RESEARCH ARTICLE

Diets High in Fruits and Low in Gum Exudates Promote the Occurrence and Development of Dental Disease in Pygmy Slow Loris (*Nycticebus pygmaeus*)

Francis Cabana,[1,2]* and K.A.I. Nekaris[1]

[1]*Nocturnal Primate Research Group, Oxford Brookes University, Headington Campus, Gipsy Lane, Oxford, OX3 0BP, United Kingdom*
[2]*Paignton Zoo Environmental Park, Paignton, Devon, TQ4 7EU, United Kingdom*

Asian slow lorises are found in zoos and rescue centres worldwide with *Nycticebus pygmaeus*, the pygmy slow loris, boasting the largest population in captivity. Diet are reportedly high in fruit and concentrates and low in insects and exudates. Wild feeding studies place insects, nectar, and gums as the most important diet components. Captive populations also show high incidences of health afflictions, many of which may be caused by nutrition. Our study, aims at identifying a causative agent within the diets of *N. pygmaeus* in regards to diseases prominent within captive populations. We sent out 55 diet and health questionnaires to institutions worldwide. Returned diets were nutritionally analyzed. Nutrient values and proportions of each ingredient were used in a principle components analysis. Resulting factors were used as variables in a binary logistic regression (BLR), with dental disease as the dependent variable. 39 questionnaires were returned with a total of 47 diets. 20 (51.7%) institutions reported the presence of diseases with dental issues being prominent. Factors that were significant in the principle components analysis included gum, nectar, protein, acid detergent fibre, calcium, ash, phosphorus, potassium, Ca:P, magnesium, vitamin D, and energy. Gum was the only significant predictor in the BLR. Lastly, a chi square test for association was performed with the presence of dental disease as the dependent variable and the amount of fruit in the diet. The combination of high fruits and little to no gum promotes the occurrence of dental diseases. Current captive diets do not reflect the evolutionary adaptations of *Nycticebus* primates. Zoo Biol. XX:1–7, 2015.

Keywords: exudativore; gummivore; nutrition; primate

INTRODUCTION

Questionnaires have become an important method of gathering information in the zoo community. Such methods have been used to suggest beneficial husbandry methods [Wright et al., 2011; Fuller et al., 2013; Rose and Roffe, 2013], identify different research or enrichment methods used and their effectiveness [Fuller et al., 2011; Huber and Lewis, 2011], and to survey the health or behavioral issues within a species and success rates of treatments [Montaudouin and Le Pape, 2005; Lewis et al., 2010]. Surveys have also been used in conjunction with veterinary or post-mortem reports, in hopes of identifying predictors or possible causes of specific health ailments as shown by Fuller et al. [2014]. Fuller et al. [2014] focussed on lorisid primates within Association of Zoo and Aquariums (AZA) institutions and concluded that more than half of the reports that were studied showed evidence of renal pathology. One fifth of the samples showed signs of cardiovascular, gastrointestinal, endocrine, and metabolic or immunologic diseases. One main hypothesis theorised by the authors in an attempt to explain why so many lorisids in captivity show signs of illness, was nutrition, speculation which was first brought up by Debyser [1995].

Asian slow lorises are found in zoos and rescue centres worldwide with *Nycticebus pygmaeus*, the pygmy slow loris,

*Correspondence to: Francis Cabana, Paignton Zoo Environmental Park, Totnes Road, Paignton, Devon, TQ4 7EU, United Kingdom.
E-mail: francis.cabana@paigntonzoo.org.uk

Received 08 May 2015; Revised 25 August 2015; Accepted 25 August 2015

DOI: 10.1002/zoo.21245
Published online XX Month Year in Wiley Online Library (wileyonlinelibrary.com).

boasting the largest population in captivity. These vulnerable primates [Streicher et al., 2008] are largely fed a diet high in fruit and concentrates [Fitch-Snyder and Schulze, 2001]. Starr et al. [2013] report feeding observations to be 40% insects, 30% nectar and, 30% exudates and sap. The ingestion of fruit was rare and opportunistic. A plant exudate has been defined in different ways to include or exclude different substances produced by plants. The definition used in this paper is from Nussinovitch [2009] which describes an exudate as a fluid which oozes out of wounds in injured trees and hardens upon exposure to air. Namely this includes gums, resins, latex, and chicle but excludes sap. No slow loris has yet been observed ingesting resins, presumably due to the high load of terpenoids and other plant secondary metabolites [Nekaris, 2014].

While feeding fruits may seem like a diet that is richer in nutrients and energy than exudates, Cabana and Plowman [2014] showed that a naturalistic diet can be palatable and promoted the occurrence of natural behaviors as well. Breeding is monitored by the Species Survival Plan (SSP) and by the European Endangered species Program (EEP) from North America and Europe, respectively. Individual *N. pygmaeus* are recommended to breed or not and to be moved to other institutions to ensure genetic diversity. Yet breeding is successful only for a few key collections and health ailments are common [Debyser, 1995; Fitch-Snyder and Schulze, 2001; Fuller et al., 2014]. All studies state nutrition as a possible causative agent of low breeding success and important presence of illness, however no attempts at providing empirical evidence were attempted.

Fruits are known to be prevalent within the diets slow lorises, both in zoos and in rescue centres, with gum exudates being used more as enrichment and not a dietary staple [Fitch-Snyder and Schulze, 2001]. Health issues have been reported to be widespread, with dental issues being the most prominent. Our study aims at identifying the current trends in captive populations of *N. pygmaeus* worldwide, extracting information about the extensiveness of health issues and indentifying a causative agent within the nutrition of *N. pygmaeus*.

MATERIALS AND METHODS

After permission and endorsements from the AZA and EAZA Prosimian Taxon Advisory Group (TAG) were obtained, questionnaires were sent via e-mail to every zoo with at least one *N. pygmaeus* which is included in the AZA species survival plan (SSP) and EAZA European Endangered Species Plan (EEP). Questionnaires were also sent to zoos and rescue centres in Vietnam, Indonesia, and Thailand. The questionnaires were filled in by keepers, curators, and veterinarians, however, we asked that our main person of contact at each institution liaise with the relevant authorities for the different parts of the questionnaire. In this questionnaire we asked about the identification of each individual *N. pygmaeus*, as well as its daily husbandry pertaining to diet, and current diet; if the current diet was less than 3 months old, we asked participants to provide data on the previous diet. Husbandry questions were limited to how often food was presented per day, on what surface or container was used to present the food and was there a seasonal change in diet. In addition, we requested details of all health problems diagnosed during the feeding of the current diet, namely dental, digestive, skeletal, renal, and liver diseases as well as pelage/fur conditions. The questionnaire also allowed and encouraged the inclusion of extra information about health issues we did not consider or mention.

Diet menus listed on our returned questionnaires were analyzed for nutrition concentrations using the Zootrition v2.6 (St. Louis Zoo) software. We used the USDA nutritional data for ingredients listed in American Zoo diets. Ingredients formerly analyzed from Paignton Zoo, UK and entered into our Zootrition database were used for all European Zoos. Nutrient information of food items analyzed by us, within Indonesia at the Indonesian Institute of Science Nutrition Laboratory (LIPI) were used for Asian Zoo ingredients.

We ran a principle components analysis (PCA) using every nutrient value for each diet that is accounted for by at least 85% of the ingredients by dry mass, in order to identify nutrients which are responsible for the highest variance of nutrient contents [Jolliffe, 2002]. The results of the PCA were then used as possible predictors in a binary logistic regression (BLR), using the presence or absence of an illness as the outcome [Hosmer and Lemeshow, 2000]. We also used a chi-square test for association to specifically investigate the effects of fruit within the diet. We assigned each collection a grade of 1, 2, or 3 to reflect none to little, medium, and high amounts of fruit respectively. These classifications were determined by removing or adding one half standard deviation to the overall mean of fruit proportion. All statistical analyzes were conducted using SPSS version 22.0 (IBM Software). Reported health issues were linked to a diet and not to an individual slow loris, therefore, results will be reported as per collection for descriptive questions and as per diet for analysis results.

The questionnaire used received full approval from the Oxford Brookes University Research Ethics Committee (Registration number 150900).

RESULTS

We sent a total of 55 questionnaires (19 to AZA collections, 28 to EAZA collections, and 8 to Asian Collections). A total of 39 (71%) were returned (18 from AZA, 13 from EAZA, and 8 from Asian Collections) representing 160 individuals (31.3% from AZA, 21.3% from EAZA, and 47.4% from Asia). Some collections had multiple diets in place for specimens with specific cases such as obesity so we analyzed a total of 47 diets worldwide. Table 1 shows the different food categories and how many collections include them in their diets as well as their average

proportion by weight in all analyzed diets. Nutrition information for the diets are found in Table 2. Dental health issues were the most prominent being found in 20 (51.3%) of the collections (Fig. 1). Most of the diets were fed in bowls or plates fixed on branches (71.8%) followed by bowls/plates on a shelf (20.5%). Very few institutions placed the food directly on the shelf (7.7%). The lorises were most often fed only once/day (59.0% of institutions), followed by twice/day (25.6%) and only 15.3% of institutions divided the daily diet into three feeds. Seasonality was virtually absent with no collections altering the diet to reflect the natural life history of *N. pygmaeus.* Three (7.8%) institutions did alter the diet seasonally to counter seasonal weight gain and loss.

For purposes of the PCA, the nutrients used as variables were from each individual diet and not averaged by collection. All nutrient concentrations on a dry matter basis as well as proportions of each food item category on a fresh weight basis for each diet were used in the PCA, totalling 31 different factors. Simple structure was obtained with 11 of these factors (Calcium, Ca:P ratio, Ash, Magnesium, Vitamin D, Crude Protein, Gum, Potassium, Acid Detergent Fibre (ADF), Nectar, and Energy) which loaded onto 4 components. Results of the rotated component matrix is visible in Table 3. The variables retained explain 71.01% of the total variance. We found multi-collinearity between some of our variables. A strong correlation in this case is defined as an r value greater than or equal to 0.700. Ash and Calcium ($r = 0.718$), Calcium and Ca:P ratio ($r = 0.849$) all correlated strongly so both Ash and Ca:P ratio were removed from the BLR.

We ran a binary stepwise logistic regression analysis using the stepwise "Forward Wald" method to test which variable could have been a predictor of presence/absence of dental disease. Nine possible predictors within 47 different diets were used in the BLR. Overall the BLR model was significant ($\chi^2 = 38.872$, $P \leq 0.001$), with presence or absence of gum being a significant predictor (Wald = 0.031, df = 1, $P = 0.039$) to the occurrence of dental disease (Table 4). The model interpreted 56.8% of cases correctly in the first step and 84.1% of cases correctly in the second step.

We further explored the status of fruit in a chi-square test for association between amount of fruit in diet and presence of dental disease. The values used for the different levels of fruit for each collection are as follows: level 1 comprises of values including and less than 28.84, level 2 is including and between 28.85–52.96, and level 3 is anything equal to and greater than 52.97. All expected cell frequencies were greater than five. There was a statistically significant association between amount of fruit in diet and presence of dental disease $\chi^2(2) = 11.113$, $P = 0.004$ and Cramer's V showed the association to be strong $V = 0.486$, $P = 0.004$.

DISCUSSION

As a general rule, fruit is a staple part of captive diets of *N. pygmaeus* and exudates are not. Our results show that high amounts of fruit were associated with the occurrence of dental disease, and the absence of gum was also shown to be a predictor in its occurrence. Teeth issues were the most

TABLE 1. Collections that use at least one food category item in any of their diets for *Nycticebus pygmaeus* and the average proportion of each category in all diets based on fresh weight, indicating that fruit is prevalent in diets worldwide and exudates are lacking

Food item category	Number of collections #(%)	Average proportion by fresh weight % (SD±)
Concentrate	26 (66.7)	17.6 (1.5)
Fruit	33 (84.6)	40.9 (24.1)
Vegetable	29 (74.4)	25.8 (22.7)
Animal product	18 (46.2)	6.5 (8.1)
Dairy product	7 (17.9)	0.1 (2.7)
Invertebrate	31 (79.5)	7.3 (6.6)
Gum exudate	14 (35.9)	2.9 (5.2)
Grain or grain-based product	3 (7.7)	0.6 (2.5)
Nectar	5 (12.8)	0.2 (0.6)
Other	6 (15.4)	0.3 (0.9)

Total collections $n = 39$. Total diets $n = 47$. Concentrates include pellets or canned food, animal products include raw or cooked meat, eggs, chicks and pinkies; Dairy products include yogurt, cheese and pudding; Grains include rice, bread and pasta; Other includes honey, peanut butter, seeds and nuts.

TABLE 2. Average, standard deviation and min-max values of the nutrient concentration of diets of *Nycticebus pygmaeus* on a dry matter basis

Nutrient	Units	Mean	SD	Min.	Max.
Ash	%	4.98	1.03	2.70	7.29
C. F.	%	8.58	3.42	2.55	18.30
C. P.	%	19.64	5.19	6.70	30.91
Ca	%	0.55	0.27	0.04	1.04
P	%	0.45	0.15	0.08	0.74
Fe	mg/kg	100.81	77.83	1.02	342.95
Mg	%	0.13	0.04	0.05	0.24
Cu	mg/kg	11.54	6.38	1.90	26.71
K	%	1.04	0.33	0.25	1.91
Se	mg/kg	0.59	1.47	0.02	8.01
Na	%	0.21	0.10	0.05	0.43
Zn	mg/kg	47.39	34.79	0.78	126.92
Vit C	mg/kg	683.09	516.41	66.11	2291
Vit D	IU D/g	5.46	4.85	0.58	21.25
Vit E	mg/kg	105	77.79	17.55	306.81
NDF	%	9.98	5.31	0.85	24.16
ADF	%	5.28	3.45	0.21	15.75
NSC	%	57.04	10.21	40.07	85.54
Ca:P		1.14	0.36	0.30	1.84
Energy	Kcal/day	75.57	36.5	24.04	178.00

Number of diets = 47. All values used for the above values were represented by at least 85% of the total dry matter content for each diet. C.F., crude fat; C.P., crude protein; Ca, calcium; P, phosphorus; Fe, iron; Mg, magnesium; Cu, copper; K, potassium; Se, selenium; Na, sodium; Zn, zinc; NDF, neutral detergent fibre; ADF, acid detergent fibre; NSC, non-structural carbohydrates.

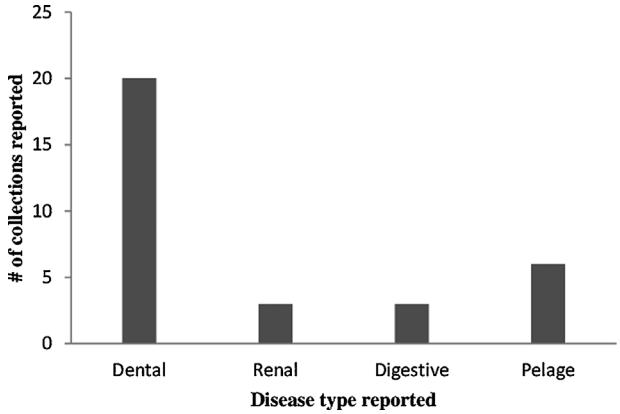

Fig. 1. Health afflictions reported by zoos and rescue centres worldwide showing the prevalence of dental diseases in captive populations. Results are based on replies from the questionnaire survey ($n = 39$).

abundant health affliction, found in 51.3% of all collections. Streicher [2004] hypothesized that diets high in fruit promote dental problems in captive *N. pygmaeus* and providing them with gouging opportunities could help remove dental plaque and combat these effects. Although we cannot comment on the validity of these assumptions, our data supports the premise of Streicher's hypothesis. The genus *Nycticebus* has specialist morphological adaptations, similar to the gummivorous marmosets *Callithrix* and *Cebuella* [Hladik, 1979; Tan and Drake, 2001]. Their dentition is particularly useful for the harvesting and processing of gum exudates. Their incisors and canines are specialised to form a toothcomb [Nekaris et al., 2010; Nekaris and Bearder, 2011]. The large procumbent lower premolars are also used in the gouging process, acting as a pivot point for the other teeth to be able to dig out the lignin from trees to stimulate gum flow [Nekaris et al., 2010]. The incredible stress placed upon the teeth is indicated by stress fractures that appear in older animals, yet broken teeth have rarely been observed in wild slow lorises which gouge nightly [Nekaris, 2014]. Dental disease has not yet been reported in wild lorises. Providing gum to captive *N. pygmaeus* had a marked effect in the reduction of gingivitis [Streicher, 2004]. There are many contact points between the broken cambium of the tree during gouging and/or the tree's gum during intake that may act as a source of friction and remove any plaque. Gum provided to captive lorises is either spread on branches or placed into drill holes of thick branches [Gray et al., 2015]. It is uncommon for a captive slow loris to gouge offered branches. Instead, they are observed only processing the gum with minimal interaction with the wood. An alternate hypothesis is the high amounts of plant secondary metabolites from the gum in conjunction with the mechanical contact between bark and tooth has a beneficial effect on teeth health [Nussinovitch, 2009]. *Nycticebus pygmaeus* has been observed feeding largely on insects, gum exudates, and nectar [Starr and Nekaris 2013; Streicher et al., 2013]. Fruit forms an insignificant part of their diet and even if they were to ingest fruit in the wild in an important quantity, fruit found in nature has a significantly different chemical composition than the fruits zoos and rescue centres use in their collections [Oftedal and Allen, 1997; Schwitzer and Kaumanns, 2003]. Cultivated fruits are higher in soluble carbohydrates and lower in protein, fiber fractions and microminerals when compared to "wild" type fruits. The main contribution of fruit in captive primate diets is water and soluble sugars that translates into energy [Plowman, 2013]. Too much of this may be the root cause of dental disease.

Caries and other dental diseases are known to be caused by bacterial plaque [Sheiham, 2001]. The microflora which inhabits this yellow plaque produces organic acids which effectively lowers the pH of the saliva and erode the surface of the teeth, the enamel, to eventually expose in inner

TABLE 3. Results of the principle components analysis rotated components matrix on the nutrient values of *N. pygmaeus* diets

	Component			
Factors	1	2	3	4
Calcium	**0.953**	0.070	−0.064	−0.089
Ca:P	**0.844**	−0.049	0.041	−0.174
Ash	**0.737**	0.293	0.230	0.162
Magnesium	**0.703**	−0.018	0.021	0.276
Vit D	0.066	**0.858**	−0.089	−0.227
Protein	0.089	**0.785**	−0.055	0.197
Gum	0.013	**0.739**	0.094	0.074
Potassium	−0.085	0.126	**0.873**	−0.012
ADF	0.224	−0.17	**0.818**	−0.045
Nectar	−0.145	0.251	0.037	**0.783**
Energy	−0.196	0.146	0.087	**−0.727**
Eigenvalue	2.922	2.068	1.483	1.339
% Variance explained	26.560	18.800	13.481	12.173

ADF, acid detergent fiber (sum of cellulose, hemi-cellulose, and lignin). Values are loadings of the variables on each of the four principal components derived. Bold values indicate the largest absolute loading per factor.

TABLE 4. Logistic regression analysis of the occurrence of dental disease as a function of diet nutrients and proportion of food items where only presence of gum was a significant predictor

Variables	Wald/score	Df	Sig.
Calcium	1.805	1	0.179
Vitamin D	0.091	1	0.763
Magnesium	0.040	1	0.842
Protein	2.655	1	0.103
Potassium	1.369	1	0.242
ADF	1.489	1	0.222
Energy	1.071	1	0.301
Gum	4.281	1	0.039[a]
Nectar	0.000	1	0.998

[a]Nutrient values used were on a dry matter basis within the diets while the food category proportions within each diet was on a fresh weight basis.

dentine layer. This acidification renders the remineralisation activity of saliva non-competitive and leads to open cavities that are prone to infection [Meurman and Cate, 1996]. This plaque gains a foothold when concentrations of soluble carbohydrates (sugars and starches) are high and also constant [Brathall, 1996]. Sugars can also augment the production of the plaque matrix itself, as well as fuel the production of organic acids by feeding the problematic acidogenic microflora [Sheiham, 2001]. Without this intake of fermentable sugars, the caries in question would not be produced. Fruit has specifically been identified as a possible cariogenic agent [Moynihan, 1998]. Dental diseases linked with sugar intake in humans are caries, root caries (which leads to infections), gingivitis, and facial and mandible abscesses, all of which have been identified in captive slow lorises [Debyser, 1995; Fitch-Snyder and Schulze, 2001; Sheiham, 2001; Fuller et al., 2014].

As well as a specialised dentition adapted for gouging, the genus *Nycticebus* also possesses a specialised gut morphology. They are described as having a shorter duodenum and a relatively long and thick large intestine and a caecum [Stevens and Hume, 2001]. The presence of these microbial chambers gives reason to assume they possess the microbiota capable of fermenting plant fiber and perhaps even chitin. Gum exudates contain a high amount of soluble fiber such as pectins and fructans that can only be digested with the symbiosis relationship of these microorganisms [Nussinovitch, 2009]. If *Nycticebus* is adapted to digest food items high in fiber, not providing gum in lorises' diets could have a detrimental effect on their health. *Cebuella and Callitthrix* are also gummivorous small primates and are known to suffer from a wasting disease in captivity. Gore et al. [2001] posits that a lack of fiber in the diets is responsible for the inflammation of the intestine that leads to nutrient malabsorbtion. Although, wasting disease has not yet been described in captive lorises, the presence of fiber itself may carry out indispensible physiological processes in the gut. There is a condition where lorises which suffer from poor welfare are emaciated, wet and have sunken eyes, however, the entire husbandry of these animals is inadequate so it is difficult to diagnose this as wasting (Nekaris, pers obs). *Nycticebus* have relatively thick masseter muscles that could possibly atrophy in captivity if not given the opportunity to gouge [Perry and Harstone-Rose, 2011]. Lorises forage by climbing up and down every branch and trunk of gum trees within their territory [Starr and Nekaris, 2013]. If an already open gouge hole has gum, the gum will be eaten, and fresh scrapes will be made so the hole keeps producing gum similarly to how it has been described for galagos [Bearder and Martin, 1980; Nekaris et al., 2010]. It is more energetically expensive to create a new gouge hole than to harvest pre-existing ones, therefore, the creation of new gouge holes in an existing territory is rare [Vinyard et al., 2009]. The actual gouging action may have little to do with dental health and more to do with the actual oral processing of exudates. Insects are caught and ingested opportunistically throughout the night and wholly ingested [Streicher, 2009; Starr and Nekaris, 2013; Streicher et al., 2013]. When wild born *N. pygmaeus* were confiscated at customs and sent to a rescue centre for rehabilitation and release, Streicher et al. [2013] fed them a diet of fruit, insects and animal products. Once in soft release, the primates had the opportunity to eat from a large variety of food items. They chose naturalistic "wild" type food items significantly more than most fruits, animal products or dairy. There is ample evidence that *N. pygmaeus* are adapted to ingest and process diets high in gum exudates and insects.

The nutrients from the analyzed diets had a wide range and no sets of guidelines unified them. Fitch-Snyder and Schulze [2001] produced the only husbandry manual for lorisine primates and suggested using the nutrient recommendations for Old World monkeys [NRC, 2003] that were originally identified from rhesus macaques (*Macaca mullatta*). These recommendations are for a medium-sized primate with an opportunistic and generalist feeding behavior. *Nycticebus* is on the other end of the feeding continuum [Nekaris, 2014]. It would seem counter intuitive that these recommendations are fit for purpose for the lorisines. No evidence based recommendations for lorisines or closely related species such as galagos currently exist and having some semblance of quality control is also important. The average content of crude protein is 19.64% and ranges from 6.7–30.91%, whereas the OWM recommendations are stated at 17–28% [NRC, 2003]. This is also a large range and with a diet high in insects, *Nycticebus* are believed to have high protein requirements although this is purely speculative. Similar hypotheses were made for callitrichids, however, was debunked by Mitura et al. [2012] whose study showed pathologies only appearing in *Callithrix* receiving diets less than 6% high quality crude protein. One long term study showed a diet of 15% crude protein on a dry matter basis is adequate for maintenance, normal breeding, and social behaviors [Flurer and Zucker, 1985]. Calcium is often thought to be a limiting nutrient in small insectivorous primates such as callitrichids [Smith, 2000]. The average amount of calcium in the *N. pygmaeus* diets is 0.55% and ranges between 0.04–1.04%. OWM recommendations, incidentally, is also 0.55% [NRC, 2003]. Multiple supplements such as cricket gut loading gel or powders, insect mineral dusters and mineral supplements spread over the fruit as well as the presence of concentrate feeds ensures minerals are found in abundant concentrations. Gum becomes increasingly important for collections that cannot afford concentrate feeds or supplements. The calcium found in wild gums would naturally help balance out the high phosphorus concentrations found within insects [Bearder and Martin, 1980; Heymann and Smith, 1999]. Calcium is found in the chitinous exoskeleton of some insects, however it has not yet been established if *Nycticebus* can digest chitin in any significant amount. Indeed the gastric mucosa of *N. coucang* was reported to contain chitinolytic enzymes; no information is available on the provenance or effectiveness of these enzymes (Stevens and Hume 1995). Callitrichid

research in the wild have often reported individuals removing the most chitinous parts of an insect before consumption such as wings or legs [Heymann and Smith, 1999]. This is not true for wild *Nycticebus,* which ingests insects whole, and suggests they may possibly have a use for chitin, possibly as an energy and/or calcium source [Starr and Nekaris, 2013]. Some captive bred individuals may remove the wings of some insects before consumption, but we regard the wild type as the "golden standard." A variety of insects should be presented to *N. pygmaeus* rather than relying on a single species of cricket or mealworm as different nutrient contents over a week may help to balance out intake and assimilation. Wild *Nycticebus* nutrient intake is mostly from a short specialist list of food categories and their captive diets should reflect that fact.

In terms of husbandry, the questionnaire results shed some insight as to the current practices of keeping *N. pygmaeus.* Free ranging *N. pygmaeus* forage for the majority of their activity budgets [Starr and Nekaris 2013]. Easily consumed diets in captivity are estimated to take up roughly 10% of their active periods when food was presented once per day, leaving more time for abnormal behaviour patterns to be performed [Cabana and Plowman, 2014]. The questionnaires received indicated the majority of collections fed their slow lorises once per day. Because of the large disparity between foraging times in the wild and in captivity, we believe this to be inadequate and would recommend two or more feeds per day. The provision of gum also significantly extended feeding time [Fitch-Snyder and Schulze, 2001; Cabana and Plowman, 2014; Gray et al., 2015]. Bowls or plates were reported to be used in over 92.3% of collections. Ideally there would be many bowls all around the enclosure to promote an uneven and random distribution of food to possibly stimulate natural foraging behaviours [Montaudouin and Le Pape, 2005]. In terms of diet variation, both Streicher [2004] and Starr and Nekaris [2013] reported a very strong seasonal effect on free ranging *N. pygmaeus* diets, accompanied by a period of weight gain and loss. The effects of mimicking these changes in captivity have yet to be quantified so we do not promote or discourage its application at this moment.

Creating an ideal diet for a wild animal in a captive setting can be a challenge, especially for specialist species. It is difficult to recreate a wild diet, however recreating the nutrients found within this diet is possible. Perhaps the nutrients should be used as the structural framework for the diet creation and specific food items should be chosen to be as close as possible to "wild" type food items [Clauss et al., 2008]. If a collection cannot provide a large enough variety of insects, replacing a portion of this food category could be attained by using a nutrient dense concentrate such as pellets, eggs, or a canned food. Insects should be gut loaded with a high calcium insect food. Nectar is easily replaced by providing a small amount of dilute juice or using a bird nectar powder and adjusting the sugar concentration to range between 22–30% (pers. obs). Vegetables may be included to ensure the diet will not lead to an energy deficit, and as a source of fiber. Gum exudate is more difficult to replace because of its unique chemical composition of soluble fiber, high Ca:P ratio, and cocktail of secondary metabolites [Smith, 2000, 2010]. Luckily, gum arabic from the *Acacia senegalensis* can be sourced in raw or refined form in most countries because of its use in the food and cosmetic industries. In tropical countries where purchasing is an issue, gum can be harvested from trees on the site using a variety of techniques from [Nussinovitch, 2009]. As shown by Cabana and Plowman [2014], it is possible for a "wild" type diet of gum, nectar, insects and vegetables to be both palatable and nutritionally appropriate.

CONCLUSIONS

1. Anecdotes, not empirical evidence, have been the basis for shaping diets of *N. pygmaeus* in captivity.
2. With a clear lack of guidelines and nutrient recommendations, the current status of nutrition for lorisines does not reflect their natural feeding ecology, morphology or physiology.
3. The captive diets are generally high in fruit and low in exudates, which lorisine primates have evolved to harness, process and digest. Not providing them with this food source can have serious health consequences.
4. Nutrient recommendations need to be identified and validated. Specialist digestive capacities should also be analyzed, specifically for soluble fiber and insect chitin.
5. A causal link was identified between the presence of fruit and lack of gum in the diet and the occurrence of dental disease. Captive diets should not rely on fruits and instead use gum Arabic and a variety of insects as their base.

ACKNOWLEDGMENTS

We would like to thank Longleat Safari and Adventure Park, Whitley Wildlife Conservation Trust, Primate Society of Great Britain, and International Primatological Society Captive Care Working party, Nacey Maggioncalda Foundation, University's Federation for Animal Welfare, Disney Worldwide Conservation Fund, Colombus Zoo, Phoenix Zoo, Cleveland Zoo and Zoo Society, Shaldon Wildlife Trust, Shepreth Wildlife Park, Sophie Danforth Foundation, Conservation International Primate Action Fund, and Mazuri Zoo Feeds for their support with various elements of this ongoing research. We are also grateful to the AZA and EAZA Prosimian TAGs for their endorsements and all collections that replied to our questionnaire, as well as to D. Whitton, G. Donati, E. Dierenfeld, and A. Plowman for advice. We also would like to extend our thanks to two anonymous reviewers for their comment.

REFERENCES

Bearder SK, Martin RD. 1980. Acacia gum and its use by lesser bushbabies, *Galgo senegalensis* (Primates: Lorisidae). Int J Primatol 1:103–128.

Brathall D. 1996. Dental caries: Intervened-interrupted-and interpreted–concluding remarks and cardiography. Eur J Oral Sci 104:486–491.

Cabana F, Plowman A. 2014. Pygmy slow loris *Nycticebus pygmaeus*-natural diet replication in captivity. End Sp Res 23:197–204.

Clauss M, Streich WJ, Nunn CL, et al. 2008. The influence of natural diet composition, food intake level, and body size on ingesta passage in primates. Comp Biochem Physiol Part A 150:274–281.

Debyser IWJ. 1995. Prosimian juvenile mortality in zoos and primate centers. Int J Primatol 16:889–907.

Fitch-Snyder H, Schulze H. 2001. Management of lorises in captivity: A husbandry manual for Asian lorisines (Nycticebus & Loris spp.). Center for Reproduction of Endangered Species, Zoological Society of San Diego.

Flurer C, Zucker H. 1985. Long-term experiments with low dietary protein levels in callitrichidae. Primates 26:479–490.

Fuller G, Margulis SW, Santymire R. 2011. The effectiveness of indigestible markers for identifying individual animal feces and their prevalence of use in North American zoos. Zoo Biol 30:379–398.

Fuller G, Kuhar CW, Dennis PM, Lukas KE. 2013. A survey of husbandry practices for Lorisid primates in North American zoos and related facilities. Zoo Biol 32:88–100.

Fuller G, Lukas KE, Kuhar C, Dennis PM. 2014. A retrospective review of mortality in lorises and pottos in North American zoos, 1980–2010. Endanger Species Res 23:205–217.

Gore MA, Brandes F, Kaup FJ, et al. 2001. Callitrichid nutrition and food sensitivity. J Med Primatol 30:179–184.

Gray AE, Wirdateti, Nekaris KAI. 2015. Trialling exudate-based enrichment efforts to improve the welfare of rescued slow lorises Nycticebus spp. Endang Species Res 27:21–29.

Heymann EW, Smith AC. 1999. When to feed on gums: Temporal patterns of gummivory in wild tamarins, *Saguinus mystax* and *Saguinus fuscicollis* (Callitrichinae). Zoo Biol 18:459–471.

Hosmer DW, Lemeshow S. 2000. Applied logistic regression. 2nd edition. New York, NY: John Wiley.

Hladik CM. 1979. Diet and ecology of prosimians. In: Doyle GA, Martin RD, editors. The study of prosimian behavior. New York, NY: Academic Press. p 307–357.

Huber HF, Lewis KP. 2011. An assessment of gum-based environmental enrichment for captive gummivorous primates. Zoo Biol 30:71–78.

Jolliffe I. 2002. Principal component analysis. New York, NY: John Wiley & Sons, Ltd.

Lewis DK, Sheperdson DJ, Owens TM, Keele M. 2010. A survey of elephant husbandry and food health in North American zoos. Zoo Biol 29:221–236.

Meurman JH, Cate JM. 1996. Pathogenisis and modifying factors of dental erosion. Eur J Oral Sci 104:199–206.

Mitura A, Liebert F, Schulumbohm C, Fuchs E. 2012. Improving the energy and nutrient supply for common marmoset monkeys fed under long-term laboratory conditions. J Medic Primatol 41:82–88.

Montaudouin S, Le Pape G. 2005. Comparison between 28 zoological parks: Stereotypic and social behaviors of captive brown bears (*Ursus arctos*). App Anim Behav Sci 92:129–141.

Moynihan PJ. 1998. Update on the nomenclature of carbohydrates and their dental effects. J Dentistry 26:209–218.

Nekaris KAI. 2014. Extreme primates: Ecology and evolution of Asian lorises. Evol Anthr 23:177–187.

Nekaris KAI, Bearder SK. 2011. The strepsirrhine primates of Asia and Mainland Africa: diversity shrouded in darkness. In: Campbell C, Fuentes A, MacKinnon K, Bearder SK, Stumpf R, editors. Primates in Perspective. Primates in Perspective. Oxford: Oxford University Press. 2nd Ed. p 24–45.

Nekaris KAI, Starr CR, Collins RL, Navarro-Montes A. 2010. Comparative ecology of exudate feeding by lorises (*Nycticebus, Loris*) and pottos (*Perodicticus, Arctocebus*). In: Burrows AM, Nash LT, editors. The evolution of exudativory in primates. Chicago, IL: Springer. p 123–137.

NRC 2003. Nutrient Requirements In: Grossblatt N, editor. Nutrient requirements of nonhuman primates second revised edition. Washington, DC: The National Academies Press. p 191–194

Nussinovitch A. 2009. Plant gum exudates of the world: Distribution, properties, and applications. Chicago, IL: CRC Press.

Oftedal OT, Allen ME. 1997. The feeding and nutrition of omnivores with emphasis on primates. In: Kleiman DG, Allen ME, Thompson KV, editors. Wild mammals in captivity: Principles and techniques. Chicago: University of Chicago Press. p 148–157.

Perry J, Harstone-Rose A. 2011. The jaw adductors of strepsirrhines in relation to body size, diet, and ingested food size. Anatom Rec 294:712–728.

Plowman A. 2013. Diet review and change for monkeys at Paignton Zoo Environmental Pak. J Zoo Aquar Res 1:73–77.

Rose EP, Roffe SM. 2013. A case study of Malayan tapir (*Tapirus indicus*) husbandry practice across 10 zoological collections. Zoo Biol 32:347–356.

Schwitzer C, Kaumanns W. 2003. Foraging patterns of free-ranging and captive primates- implications for captive feeding regimes. In: Fidgett A, Clauss M, Ganslober U, Hatt JM, Nijboer J, editors. Zoo Animal Nutrition Vol. II. Amsterdam, NE: Furth: Filander Verlag. p 247–265.

Sheiham A. 2001. Dietary effects of dental diseases. Pub Heal Nutr 4:569–591.

Smith AC. 2000. Composition and proposed nutritional importance of exudates eaten by saddleback (*Saguinus fuscicollis*) and mustached (*Saguius mystax*) tamarins. Int J Primatol 21:69–83.

Smith AC. 2010. Influences on gum feeding in primates. In: Burrows AM, Nash LT, editors The evolution of exudativory in primates. Chicago, Il: Springer. p 109–122.

Starr C, Nekaris KAI. 2013. Obligate exudativory characterizes the diet of the pygmy slow loris Nycticebus pygmaeus. Am J Primatol 75:1054–1061.

Streicher U. 2004. Aspects of ecology and conservation of the pygmy slow loris *Nycticebus pygmaeus* in Vietnam. [Dissertation] Ludwig-Maximilians Universitat Munchen.

Streicher U. 2009. Diet and feeding behavior of pygmy lorises *(Nycticebus pygmaeus)* in Vietnam. Viet J Primatol 3:37–44.

Streicher U, Thanh NV, Nadler T, Timmins RJ, Nekaris A. 2008. *Nycticebus pygmaeus*. The IUCN Red List of Threatened Species. Version 2014. 3. <www.iucnredlist.org>. Downloaded on 15 April 2015.

Streicher U, Wilson A, Collins RL, Nekaris KAI. 2013. Exudates and animal prey characterize slow loris (*Nycticebus pygmaeus*, *N. cougang* and *N. javanicus*) diet in captivity and after release into the wild. In: Masters J, Genin F, Crompton R, editors. Leaping ahead: advances in prosimian biology. New York, NY: Springer.

Stevens CE, Hume ID. 2001. Comparative physiology of the vertebrate digestive system second edition. New York, NY: Cambridge University Press.

Tan CL, Drake JH. 2001. Evidence of tree gouging and exudate eating in pygmy slow lorises *(Nycticebus pygmaeus)*. Folia Primatol 72:37–39.

Vinyard CJ, Wall CE, Williams SH, et al. 2009. In: Ford SM, Porter LM, Davis LC, editors. The evolutionary morphology of tree gouging in marmosets. In New York, NY: Springer. p 395–409.

Wright DJ, Omed HM, Bishop CM, Fidgett AL. 2011. Variations in Eastern bongo (*Tragelaphus eurycerus isaaci*) feeding practices in UK zoological collections. Zoo Biol 30:149–164.