or reptile scale. We could not trace gums or nectar in fecal samples. We grouped plant matter (fruit, flowers, bamboo, fungi) and identified arthropods by taxonomic order. We used chi-square tests to evaluate the differences amongst categories in SPSS V19.0 to analyze data.

We adhered to all legal requirements of the Kingdom of Cambodia.

RESULTS

Over the course of 365.06 hr of observation, we collected 168 feeding observations. The observed proportion of each food type consumed across both study periods is shown in Figure 4. Overall, exudates accounted for over 50% of feeding time. We assessed 189 sub-samples from nine pygmy loris fecal samples. The proportion of each food item in fecal samples is shown in Table I and indicates that arthropods are an important component of the diet, prevalent in 81% of scats. Evidence of exudate consumption was present in 98% of scats containing plant material.

Animals fed on terminal tree branches, middle of branches, tree trunks, in bamboo, and in undergrowth (Fig. 5). The greatest frequency of feeding occurred equally between the terminal branches of trees (insects and nectar) and on the trunk (exudates). Animals were observed feeding alone, except for three instances. Twice we observed two pygmy lorises spaced 1 m apart feeding on fruit from the vine *Salacia chinensis*; this vine fruited throughout the site in March and April. The second observation occurred on an unidentified tree species, which exuded large quantities of gum (Fig. 6b) and an adult male and female fed alongside each other, which was followed by a long bout of allogrooming.

In terms of animal prey, lorises fed more frequently on small prey items than on medium-

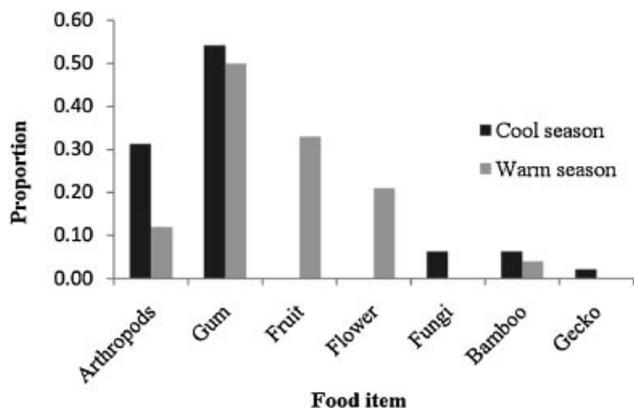


Fig. 4. Proportion of food types pygmy lorises were observed to consume in the Seima Protected Forest, Cambodia, over 6 months in 2008 and 2009.

TABLE I. Proportion of Food Items Identified in Nine Scats Collected From Captured Pygmy Lorises

Food item	Proportion of scats	Proportion of sub-samples
Plant material	0.98	0.74
Animal bone	0.01	<0.01
Animal hair	0.42	0.07
Reptile scale	0.01	<0.01
Arthropods	0.81	0.19
Order		
<i>Diptera</i> [true flies]	0.1	0.01
<i>Coleoptera</i> [beetles]	0.9	0.06
<i>Hymenoptera</i> [wasps, bees, ants]	0.1	0.01
<i>Hemiptera</i> [cicadas, leafhoppers, aphids]	0.2	0.01
<i>Neuroptera</i> [net-winged insects, lacewings]	0.1	0.01
<i>Trichoptera</i> [moth like insects-sedge-flies]	0.2	0.07
<i>Lepidoptera</i> [moths and butterflies]	0.6	0.17

Twenty sub-samples were taken from each scat to identify the relative frequency of food items in scats.

sized and large prey ($\chi^2 = 30.2$, $df = 2$, $P = <0.001$). Food items in general were primarily removed orally (58.2%, $n = 46$, $\chi^2 = 25.24$, $df = 2$, $P = <0.001$) from the substrate, followed by grabbed with one (29.1%, $n = 23$) or both (12.6%, $n = 10$) of the animals hands.

Lorises picked and/or licked the inside of flowers during March and appeared to be consuming nectar. Pollen was visible on the face of animals that were videoed consuming floral parts. Flowering trees were revisited up to three times in a single night, and multiple sites were also visited.

During feeding bouts, lorises appeared to search for exudate sources through visual and olfactory inspection of plant surfaces. As this is the first time this behavior has been described, we define it as moving rapidly over a tree surface visually scanning

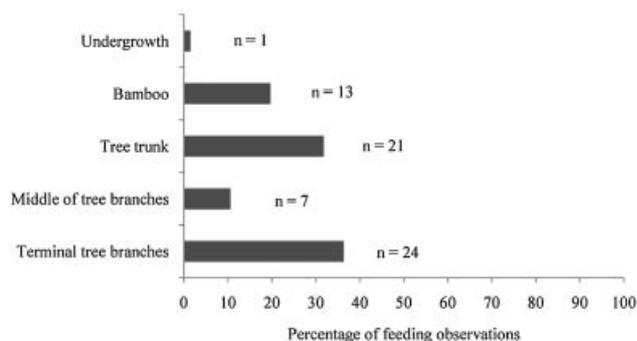


Fig. 5. Substrates pygmy lorises were observed to consume food items on ad libitum feeding observations.

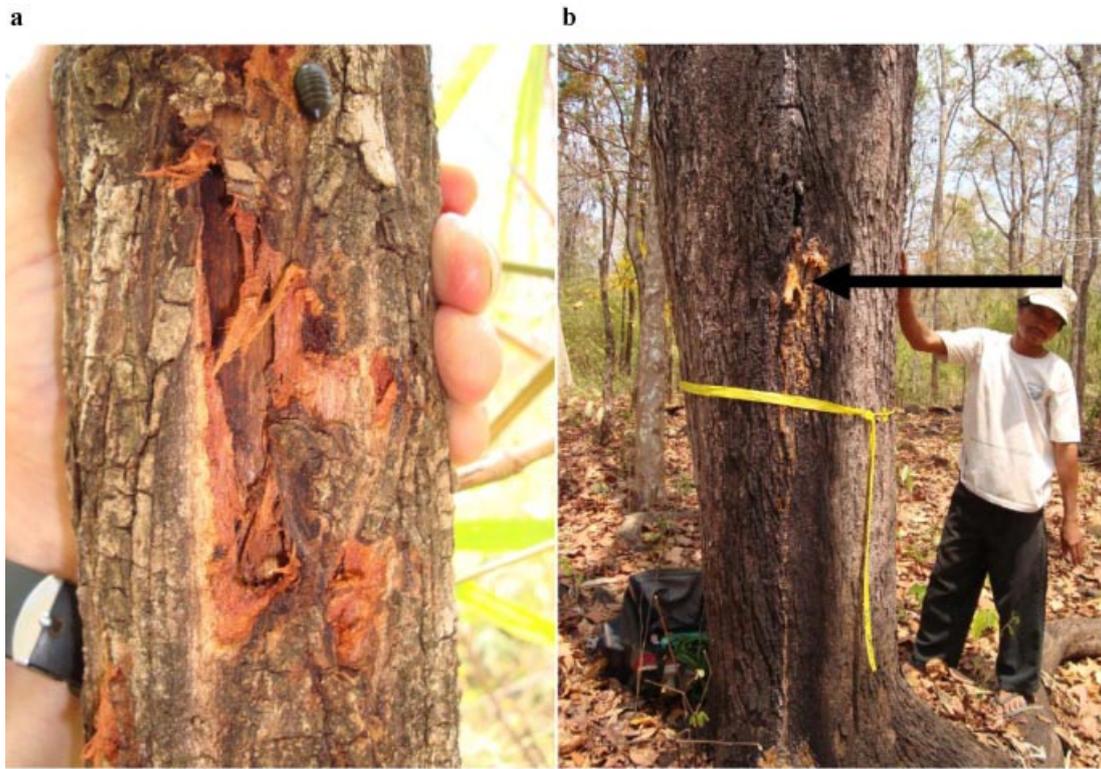


Fig. 6. **a:** Gouge marks made by a radio-collared pygmy loris in the main trunk of a tree. **b:** Feeding tree exuding large quantities of gum (indicated by an arrow).

or sniffing a surface, intermittently biting droplets of gum or stopping to gouge a surface. This “active” behavior is opposed to opportunistic finding of an exudate source. Mean searching time averaged 134 sec but ranged from 7 to 913 sec. Pygmy lorises consumed exudates in an orthograde posture [the head faced up or down] when they were situated on a vertical substrate, but also could stand quadrupedally over an exudate source. During gouging, which lasted an average of 28 sec, lorises broke bark, producing a noise audible even from a distance of 10 m. During scraping and gouging, the bark may curl up as if by a chisel, and the pygmy loris turns its head from side to side to spit it out. The animals also gouged bamboo to reveal insects and scraped lichens and fungus off the surface of old culms. During the latter process, the animal scraped or gouged while pressing its feet against the bamboo culm, which sometimes shook the bamboo, which was audible up to 100 m.

On trees without active wounds, animals raced up and down a single trunk, making up to 20 trial holes ($n = 20$, mean = $13 \pm 5SD$) with their toothcomb that did not appear to yield exudates. The study animals visibly pushed their lower anterior teeth (toothcomb) into the superficial layer of trees or lianas when gouging. Exudates were brought into the mouth by scooping (also with the toothcomb), or by licking it with the tongue. Licking occurred on the

surface of the tree, or with the animal pressing its face hard against the bark and pushing its tongue deep in the hole.

Scraping often lasted only 2 or 3 sec, with the animal picking up droplets of exudates as it moved around a trunk in a serpentine motion. At very large tree wounds, they spent up to 43 min consuming exudates. The wound shown in Figure 6b produced large quantities of gum more than twice the body length of a pygmy loris, and the study animals removed these with the toothcomb and then held them in their hands, intermittently licking them or biting them exclusively with the rear teeth, followed by intense chewing for periods of 54 sec. Animals were vigilant at these large wounds and scanned the environment while chewing.

We recorded 19 video clips of exudate feeding that averaged 28 sec (± 13.9 sec). Animals rapidly moved between a sequence of gouging (3.1 sec) or biting (mean = 4.6 sec), licking (mean = 3.8 sec), and chewing (mean = 6 sec). Of these clips, 7 showed that while gouging and licking, animals wiped their chin or the sides of their face rapidly over the gouge mark.

DISCUSSION

Our data indicate that the pygmy loris consumes a diverse range of food items in the study area. Most

notable was that almost 50% of feeding observations were of exudates, consumed in both the cool and the warm season. Although these results may be biased by difficulties in observing feeding when the lorises are high in the tree crown, these findings suggest that pygmy lorises, like other slow lorises, are obligate exudativores, exhibiting a feeding specialization relatively rare across primates [Smith, 2010], along with callitrichines (*Cebuella*, *Mico*, and *Callithrix*) [Coimbra-Filho & Mittermeier, 1978], fork-marked lemurs (*Phaner furcifer*) [Schulke, 2003], and needle-clawed galagos (*Euoticus*) [Bearder & Martin, 1980b; Fig. 1].

The proportion of exudate consumption was only marginally higher during the cool season, despite field temperatures reaching as low as 13.7°C on night-follows [Starr et al., 2012], suggesting exudates formed a regular part of the diet. Other foods were fed on seasonally. The consumption of fungi and animal parts was only observed during the cool season, and these foods appeared to be replaced by fruit and flowers during warmer periods. Gum feeding has been observed to increase in the southern lesser galago (*Galago moholi*) in South Africa during colder months, and Bearder & Martin [1980a,b] proposed that exudates, which are available year-round, serve as a fall back food for *G. moholi* during the cold season when more preferred foods are scarce. We feel this is not the case for pygmy lorises.

Hladik [1980] suggests that once a strepsirrhine reaches the size threshold of the pygmy loris (0.2–0.7 kg), it is not possible to subsist on insects alone, and the diet must be supplemented with gums and fruits. The majority of the arthropods identified from the fecal samples were remains from the orders Coleoptera and Lepidoptera. We did not identify any Hymenoptera (ants or termites), however, the sample size was small (N = 9). We inspected the bamboo that that animals had licked or gouged and found them to be full of ants and termites, and it may have been these that pygmy lorises were consuming Hymenoptera that was not detected in their feces. These observations occurred in dead bamboo thickets that were often covered in a thick layer of lichen, which may also be food for the pygmy loris. Although head-shaking, sneezing, slobbering, or urine washing when consuming possibly toxic invertebrates has been observed in the Mysore slender loris in India [Nekaris & Rasmussen, 2003] and the pygmy loris in Vietnam [Streicher et al., 2012], it was never observed in our site. Pygmy lorises were observed consuming animal prey frequently, and evidence of reptile and mammal prey in their diet shows they are well-adapted for nocturnal hunting. Animals consumed fruit from the vine *S. chinensis* and this was documented during field surveys, when multiple animals were found exploiting this vine [Starr et al., 2011]. This vine was abundant throughout the site, and may be useful for locating animals in future radio-tracking studies

when it is fruiting from March to May. Having pointed out that pygmy lorises do rely on these other resources, nectar, and fruit eating were very obvious and relatively easy to observe in the field and during our study were extremely unlikely to be under-recorded. In contrast we are certain that if visibility were better, we would have seen more prey capture events. Nevertheless, regardless of the role of insect feeding plays in pygmy loris feeding ecology, these primates exhibit clear-cut morphological adaptations towards exudativory.

The need for exudates in the pygmy slow lorises diet is further exemplified by the extreme difficulty faced until now by zoos attempting to manage this species. As of December 2012, 202 individuals were kept in ISIS-accredited zoos, producing only 11 offspring. The captive population is plagued by ill health, the most common problem of which is dental disease, which some have ascribed to too much soft food in their diet [Sutherland-Smith & Stalis, 2001]. Severe obesity also has been an issue for pygmy slow lorises, which have traditionally been fed in captivity on a diet of more than 55% produce [Ratajszczak, 1998; Sutherland-Smith & Stalis, 2001]. Despite a tendency to move towards feeding animals vegetables rather than sugar-rich fruits, some zoos have decided not to display pygmy lorises publicly due to morbid obesity [Johann, pers. comm.]. Gum arabic has traditionally been offered only as enrichment, and has even been included in a list of “items beyond the scope of most regular diets” in an Asian loris husbandry manual [Bottcher-Law, 2001, p. 87]. Streicher [2004] found that wild-caught pygmy lorises captured for the wildlife trade did not have dental problems if given sufficient branches to gouge, whereas, those fed only on European diets showed recurrent problems with tartar and gingivitis. She suggested that allowing animals to have adequate resources for gouging was vital for keeping them healthy in captivity, and that lack of such resources would directly result in dental disease, through non-abrasion of teeth and limited stimulation of the gums [Streicher, 2004]. We believe that ill health seen by animals deprived of gum and gouging in captivity is further evidence that *N. pygmaeus* is an obligate exudativore.

A better understanding of the diet of *N. pygmaeus* is becoming vital for conservation efforts. Pygmy lorises are listed as vulnerable in the IUCN Red list [Streicher et al., 2008], and in Appendix 1 of CITES based on an increasing and unsustainable trade of this species for traditional medicine and the illegal pet trade [Nekaris & Nijman, 2007], and habitat loss and degradation [Streicher et al., 2008]. The dire threats to pygmy lorises require improvement in their captive breeding and management as a safeguard for this species. The observed diversity of food items consumed by pygmy lorises in this study, particularly their reliance on exudates, provides a

scientific basis for improving the diet of captive animals, as well as high-lighting the importance of substrates for gouging.

At the same time, information about diet can be used to inform conservation policies at the local level. Sussman [1978] showed the importance of lemurs as pollinators to many Malagasy trees. Pygmy lorises consumed floral nectar, and nectar-producing parts of flowers. Animals have relatively large home ranges (10.38–33.80 ha) for such a small-bodied primate [Nekaris and Starr, 2013], and consume fruits that are also used by local people for food and medicine [Nekaris et al., 2010a; Starr et al., 2011]. If it can be demonstrated that they are responsible for pollinating these trees, this information may be a useful conservation tool to counteract the heavy local trade in this species [Nekaris et al., 2010b; Starr et al., 2010].

The question that remains is why would slow lorises be so distinct from most other extant Lorisiformes in terms of their dietary adaptations? The answer may lie in the early origin and diversification of the genus *Nycticebus*. Although the earliest fossil record of the Lorisidae present in Asia dates to 8 mya [Rasmussen & Nekaris, 1998], molecular data show that the last common ancestor between *Nycticebus* and another member of the Lorisiformes, *Loris*, may date to 30 mya, with the currently recognized species of *Nycticebus* diverging at approximately 16 mya [Nekaris and Roos, unpublished data]. Around this time, the climate in Southeast Asia dramatically fluctuated, with savannah-like landscapes and open woodlands appearing [Bird et al., 2005; Morley & Flenley, 1987]. Such a dramatic change in environment with reduction in tropical food resources may have been the impetus to select for specialized gouging adaptations in the slow lorises.

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