

RESEARCH ARTICLE

Improving Diet and Activity of Insectivorous Primates in Captivity: Naturalizing the Diet of Northern Ceylon Gray Slender Loris, *Loris lydekkerianus nordicus*

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Data on in-situ diet and nutritional requirements should inform the provision of food to captive insectivorous primates. Despite the growing availability of such information an over-reliance on commercially available primate foods and fruit continues in many captive establishments. Wild slender lorises are almost exclusively insectivorous, yet captive conspecifics are fed a primarily frugivorous diet that is likely to contribute to behavioral and health problems. We investigated the effect of naturalizing diet in the Northern Ceylon grey slender loris (*Loris lydekkerianus nordicus*) by providing live insect prey to a captive group of five individuals. We calculated activity budgets in accordance with six established categories and recorded positional behaviors. We collected data over 30 hours for each of three conditions: pre-enrichment, enrichment, post-enrichment. We hypothesized that increased opportunity for the display of natural behaviors would be stimulated by the dietary enrichment of live insects and made the following predictions; 1) Percentage time spent foraging would increase and time spent inactive would decrease; 2) behavioral repertoires would increase; 3) foraging patterns would be more constant over time with reduced feeding-time peaks. We analyzed time budget and behavioral changes using Friedman tests. We found significant changes in activity budgets with inactivity reduced and foraging levels increased to levels seen in wild slender lorises. We found a significant increase in postures used in foraging and a wider behavioral repertoire. We discuss the benefits of providing free-ranging live food in relation to enhancing the temporal-spatial distribution of food acquisition, satisfying nutritional requirements, balancing energy intake, and expenditure, expanding sensory stimulation, and promoting behavioral competence. We discuss our findings in relation to other insectivorous primates. Zoo Biol. XX:XX–XX, 2015.

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INTRODUCTION

Considering wild foraging ecology when designing diets for captive primates is vital to animal health, longevity, and feeding schedules [Crissey and Pribyl, 1997; Schwitzer and Kaumanns, 2003; Baer et al., 2010]. Scott et al. [1999] formally recommended that food supplied to zoo animals should be appropriate for the species, meet the biological and behavioral needs of the animals and support natural feeding behavior. Captive diets should be appropriate both in regard to content and presentation e.g., frequency of feeding and method of delivery [Young, 1997]. In order to meet the behavioral or ethological needs of captive animals feeding should derive from natural foraging behavior [Hughes and Duncan, 1988].

The extent of insectivory in primates ranges from flexible omnivores that feed on insects when resources are scarce [*Saimiri*, Rosenberger, 1992], those that take insects

opportunistically [*Callicebus*, *Aotus*, Rosenberger, 1992], species heavily reliant on invertebrates [*Saguinus geoffroyi*, Garber, 1980; *Cebuella pygmaea*, Soini, 1982; *Cebus olivaceus*, Robinson, 1984], and primarily insectivorous or faunivorous taxa [*Tarsius* spp, Niemitz, 1984; *Galagoidea* spp, *Arctocebus* spp, Nekaris and Bearder, 2011]. Generally

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body size imposes an upper limit on primate insectivory [Hawes and Peres, 2014]; within galagos smaller-bodied taxa are more insectivorous with larger species tending to supplement their diets with exudates and fruits [Nekaris and Bearder, 2011; Burke and Lehman, 2014].

Insectivory in wild slender lorises (*Loris* spp.) is consistently reported to be over 90% [Rhadakrishna and Singh, 2002; Nekaris and Rasmussen, 2003; Kumara et al., 2005; Nekaris, 2005; Kar Gupta, 2007; Bernede, 2009]. Lorises have been observed to feed on a wide range of prey including nine orders and 17 families of insects as well as spiders, molluscs and small vertebrates [Nekaris and Rasmussen, 2003]. Previously, only members of the genus *Tarsius* were known to be 100% faunivorous, with arthropods accounting for approximately 90% of their diet [Niemitz, 1984]; the red slender loris too has only been observed to eat animal prey [Nekaris and Jayewardene, 2003; Bernede, 2009]. Wild slender lorises spend more than one third of their activity time feeding or foraging [Nekaris, 2001]. Slender lorises typically use a “one-hand grab” to catch insects and predominantly take small- to medium-sized prey in relation to hand size [Nekaris, 2005]. The availability of insects affects slender loris distribution with their densities positively associated with agricultural pest abundance [Singh et al., 2000] and with insect presence [Nekaris and Jayewardene, 2004]. Nekaris, [2000] in her long-term study in India found that slender loris group size was positively correlated with insect density.

Two reviews of captive slender loris husbandry found that diets consisted of fruit and vegetables, specialist primate feed, and small quantities of supplementary insects, milk, eggs, honey, or cat food [Fitch-Snyder and Schulze, 2001; Elvidge, 2013]. Elvidge, [2013] reviewed husbandry methods in EAZA institutions and found that although three of the four zoos provided insects to their gray slender lorises, these supplemented a primarily frugivorous diet. Slender lorises show morphological, physiological, and behavioral adaptations to insectivory (Table 1) and are ill-equipped to deal with a frugivorous diet, a trait noted by one of the first individuals to keep lorises, who wrote: “*I feel sure that the direct cause of failure in so many attempts to keep these little animals, for any length of time, in captivity is attributable to their having been fed chiefly on fruit, with insufficient quantity of fresh animal and insect food to keep them in good health*” [Phillips, 1931].

Despite the importance of naturalistic diets to health and well-being, the dietary needs of captive slender lorises continue to be largely neglected. Captive breeding of slender lorises has had limited success primarily due to environmental stress, disease, and nutritional problems [Fitch-Snyder and Schulze, 2001; Fuller et al., 2013]. A recent survey of the causes of death in captive Northern Ceylon gray slender loris, *Loris lydekkerianus nordicus* found a range of lethal disorders including: gastrointestinal, hepatic and biliary, ocular, renal, respiratory, and multi-systemic, which the authors linked at least partially to diet [Fuller et al., 2014].

It has been proposed that zoos should not only conserve species genetic diversity but should also maintain individual animals’ behavioral competence such as key survival skills [Seidensticker and Doherty, 1996]. Insectivores spend considerable time hunting and presenting such animals food in containers at set feeding times is likely to reduce activity and competence whereas provision of live prey creates opportunity for foraging and honing skills throughout the active period. Provision of insects to captive primates has been shown to influence behavior; activity levels were increased in *Perodicticus potto* by dispersing food and providing a cricket dispenser placed into a hollow log on the floor and behavioral repertoires including sexual behavior were also promoted [Frederick and Fernandes, 1996]. Provision of foraging opportunities tailored to the known foraging behavior of other insectivorous primates is likely to improve their captive experience by stimulating expression of their natural behaviors. Moustached tamarins *Saguinus mystax* are active foliage gleaners that grab prey from leaves and branches whereas the saddleback tamarins *S. fuscicollis* use manipulative foraging directed at blind microhabitats such as tree bark, leaf litter and woody crevices [Peres, 1992]. Aye-ayes *Daubentonia madagascariensis* use their specialized feeding finger to tap-locate prey and extract them from inside branches [Erickson et al., 1994]. Owl monkeys *Aotus nancymae* catch prey by grabbing them from the air or by clamping them against a substrate [Wolovich et al., 2010].

Naturalizing the foraging task of insectivorous primates is likely to support predation skills; the quality of captive hunting is less clear. In a study of golden lion tamarins *Leontopithecus rosalia*, Castro et al., [1998] found captive animals were less efficient foragers than their wild counterparts. The closer the match between captive and wild environments the more likely the animals are to retain key survival skills; maintenance of such abilities would help to preserve behavioral competence through generations of captive breeding.

Provision of free-ranging live foods to insectivorous primates offers enrichment in several sensory domains. Animals have an innate “template” of their food characteristics and/or they learn to recognize food as juveniles [Young, 2003]. Many species form a “search image” or heightened reception to prey characteristics [Plaisted and Mackintosh, 1995]. It is likely that insectivores are highly attuned to a variety of insect characteristics; insects differ in taste and texture as well as stimulating vision, hearing and olfaction. Horsfield’s tarsier *Tarsius bancanus* young are able to catch insect prey from age six weeks [Niemitz, 1984], and Mysore slender lorises consume noxious insect prey as young as 8 weeks [Nekaris, unpub. data]. Nocturnal insectivorous primates primarily use hearing to locate prey [tarsiers, Niemitz, 1984; mouse lemurs, Atslis, 2000; galagos Nekaris and Bearder, 2011]. Lorises use scent detection to locate slow-moving odorous arthropods [Rasmussen and Nekaris, 1998] although they are primarily visual predators able to locate prey from considerable distances [Nekaris, 2005].

TABLE 1. Morphological, physiological, and behavioral adaptations of *Loris* to insectivory, demonstrating the previously overlooked yet intense specialization of these primates

	Morphology	Physiology	Behavior
Prey location	Marked optic convergence, able to locate prey from considerable distances ^h	Dual chemosensory systems; olfactory and vomeronasal ^d	Visual tracking of prey ^g
Hunting/capture	Convergent position of all fingers for dynamic prey grabbing ^c	Dichromatic vision to detect camouflaged prey ^f	Travel in irregular patterns to avoid local depletion of invertebrate prey ^c
	Flexible pelvic girdle and tensile forces on the limbs ^k		Stealth minimizes disturbance of evasive prey ^g
	Retia mirabilia of proximal limb vessels ^e ; enables suspensory postures		Bipedal and monopodal hang postures to grab flying insects using one or two hand grab ^g
Ingestion	Modified dentition ^{ab}	Ability to process arthropods with distasteful chemicals or potential to inject venom ^f	Procurement of ants by novel feeding technique ⁱ
	Ability to eat hard foods ^j		Acrobatic suspensory postures to catch prey ^l
Digestion	Relatively small intestine for a diet of concentrated nutrients ^b	Reduced basal metabolic rate ^h	Hands used to dismember prey, or hold prey whilst teeth remove inedible parts e.g. wings of cicadas ^g .

^aWhite (2009).^bSwindler (2002).^cHladik (1979).^dGarrett et al. (2013).^eOzanne and Bell (2003).^fTan and Li (1999).^gNekaris (2005).^hRasmussen and Nekaris (1998).ⁱKumara et al. (2005).^jPhillips (1931).^kCrompton et al. (1987).^lNekaris (2002).

The primary reason for naturalizing the diets of captive animals is to maintain their health and well-being. Appropriate diets are particularly important for expectant and lactating mothers and neonates; the mortality in newborn lorises and pottos is high [Fuller et al., 2014]. Slender lorises have a reduced metabolic rate [Müller et al., 1985; Rasmussen and Izard, 1988]; an inappropriate frugivorous diet has great potential to cause weight gain and metabolic dysfunction due to hypo-metabolism. Captive slender lorises frequently suffer dental problems [Plesker and Schulze, 2013], whilst ocular problems and renal pathology was found in 50% of captive lorises and pottos post-mortem [Fuller et al., 2014]. Slender lorises are generalist insectivores, taking a wide variety of prey; whilst care must be taken when introducing new food items that have the potential to induce adverse reactions, lorises are known to eat a variety of noxious insects that can be toxic to other animals [Nekaris, 2005] thus they are likely to be particularly adaptable and indeed are physiologically adapted to such prey.

Zoo collections include many species whose natural diet would include insects. The necessity to meet the dietary needs of obligate insectivores such as Pholidota and Tubulidentata is clear whereas the diet of predominantly insectivorous primates (e.g., Galagidae, Perodicticinae, Cheirogaleidae, and partial insectivores such as Callitrichinae) are less evident. Our study uses *L. l. nordicus* as a model for the husbandry of arboreal insectivorous primates. We investigated the effect of live food enrichment on the activity budget and positional behavior of gray slender lorises housed at ZSL London Zoo. We anticipated that enhancing their ability to forage and feed in a manner similar to their wild counterparts would improve their well-being. We formulated three predictions:

Prediction 1—*Activity level and diet*: We predict that when provided with live prey, the percentage time slender lorises spent foraging would significantly increase, with a subsequent decrease in inactivity.

Prediction 2—*Behavioral repertoire and diet*: We predict that lorises' behavioral repertoires, particularly in

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regards to positional behaviors, would significantly increase when live prey are provided to them.

Prediction 3—*Temporal-spatial change and diet*: We predict that provision of live prey would produce significantly greater consistency in foraging, thus reducing artificial “feeding time” peaks.

MATERIALS AND METHODS

Subjects and Enclosure

The study animals were five female slender lorises housed together off-exhibit at the Clore nocturnal house London Zoo. All animals were related; the group comprised a mother and four daughters. The enclosure measured approximately 2.1 m (height) by 4.4 m (length) by 1.5 m (width). Humidity was between 60–77% and temperature 22–24 °C. Substrates included a complex of predominately small- to medium-sized branches. Lorises were on a reverse lighting cycle and tended to wake when lights were turned off at approximately 10.00 am. The illumination was 18w T8 thin with a blue sleeve cover and an intensity of T5 12 watt. The normal feeding regime included two feeds per day at approximately 11.00 and 14.00 hours, food was presented in coconut bowls suspended from substrates (Table 2).

Data Collection

Zoo opening hours (10.00 am–4.00 pm) dictated the observational duration of six hours per day. We collected data for five consecutive days for each of three conditions; pre-enrichment, (usual diet) enrichment (usual diet plus live insects), post-enrichment (usual diet).

To test prediction 1 we collected data via instantaneous point sampling [Altmann, 1974], at five-minute intervals for each of the five animals. To enable direct comparison with the activity budgets of wild loris, we selected categories to match field studies [Nekaris, 2001]. Activity categories comprised: inactive (rest motionless or sleep), travel (directed movement, animal not looking

for food), feed (consumption of food item), forage (animal actively looking for food), groom (cleaning own or others' fur by mouth), other (urine wash, scent mark, play, fight).

To test prediction 2 we recorded the lorises' positional behaviors on each sampling point, following Schulze and Meier, [1995] and Nekaris, [2001]: sit, quadrupedal walk, sleeping ball, bridge, climb up, climb down, quadrupedal stand, cling, bipedal hang, bipedal stand, tripedal hang, quadrupedal hang, and quadrupedal walk hanging. The category of “other” was used to denote any postures distinct from published ethograms. To test prediction 3 we measured the spatial and temporal distribution of live food by recording the time and location (floor, trunk/crevice, branch) of all observed captures.

Prey Selection

In order to select the most appropriate species for the enrichment we considered several factors including those impacting on animal keepers, husbandry, and enrichment value. Six criteria were considered; nocturnality, nutritional value, sensory value, pest status of any escapees, availability, and ease of handling. We evaluated a variety of potential species including moths, beetles, locusts, meal worms, crickets, spiders, and ants. The diversity of species eaten by lorises, including noxious taxa, indicated that palatability and potential harm by adverse reaction were not priority selection criteria. Crickets were found to fulfill all key criteria and therefore the common black cricket, *Gryllus assimilis* was chosen [c.f. Walker and Masaki, 1989]. Crickets are also cost-effective; approximately \$2.60/£1.70 per 100 crickets [Livefoodsdirect, 2015].

Prey Provision

In order to simulate natural foraging conditions the prey were free-released into the enclosure and scattered by hand to maximize their distribution. They were provided

TABLE 2. Typical ZSL diet regime for slender lorises, weights are per animal per day

Food item	Weight fed (g)	Presentation
Mazuri primate pellet ^a	20.0	Ingredients mixed and fed am
Kit-e-Kat cat food	15.0	
Banana	6.0	
Honey	0.75	
Apple	6.0	Fed chopped into 2 cm ³ pieces pm
Pear	4.0	
Grape	4.0	
Soft fruit - melon, mango, papaya, grape	6.0	
Raisins	0.5	Fed scattered around the enclosure 2 times a week
Live food - meal worms, <i>locusts</i>	10	Meal worm dispenser

^aPrimate pellet, cat food and banana are mixed together for the morning feed. Raisins are fed twice a week on a Monday and Saturday (2 g per day). Some food is lost to pests (mice) from within their enclosure.

TABLE 3. Nutrient content of three different diets for slender lorises, the captive diet fed during this study at ZSL, the diet enriched with crickets and a hypothetical diet if the added insects were all fully gut loaded, all on a dry matter basis

Diet	Ash (%)	Protein (%)	Fat (%)	Carbohydrates ^a (%)	Ca (%)	P (%)	Na (%)	Energy (kcal/kg)
ZSL diet	4.83	15.53	5.00	84.30	0.75	0.46	0.21	88.42
Enriched diet	4.91	20.04	5.80	69.25	0.69	0.51	0.24	102.63
Enriched GL	5.41	19.95	5.63	69.01	0.79	0.50	0.25	102.42
Recommendation		8.00	2.50		0.55	0.33		

^aCarbohydrate value was calculated by removing Ash, Protein and Fat from 100.

each morning at approximately 10.00 am. A total of approximately 200 crickets were released over the five days of the enrichment condition (approximately 40 each day). Lorises were offered their regular diet in conjunction with the insect enrichment; they continued to consume the regular diet but to a lesser extent.

Data Analysis

We collected a total of 5,100 instantaneous sample points; approximately 1,800 per condition. To examine changes in activity budgets (Prediction 1) we used Friedman ANOVAs to analyze hourly data for each of the activities by condition [Friedman, 1937]. We conducted the analyses using SPSS v21.0 with probability set at the $p \leq 0.05$ level. We used Friedman ANOVAs to analyze hourly data for each of the positional behaviors by condition [Friedman, 1937] and compared the rates of “other” positional behaviors (Prediction 2). To test the 3rd prediction, we compiled foraging profiles by calculating the mean time spent foraging per hour for each of the three conditions. We recorded the number of crickets eaten per hour during the active period.

We calculated the nutrient contents of each diet using Zootrition (St. Louis Zoo) and its database of ingredients. We analyzed the following three diets: the current ZSL slender loris diet, as presented; the same diet with the added crickets; the same diet with the addition of gut-loaded crickets. No nutritional information for *Gryllus assimilis* was available, therefore *Acheta domesticus* was used for the normal and gut loaded values from Bernard and Allen [1997] (Table 3).

RESULTS

Prediction 1: Foraging significantly increased and inactivity was significantly reduced ($X^2 = 524.08$, $df = 10$, $p \leq 0.001$) during the enrichment condition. Foraging levels more closely matched the foraging levels of wild lorises (Table 4).

Prediction 2: Percentage of time spent in postures typically used during foraging (quadrupedal hang, quadrupedal walk, climb up, and climb down) increased and certain resting postures (sleeping ball and sitting) decreased significantly during the enrichment condition ($X^2 = 550.615$, $df = 26$, $p \leq 0.001$). Observations of “other” positional behaviors rose from 0.2–3% during enrichment.

Prediction 3: Inactivity was consistently lower throughout the day during enrichment (Figure 1a). During enrichment foraging levels gradually declined throughout the day but remained higher than at any point during pre- and post-enrichment (Figure 1b).

A total of 161 consumptions were observed of approximately 200 crickets released; the number of crickets captured per hour decreased over time however lorises continued to make captures more than five hours after crickets were released. The temporal distribution of cricket consumption gradually decreased, percentage of observed captures per hour post-release were; 50%, 21%, 12%, 7%, 6%, 4%.

DISCUSSION

Prediction 1 was supported; naturalizing the diet significantly increased foraging and reduced inactivity. During the pre-enrichment condition lorises spent the

TABLE 4. Activity budget of captive slender lorises compared with that of wild Mysore slender loris; mean percentage of time spent in each activity by condition

Activity	Wild <i>L. l. lydekkerianus</i> ; Nekaris (2001)	Pre-enrichment N = 5 (1675 sample points)	Enrichment N = 5 (1725 sample points)	Post-enrichment N = 5 (1700 sample points)
Inactive	43	46 ± 0.15	29 ± 0.08	59 ± 0.15***
Travel	22	20 ± 0.11	21 ± 0.09	13 ± 0.07
Feed	1	8 ± 0.07	6 ± 0.03	5 ± 0.02
Forage	27	9 ± 0.06	24 ± 0.11	10 ± 0.06***
Groom	6	8 ± 0.5	11 ± 0.08	8 ± 0.04
Other	1	8 ± 0.06	9 ± 0.05	6 ± 0.04

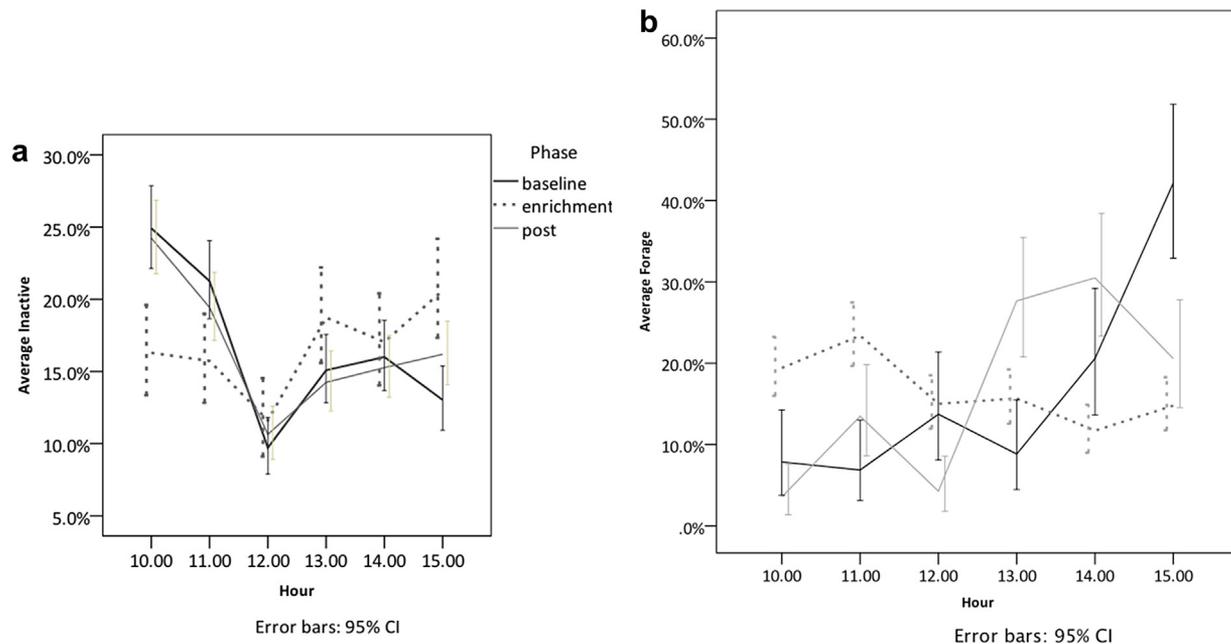


Fig. 1. a: Inactivity profile of captive slender lorises to show the mean time animals spent inactive per hour by condition. Friedman $X^2 = 12.00$ $P \leq 0.01$. b Foraging profile of captive slender lorises to show the mean time animals spent foraging per hour by condition. Friedman $X^2 = 9.00$ $P \leq 0.01$.

majority of their time inactive, enrichment significantly reduced inactivity to approximately one third with inactivity more evenly distributed throughout the active period. Wild *L. l. lydekkerianus* have been found to spend approximately 43% of their time inactive with this level being relatively stable throughout the night [Nekaris, 2001]. Radhakrishna and Singh, [2002], using a more stringent definition of inactive, found an inactivity level of 27% in *L. l. lydekkerianus*. Thus inactivity during enrichment more closely matched in-situ activity patterns; the increase in activity was primarily due to higher levels of foraging and might also have been promoted by higher energy intake from their diet.

Time-budgets are a reliable way to measure the cost an animal is prepared to pay for the opportunity to perform different behaviors i.e., they can be used as a measure of the importance of that behavior to the animal [Dawkins, 1988]. The most significant behavioral change during the enrichment condition was foraging, which increased to four times the pre-enrichment level. In-situ Mysore slender lorises spend around 27% of their time foraging [Nekaris, 2001] thus during enrichment a foraging level comparable with wild slender lorises was achieved. Foraging returned to pre-enrichment levels following withdrawal of free-ranging prey. In other animals that hunt their prey foraging was found to increase during both enrichment and post-enrichment phases; in small cats [Shepherdson et al., 1993] cheetahs *Acinonyx jubatus* [Williams, 1996] and bush dogs *Speothos venaticus* [Ings, 1997]. This is likely to be due to behavioral activation whereby the animal discovers an outlet for its behavior that it continues to display in the absence of the

initial trigger [Haskell et al., 1996]. Behavioral activation was not found in the slender loris.

Prediction 2 was supported; we found that significant changes were made to the lorises' behavioral repertoire including the emergence of novel postures. All twelve postures shown by wild slender lorises were represented by the captive animals within each of the study conditions. Five significant changes occurred during the enrichment condition. i) Lorises tended to "climb down" more as they often located a cricket from the upper branches and used a fast vertical route to reach the prey. ii) Bipedal hang was used more commonly. This posture was frequently employed to access prey from the ground using a one-hand grab whilst suspended from a low branch. This technique mirrored that described for wild *Loris* as the common capture technique for slow moving prey [Nekaris, 2005]. iii) Cling was used substantially more often, this position was frequently employed whilst foraging; lorises clung to small- or medium-sized branches and scanned to locate prey. This posture was used considerably more frequently than by wild animals, perhaps due to the limited travelling opportunities in a captive environment. iv) During enrichment "sleeping ball" was reduced to levels seen in wild Mysore slender loris. v) The category of "other" was used significantly more during enrichment due to increased behavioral repertoires. Three novel postures were exhibited during enrichment; *monopodal hang*, in which the animal supports itself suspended by one leg, *horizontal cantilever*; the animal raises itself suspended to between 45–90 degrees via its hind limbs and *transverse bipedal stand*; the animal supports itself with one fore-limb and the opposing hind limb with the other hind

limb stretched out to maintain balance. These positions were employed primarily during foraging with monopodal hang also observed during play. It is likely that provision of live prey would promote the utilization of locomotor and morphological specializations shown by *Daubentonia madagascariensis* such as head-first descent and postural suspension [Curtis and Feistner, 1994] and encourage the full range of postural and locomotor repertoires required for active foraging in other insectivorous primates e.g., agile leaping in galagos Nekaris and Bearder, 2011] and tamarins [Garber and Pruetz, 1995]. Food-based enrichment consisting of food Kong, termite mound, and hanging food was associated with a significant increase in species-typical behaviors and increased behavioral diversity in armadillos *Dasyurus novemcinctus* and Senegal bush-babies *Galago senegalensis* [Clark and Melfi, 2012].

We observed an additional social behavior during enrichment; on several occasions lorises allowed others to take crickets from their hands and mouths without resistance or reprisal. On two occasions lorises engaged in active parent-offspring and sibling-sibling food sharing. Slender lorises were not seen to solicit for, take or share fruit or food pellets indicating that insect prey were more highly prized. Nekaris and Rasmussen, [2005], observed in-situ slender lorises “feeding amicably together”; they suggest that the abundance of prey and lack of competition might influence the higher gregariousness among lorises compared with other nocturnal primates. Captive owl monkeys *Aotus nancymaae* beg for insect prey from other conspecifics and approximately half such solicitations resulted in food-sharing Wolovich et al., 2010].

Prediction 3 was supported; increasing the temporal-spatial distribution of food enabled more consistency of foraging over time thus more closely emulating the foraging task faced by wild loris. Provision of sufficient numbers of insects allowed most to evade immediate capture and reduced “meal-time” effects. Feeding captive primates should ideally maximize both spatial and temporal distribution [Schwitzer and Kaumanns, 2003]. Food enrichments often consist of devices or dispensers that animals activate to gain food rewards e.g., meal-worm dispensers stimulated observation and foraging behavior in meerkats [Shepherdson et al., 1989]. The ZSL lorises are typically fed mealworms twice a week supplied via a static dispenser; lorises pull the mealworms from holes in a hanging cylinder. Lorises were observed to gather around the dispenser and take turns to

feed. Spatial and temporal distribution is not enhanced by this method, nor is hunting skill required, as worms are gleaned quickly and easily from a single location; in addition individual animals can monopolize the food source.

Studies of the basal metabolic rate (BMR) of *Nycticebus* and *Loris* species have found that they have a very low metabolism and do not expend as much energy as similar sized primates [Muller, 1979; Muller et al., 1985]. Lorises have a BMR of less than half of the Kleiber equation thus the most appropriate equation for the BMR for adult, non-gestating or lactating slender lorises is: $BMR = 0.5(g)^{0.75}$ where g is the animal's body mass in grams [Kleiber, 1947; Muller, 1979; Muller et al., 1985]. Basal metabolic rate does not account for any other metabolic activities such as homeothermy, performance of behaviors or digestion. The actual target energy or field metabolic rate is one and a half times greater than the BMR: $FMR = 1.5BMR$ [Jansen and Nijboer, 2003]. This value is a gross approximation, thus weight monitoring is necessary. Using an average body weight of 300 g, the estimated FMR of a slender loris is 54.04 Kcal/day. Comparison of this value with that of the current diet indicates that the energy content offered is much higher than necessary and high in soluble nutrients which is likely to promote obesity [Plowman, 2013] and possibly dental disease [Fuller et al., 2013].

Although there are currently no nutrient recommendations specifically for lorises, the recommendation for old world monkeys (OWMR) is often used [Fitch-Snyder, 2001; NRC, 2003]. These recommendations are not necessarily applicable for slender lorises that have a high protein and fat diet consisting mainly of insects [Nekaris, 2005]. The OWMR are based on rhesus macaques (*Macaca mulatta*) that have an opportunistic diet of plant and animal matter [NRC, 2003]. Crissey et al., [1997] assert that the primates' natural diet choices should be used as a parameter for captive diets because nutrient requirements are unique to each species and even species in the same niche may have different gastrointestinal morphologies. It is recommended that slender lorises have diets high in protein and fat, and perhaps chitin, and low in soluble carbohydrates. Care must be taken for the calcium and phosphorous ratios to remain balanced. The dietary requirements of insectivorous primates can be met by feeding high concentrations of calcium and other nutrients to crickets; this gut-loading produces a balanced, nutrient rich diet [Bernard and Allen, 1997; Table 5]. Body weight can be managed by manipulating the

TABLE 5. Nutrient concentrations of normal versus gut loaded crickets from Bernard and Allen [1997] on a dry matter basis. Energy concentration is provided in Gross energy

Cricket	Ash (%)	Protein (%)	Fat (%)	Carbohydrates ^a (%)	Ca (%)	P (%)	Na (%)	Energy (kcal/kg)
Normal	5.70	64.90	13.80	15.60	0.14	0.99	0.49	5.34
Gut Loaded	9.80	65.20	12.60	12.40	0.90	0.92	0.57	5.40

^aCarbohydrate value was calculated by removing Ash, Protein and Fat from 100.

balance of invertebrates provided e.g., crickets have a low fat content whereas that of waxworms *Galleria mellonella* is high [Baer et al., 2010].

Small insectivorous primates need to feed frequently and consume foods that are nutrient rich, and readily metabolized. The digestive system of slender lorises is likely to have evolved to process small quantities of food over extended periods of time rather than large quantities at “meal times” [Chivers and Hladik, 1980]. Provision of live insects enables more consistent feeding opportunities with animals being able to eat “little and often” thus balancing their energy intake and expenditure. This is in stark contrast to the typical diet which is presented in bowls at set times. Feeding peaks were found between 11.00–12.00 hours and 14.00–15.00 hours in pre- and post-enrichment conditions, coinciding with the two food provision times. Spatial distribution was maximized as lorises were able to search for prey in all areas of the enclosure, we observed that the majority of captures occurred from the floor; lorises typically used one-hand grab in bipedal or monopedal hang from a low branch. We often observed lorises intently staring into cracks and crevices, returning several times to areas where they had detected a cricket.

Temporal distribution could be further naturalized by producing periodic increases and reductions in cricket availability. Zoos might consider maintaining colonies of crickets within insectivorous primate exhibits. Crickets readily breed in warm, humid conditions thus a self-sustaining colony could potentially be established. Crickets are omnivorous and will eat a wide variety of organic materials [Masaki, 1996] thus could survive by feeding on small quantities of discarded food. Crickets reach maturity within weeks; if provided in sufficient numbers some could evade capture and provide a cyclical replenishing food resource.

Diet in captivity is subject to individual preference; slender lorises preferred the larvae stage to the adult stage of several insect species, with male and female lorises showing different insect species and life stage preferences [Clayton and Glander, 2011]. Aye-ayes *Daubentonia madagascariensis* favored fruits, vegetables, nuts, eggs, and larval insects [Carroll and Haring, 1994]. Tarsiers ate only live, moving food and showed an almost exclusive preference for crickets [Far and Good, 1988].

Given the ease of providing evidence-based food, and the known serious health consequences of poor nutrition, the persistence of inappropriate diet might be due to failure to consult published literature. A survey of approximately 200 diet plans for 50 primate species found that diets often evolved within institutions as a result of “trial and error” rather than by scientific inquiry [Kaumanns et al., 2000]. Secondly, the relative rarity of insectivorous primates might be a factor. It is possible that animals whose diet is atypical within their Order are less likely to be provided with an evidenced-based diet. The primarily exudativorous pygmy slow loris *Nycticebus pygmaeus* continues to be fed an

inappropriate diet in captivity [Cabana and Plowman, 2014]. Wild aye-ayes *Daubentonia madagascariensis* eat seeds, nectar, fungus, and insect larvae; a combination not replicated in captivity [Sterling et al., 1994]. Thirdly, whilst slender lorises have evolved numerous adaptations for foraging and feeding on insects (Table 1) their overt morphological adaptations to insectivory are less obvious than those of *Pholidota* and *Tubulidentata*.

CONCLUSIONS

1. A more naturalistic diet of live insects (specifically crickets) offered to captive slender lorises significantly increased foraging behavior and reduced inactivity to levels comparable with wild slender lorises.
2. Wider behavioral repertoires and behavioral competence was promoted when live insects were provided in their diet.
3. Ethological needs can be met by stimulating the display of natural foraging and feeding behaviors using live prey as dietary enrichment
4. Provision of live insects enables maintenance of a diverse and unpredictable insectivorous diet. This provides the opportunity for captive animals to practice and refine hunting skills and to benefit from the nutritional advantages of a natural diet.

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STATEMENT OF COMPLIANCE

We have fully complied with the “Guidelines for the use of animals in research” published in *Animal Behavior*, 43, 1992.

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