Francis Cabana, Ellen Dierenfeld, Wirdateti Wirdateti, Giuseppe Donati, K.A.I. Nekaris

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Title: The seasonal feeding ecology of the Javan slow loris (*Nycticebus javanicus*)

Francis Cabana[1 2], Ellen Dierenfeld[3], Wirdateti Wirdateti[4], Giuseppe Donati[1], K.A.I. Nekaris[1]

1 Nocturnal Primate Research Group, Oxford Brookes University, Oxford, OX3 0BP

2 Wildlife Reserves Singapore, Singapore, 729826

3 Ellen Dierenfeld Consultancy LLC, Saint Louis, USA

4 Lembaga Ilmu Pengetahuan Indonesia, Bogor, 12710

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Corresponding author: Francis Cabana, Wildlife Nutrition Centre, Wildlife Reserves Singapore, 80 Mandai Lake Road, 729826, e-mail: francis.cabana@wrs.com.sg, Office: +65 63608652, Fax: +65 3636 8365

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ABSTRACT

Objectives: To describe the strategy employed by exudativorous primates during seasonal shifts in food abundance using the Javan slow loris as a model. Males and females may cope differently as well as exploit fallback foods in different proportions.

Materials and Methods: Observing 15 free ranging Javan slow lorises over a year, we quantified their seasonal diet and nutrient intake using intake rates. We monitored phenology over five plots that were assessed monthly. We weighed animals every six months. We analysed all food items slow lorises ingested for macronutrients using the nutritional geometry framework.

Results: The slow loris diet consisted of eight food categories, with gum and insects being the major food source in terms of weight. All food items were available in the wet season and were restricted in the dry season. Males and females reacted differently to seasonal abundances with females ingesting more protein, gum, fruits and flowers and males ingesting more fibre.

Discussion: The reproductive costs of gestation and lactation may place a burden on females that requires them to alter their foraging strategy during the dry season to ensure enough protein and overall energy is ingested. The overall strategy used by these exudativorous primates is one of nutrient maximization as no nutrient was clearly preferred over another.

INTRODUCTION

Primates have evolved a variety of ways to cope with the seasonality of their habitats, specifically in regards to the flux of available nutrients and energy (Gould et al., 1999; Irwin et al., 2014). Changes in behavior leading to reduced metabolic costs (Gould et al., 2011); reduction of fat reserves (Knotts, 1998), changes in physiology i.e. torpor (Nowack et al., 2013; Pereira 1993;); alteration of home range size and/or daily distance travelled (Campera et al., 2014; Pichon et al., 2016; Sato et al., 2015); and prominently, the ingestion of less preferred (fallback food) items (McGraw et al., 2014; Serckx et al., 2015) are all strategies primates may employ to cope with energetically restrictive seasons. The term "fallback food" has been used inconsistently in the primatological literature. Fallback foods are not intrinsic, meaning a plant part is not inherently of low quality, but instead fallback foods are comparatively observed to have a lower nutritional quality (Lambert and Rothman, 2015). Following optimal foraging theory (Charnov, 1976), the highest quality food items should be selected based on what is available, given their defined constraints such as requiring substantially more handling or processing time, possessing a higher fiber concentration or higher secondary plant metabolite content. All of these factors may ultimately reduce the amount of or absorption rate of nutrients, decreasing the nutritional gains of this particular food in regards to the resources needed to process it (low quality). When compared to a food item with higher gains and/or requiring a lower processing intensity (high quality), the low quality food item is described as fallback and should only be selected when the higher quality food is not available. Such selections are relative to what other edible items are available.

Tougher or more fibrous foods have often been labelled as fallback foods, without regard for the morphological or physiological adaptations of species that consume them (Constantino et al. 2009; Lambert et al., 2004; Moura and Lee, 2004). For such species, animals may select a typical fallback food disproportionally relative to the food's abundance in a given habitat, using it as a preferred food item (Leighton, 1993; Marshall and Wrangham, 2007). Fallback foods can be further defined into "staple" and "filler". The staple fallback foods are always available and are a small yet consistent part of the overall diet. This category is in opposition with filler fall back foods, which may be available year-round or only seasonally yet very rarely become an important part of the diet, usually when preferred foods are absent (McGraw et al., 2014). Preferred food items, often ripe fruit or young leaves, can be eaten alongside the modified described staple fall back foods (Marshall and Wrangham, 2007). Many frugivorous species have to survive drastic changes in food availability, often by choosing to ingest a larger variety of plant parts as well as possibly insects (Beeson, 1989; Gould et al., 2011; Norconk et al., 2009; Ossi and Kamilar, 2006; Terborgh 1984). Less is known about how exudativorous or insectivorous primates respond to such seasonal changes.

Gums as a food resource have been reported to be of little nutritional value, containing low levels of crude protein, virtually no lipids and mostly comprising soluble fiber (Nash and Whitten, 1989). To gain energy from such food, species exploiting them must possess the capacity for fermentation, as well as the ability to cope with plant secondary metabolites (PSM). Given both of these anti-feedants (high fiber and PSMs), gum is described as a fallback food for many primate species (Smith et al., 2010), especially also because it is usually available year round and can act as a staple or filler fallback food. Increasing proportions of gums are consumed by many primate species during the dry season when fruits or young leaves are less accessible such as for the grey mouse lemur (*Microcebus murinus)*, Senegal bushbaby (*Galago senegalensis)*, the giant mouse lemur (*Mirza coquereli*), a number of tamarins (*Saguinus spp.*) and marmosets (*Cebuella* and *Callithrix spp.)*, squirrel monkeys (*Saimiri sciureus*), red-tailed monkeys (*Cercopithecus ascanius)* and yellow baboons (*Papio cynocephalus*) (Chapman et al., 2002; Dammhahn and Kappeler, 2008; Garber, 1984; Hladik et al., 1980; Oates, 1984; Porter et al., 2007; Raboy et al., 2008; Sugiyama and Koman, 1992; Stone, 2007). Gum was considered a fallback food in these studies.

Slow lorises display a suite of morphological adaptations that are centered on exploiting exudate food sources, and it is now widely accepted to categorize them as exudativorous primates (Burrows et al., 2015). Although originally suggested to be frugivorous based on comparisons with pottos (Charles-Dominique, 1977), wild field studies have clearly demonstrated that slow lorises (*Nycticebus*) are specialized exudativores (gum specialists) (Nekaris, 2014). The largest of the lorisines (1.1-2.4 kg), the Bengal slow loris (*N. bengalensis*) has been observed spending the majority of its feeding time on exudates (Pliosugnoen et al., 2010; Swapna et al., 2010), with only 4.45% time spent eating fruit (Das et al., 2014). The smaller bodied pygmy slow loris (*N. pygmaeus*) (350-550 g) has rarely been observed to ingest fruit in the wild, focusing on a diet of gum, nectar and insects (Streicher 2009; Starr and Nekaris, 2013). A three-month study of the Javan slow loris (900 g), *N. javanicus* found that the majority of feeding time was spent on exudates, insects and nectar (Rode-Margono et al., 2014). In peninsular Malaysia, Wiens et al. (2006)

found two-thirds of the diet of wild *N. coucang* (650-850 g) was exudates (Barrett, 1984; Wiens et al., 2006). None of these studies however quantified the nutritional content of slow loris diets.

Quantitative feeding ecology research has allowed for a deeper understanding of primates' differing strategies to seasonality (Norscia et al., 2006). The framework of nutritional geometry (FNG) alone has allowed for in-depth analyses of how species react during lean seasons as population or refined sex-specific strategies, especially concerning reproductive costs (Ganzhorn, 2002; Pichon and Simmen, 2015; Rothman et al., 2008). The FNG's unique characteristic allows the simultaneous portrayal of an animal's response to resource availability. For example, this method has been used to define empirically the term 'lean season' as well as quantitatively identify if any food items are being used as a fallback food with quantitative data (Felton et al., 2009; Simpson and Raubenheimer, 2002). It is an integrative framework and allows inclusion of multiple food components, and is not limited to two axes. By characterizing two of three nutritional parameters, the third can be implied in geometric space, and a three-dimensional model of major nutrient intakes can be displayed. Alternatively, the methodology can also graph the relative importance of one nutrient relative to others through time. It also allows to model single individual or entire population nutrient intakes'. With primates, this methodology has been successfully applied to Peruvian spider monkeys (*Ateles chamek* - Felton et al. 2009), Chacma baboons (*Papio ursinus* - Johnson et al., 2013), mountain gorillas (*Gorilla beringei* - Rothman et al., 2011), Bornean orangutans (*Pongo pygmaeus* - Vogel et al., 2012), guereza (*Colobus guereza* - Johnson et al., 2015) and two strepsirhines, diademed sifakas (*Propithecus diadema* - Irwin et al., 2014, 2015) andwhite-footed sportive lemurs (*Lepilemur leucopus* - Droscher et al., 2016).

In this study, we aim to describe quantitatively the seasonal feeding strategies of an exudativore, using the Javan slow loris as a model species. We examine the presence of a lean season by measuring energy intake between seasons and to determine if gum is indeed a fallback food by analyzing its usage, rather than intrinsically labelling it by using food intake rates to plot nutrient intake per season. To rule out other possible theories of fallback food usage, we report the seasonal proportions of time spent feeding on food items as well as intake for both sexes and seasons to control for sex-specific changes in food habits.

MATERIALS AND METHODS

Study site and subjects

We analyzed data from free-ranging Javan slow lorises (n=15) in an agro-forest environment on the active volcano Mt. Papandayan, surrounding the village of Cipaganti (S7°6'6"-7°7' and E107°46' - 107°46'5") in West Java, Indonesia, between June 2014 and June 2015. Nekaris initiated a long-term study in the area in 2011. The agro-forest mosaic consisted of agricultural plots interspersed among between thick rows of various trees, bamboos and undergrowth plants. This habitat enabled generally good visibility of the slow lorises despite high human presence and disturbance. Although modified, the habitat provided a variety of both preferred and avoided plant species of varying nutritional quality. We caught slow lorises by hand and collared them following previous protocols (Rode-Margono, et al., 2014) with radio collars (BioTrack, UK – 16 g on average, 1.9% of body weight). We tracked the slow lorises using a six-element Yagi antenna and SIKA receiver (BioTrack, UK) and observed them using next generation LED headlamps with a red filter (CluLite, UK). In order to calculate activity periods, we equipped four individuals (male n=2, female n=2) with ActiWatch Mini Loggers (CamnTech, Germany) on their radio collar for four months, allowing us to multiply quantified intake rates by the appropriate activity times. We set epoch lengths at every minute at 100% intensity. The field site is near the equator and day lengths vary little throughout the year (Rode-Margono, and Nekaris, 2014).

We also observed captive Javan slow lorises (n=10) at Cikananga Wildlife Rescue Centre (CWRC - S7°03'27.04" and E106° 54'36.63"), near Sukabumi, West Java, Indonesia. We conducted gum intake rate trials at CWRC on ten individually housed adult Javan slow lorises (male n=5, female n=5).

Observational data

Although Java is classified as aseasonal, we defined two clear climatic periods that we hereafter refer to as seasons. We defined the “wet season” as receiving more than 60 mm per month (November to April) (Rode-Margono and Nekaris, 2014). The “dry season” ranged between 5 and 60 mm of rainfall per month between May and October. We followed radio-collared slow lorises in two observation periods during the night, from 18:00h to 0:00h and 00:00h to 06:00 h, each covering one different animal per period. Every individual slow loris was observed on a random schedule to prevent bias, however all observations were counterbalanced throughout the wet and dry seasons. We caught each slow loris at least every six months for a health check that included weighing using a hanging clip scale (Pesola). We used values for 13 adult or sub-adult slow lorises with weight information (female n=42, male n= 29) obtained between 2012 and 2015. Females may have been gestating when weighed, resulting in higher BW. This factor is not an issue with regards to analysis as these variations may impact the nutrient intake of gestating females, and understanding this strategy is essential to comprehend their natural feeding ecology. . We used instantaneous behavior sampling (Altmann, 1974) with a 15-minute interval as well as all-occurrence feeding behavior sampling (Nekaris and Rasmussen, 2003). We collected data on a total of 256 days over the course of 12 months (1470 hours, 5.8 hours/night average), totaling 7191 instantaneous points of data. At each instantaneous sample point where the slow loris was observed feeding, we recorded the category of food being consumed and plant species. During all occurrence sampling, we recorded the category of food being ingested, plant species, and the measurement of intake. We recorded gum feeding only when a slow loris was visibly ingesting tree gum and not simply gouging the tree cambium; we recorded duration in seconds. We defined nectar feeding as a slow loris using its tongue to lap up nectar without consuming the flower; we recorded the number of flowers visited. If one flower was revisited, it was not counted again for that evening. We defined fruit feeding as a slow loris eating the non-flower reproductive plant part. We noted if the seed(s) was/were ingested or not, and recorded the leftover weight after consumption. After the slow loris moved away, we approached the left over fruit and collected the leftovers and placed them in a sealed plastic bag. It was impossible to identify the insects being eaten. We thus could only record the size of the insect in relation to the slow loris' hand(s). We thus divided insect feeding into three size categories small (much smaller than the palm of one hand, caught with mouth or one hand), medium (caught in air or on substrate with one hand with the insect being roughly the same size as the slow loris’ hand) and large (caught with two hands, insect being larger than one of the loris’ hands) with number caught consumed being recorded (Nekaris and Rasmussen, 2003). For leaf eating, we noted whether a leaf was mature or immature and how many were consumed. We defined flower feeding as the consumption of flower reproductive parts, with the amount of flowers ingested. We calculated the average amount of nectar within one *Calliandra calothyrsus* (Fabaceae*)* by sampling 100 inflorescences, totalling 451 flowers and measuring the volume of nectar within each flower using a microcapillary tube. The average quantity of nectar obtained was 22.55 (SD ±1.82) µL. The average fresh weight of each food item quantified was: 2.5 g (SD ±0.06) for flowers, 1.2 g (SD ±0.03) for young leaves, 83 g (SD ±4.20) for persimmons (*Diospyros kaki,* Ebenaceae), 990 g (SD ±130.55) for jackfruit (*Artocarpus heterophyllus*, Moraceae), 0.010, 0.60 and 1.1 g for small medium and large insects respectively.

Captive gum intake rate trials

We harvested one kg of wild gum from the Cipaganti field site and transported it fresh to CWRC. We fed each of the ten slow lorises (weight range 862 to 1020 g) 10 g of the wild gum (*Acacia decurrens,* Fabaceae, the same species we observed being ingested by the wild slow lorises) and, using a stopwatch, recorded the amount of time required to eat this 10 g. If consumption stopped, or the slow loris became disinterested, we stopped the stopwatch until ingestion resumed. We repeated this experiment on two separate occasions one week apart with each slow loris observed on the same night. We provided the gum by placing it in wooden logs, each cut to 20 cm long, with a deep longitudinal groove, 5 cm deep.

Intake rates

We used the equation (equation 1) to calculate food intake rate F (gram/hour), for individual *i*, for food item *f* and for season *s*, modified from Rothman et al. (2008). We summed the collected measurement of intake data for individual *i* of food *f* during season *s* and multiplied it by the intake rate (I) of food *f* to transfer the intake into grams. Recorded values for I (as fresh weight) are: 0.0212 g/sec for gum, 0.002255 g/flower for nectar, 50 g/fruit for persimmon, 475 g/fruit for jackfruit, 0.010, 0.60 and 1.1 g/insect for small, medium and large insects respectively, 2.5 g/flower for eucalyptus flowers (*Eucalyptus* spp.) and 1.2 g/leaf for young bamboo leaves (*Gigantochloa cf. ater*). The total sum was divided by the amount of hours (H) individual *i* was observed during season *s*.

(Eq 1) $F_{ifs} = \frac{\sum_f W_{ifs} I_f}{H_{is}}$

We averaged values obtained by equation 1 to yield average daily values for the wet and dry season for the entire study population as well as for each sex separately. Values reported include seasonal daily averages only, similar to Irwin et al. (2015) due to the widely variable counterbalancing of observations for each individual.

Phenology and insect availability

We organized five 10 m by 10 m phenology plots in random locations using a GIS map at five different altitudes inhabited by slow lorises: 1200, 1300, 1350, 1500 and 1600 m above sea level that contained 21, 14, 54, 13, 23 adult trees and bamboo species, respectively. A total of 16 different tree and bamboo species occurred within our plots, which is representative of the agro-forest environment. We did not count domestic crop plants in the phenology plots. We modified methods from Chapman et al. (1999). We numbered and labelled trees and each month scored those with a diameter at breast height (DBH) ≥ 5 cm for the amounts of young leaves, mature leaves, flowers, unripe fruits, and ripe fruits. The scoring system used included: 0 = none present, 1 = 0-50% of capacity reached and 2= ≥ 50% of the capacity was reached.

For insect availability, we calculated catch density using a malaise trap and three sticky traps twice a week for the duration of the study (Benton et al., 2002). We used both trap types in three different locations that we rotated weekly. We placed the malaise trap only in areas between trees used by the slow lorises and placed sticky traps on trunks and branches of trees often frequented by slow lorises. We divided the weight (g) caught for each month by the total weight caught over 12 months and used them as gross indicators of availability for each category. We sampled insects according to Rode-Margono et al. (2015) using a malaise trap and three different sticky traps nightly. Catch rate was so low that it was not possible to obtain a large enough mass for the three different size categories of insects recorded in this study (small, medium and large). Therefore, we combined the samples of all three insects into proportions reflecting their yearly intake; thus one analyzed sample reflected the weighted yearly intake.

For plant availability, we tallied the frequency of each plant part consumed per species of plant and averaged the values monthly to equal a mean availability score of the field site for each possible food source per month. We averaged these in turn to obtain a mean availability score for the entire study period for each food item. To determine if food items were being eaten in proportion to their availability, we plotted the mean yearly availability score for each food type against the yearly contribution of that food source for each individual slow lorises diet (based on intake weights) as per Johnson et al. (2013). We used a Spearman's Correlation test to determine if the contribution of food items to the diet correlated with their availability.

Sample collection and chemical analyses

We collected any food item for chemical analyses that we observed being ingested by any wild slow loris. We collected at least 500 g (fresh weight) of the food item from the trees actually fed on. We only analyzed the plant part ingested by the slow lorises. If more than one tree of the same species was fed on for the same food item, we took samples from many different trees and pooled the results in order to create a representative sample. We weighed samples and placed them in trays wrapped in mosquito netting and dried them in indirect sunlight for two days (24 hours' worth of sunlight) with temperatures reaching up to 32°C within the tray. We then reweighed dried samples and placed them in plastic sealed bags with silica gel packets, and then placed them in another plastic bag of silica gel. We placed all samples in a cooler in a dry equipment room until transported for laboratory analysis.
We conducted nutrient analyses in the Nutrition Laboratory of Lembaga Ilmu Pengetahuan Indonesia (Indonesian Institute of Sciences, also known as LIPI) in Bogor, West Java, Indonesia. Nutritional analyses followed Norconk and Conklin-Brittan (2004). We estimated crude protein (CP) by the Kjeldahl method for total nitrogen, multiplying results by 6.25 (Norconk and Conklin-Brittain, 2004; Pierce et al., 1958), we determined total ash by incinerating the sample (0.5 g) at 550°C overnight in a muffle furnace; we determined crude fat by ether extract for four days (Williams, 1984), free soluble sugars via phenol/sulfuric acid colorimetric assay, calibrated for sucrose (Strickland and Parsons, 1972), and total non-structural carbohydrates (TNC) by calculation (equation 3). We analysed fibers as neutral detergent fiber (NDF) and acid detergent fiber (ADF) using the Van Soest method (Van Soest, 1996).

It was not possible to collect enough nectar for standard chemical analyses, therefore, we used 85 *u*l microcapillary tubes to measure the average volume of nectar in each flower (Morrant et al. 2009), and we used a portable hand-held refractometer to estimate soluble sugar contents as per Bolten et al. (1979). We only observed the nectar of *Calliandra calothyrsus* being ingested; therefore we sampled 100 inflorescences, totaling 451 flowers. Energy values of each food item were calculated as per Irwin et al. (2012) in equation 2, by summing up the caloric energy values for each macronutrient:

(Eq 2) $E= (CP*4) + (CF*9) + (TNC*4) + (NDF*1.6)$

Where E is total energy in Kcal, CP is percentage of crude protein in DM, CF is crude fat in DM and TNC is total non-structural carbohydrates in DM. Total non-structural carbohydrate amounts were calculated by equation 3 where A is ash. Our gross estimate for TNC does not include the fiber fractions of neutral detergent fiber (NDF which is an estimate for lignin, cellulose and hemi-cellulose (Van Soest, 1994). The digestive system of *Nycticebus* is morphologically adapted to ferment some amount of plant fiber matter, although not yet quantified (Stevens and Hume, 2004). We assume the Javan slow loris is able to digest approximately 40% of NDF intake, resulting in an assimilation of 1.6 kcal/g of NDF based on the hindgut-fermenting chimpanzee (*Pan troglodytes*) (Conklin-Brittain et al. 2006). We may be overestimating our energetic modelling as this is a starting point for understanding slow loris feeding ecologies (Sayers et al. 2010).

(Eq 3) $TNC=100-A-CP-CF-NDF$

Data analyses

We determined average seasonal nutrient intake amounts (*N*) for nutrient *n* ingested by individual *i* during season *s* using equation 4. We multiplied the sum of the food intake rates (eq 1) for food *f* for individual *i* and season *s* by the fresh matter content (*M*) of nutrient *n* for food *f* were added up and multiplied by the activity period *A*. We averaged every individual average daily intake for each nutrient to determine the average daily seasonal intake of each nutrient. This was used to calculate protein energy (PE) by multiplying the crude protein amount by 4 kcal/g, and calculating the non-protein energy (NPE) by multiplying TNC by 4 kcal/g DM, NDF by 1.6 kcal/g DM, and crude fat by 9 kcal/g DM and summing.

(Eq 4) $N_{nis}=(\sum_{n} F_f M_{nf})A$

We employed right angle mixture triangles (RMT) to visualize which energy source was variable and which was controlled between the seasons. We plotted the proportions of protein, total carbohydrates and crude fat energy against each other on a scatter plot in all combinations, leaving the outlier to be interpreted as the implicit axis (Raubenheimer, 2011). We plotted the average daily PE versus NPE for both dry and wet season. We also plotted the average daily seasonal intake of protein in grams versus combination of fat and carbohydrates for males and for females in order to determine if they adopt different strategies seasonally. For this graph only we used adults, reducing numbers to n=7 (males) and n=8 (females).

After we checked that there was no multicollinearity between the independent variables by using a linear regression analysis (VIF values between 1.000 and 1.150), we used a Generalized Linear Mixed Model (GLMM) with an identity link function and inverse Gaussian distribution of the response variable (based on visual inspection) to determine the effect of sex and season on nutrient intake and proportion of the diet food items. Nutrients we tested were crude protein, crude fat, NDF, ADF, carbohydrates, TNC, total energy and protein:non-protein energy, obtained from proportions of the various diet items (gum, nectar, fruits, insects, flowers and leaves), all using the seasonal average daily intake data in grams for each individual. Individual was used as a random factor in the GLMM. We conducted all statistical analyses in SPSS 22 (IBM Software).

RESULTS

We recorded the slow lorises feeding on six plant species and various insect species (Table 1). Each plant species was used for one plant part whether it was gum, fruit, young leaf, etc. We only observed the mesocarp of fruits being eaten; slow lorises discarded the skin and seeds. Slow lorises ingested insects in their entirety; legs or wings were not removed. Lastly, we did not observe any mature leaves being eaten, only young leaves. The activity loggers revealed an average active cycle of 11.95 hours (SD ± 0.12), which we rounded up to 12 hours for the purpose of our average daily nutrient intake. Results of the captive gum intake trials resulted in a rate of 0.021 g/s (SD ±0.006) (n=10).

We found the average sugar content in *Calliandra* nectar to be 22.82 (SD ±5.12) Brix, which equates to 253 g of sugar per L of nectar, which we estimate to be 98% of DM and 22.55% as fed (AF). Average hourly intake rates for each food items' category under both seasons and also yearly were tabulated in table 2. The average seasonal proportions of each feed category of instantaneous and intake data do not match, presenting different magnitudes of consumption (fig. 1). The phenology and proportion of diet correlation were not significantly correlated (rho=0.192, P=0.070, n=84), which points to an aseasonal use of these resources (fig. 2).

The average daily intake ratio of protein (PE) and non-protein energy (NPE = fat + TNC+ NDF) for both the dry and wet seasons for each individual (wet n=15 dry n =15) is depicted in figure 3. Non-protein energy was more important during the dry season with a slope of y=1.018x, SD ± 0.38 (R^2=0.8057), where y is NPE and x is PE, than during the wet season (y=0.723x, SD ± 0.52 R^2=0.8374). The point with the highest protein content has no significant effect on the results of this figure as its removal alters the wet season ratio to y=0.793x.

We used right angle mixture triangles (RMT) to graph which macronutrient was used as a consistent and controlled energy source for both the dry and wet seasons, where the implicit axes was fat (fig. 4A), carbohydrates (fig. 4B) and protein (fig. 4C). The proportions were tightly controlled as they demonstrated similar patterns across seasons. The proportion of fat energy was constant throughout the year (~20%). The energy from protein and carbohydrates could be used interchangeably year round.

The average weight of adult female Javan slow lorises during the wet season was 930.07 g (± 71.28) versus 844.31 g (± 97.46) for the dry season. The male's weight was 898.05 g ± 74.01 in the wet season, and 887 g ± 80.93 in the dry season. Overall average weight for our study individuals over three years of data was 900.47 g (± 83.46).

The results of the GLMM show that females had a higher intake of crude protein (B=+0.314 SE= 0.7400), gum (B= +15.953 SE= 37.5419), fruit (B= +4.875 SE= 20.0763) and insects (B= +20.081 SE= 17.3900) and males had a higher intake of ADF (B= -0.840 SE= 0.4437); season had a significant effect on ADF (B= -1.328 SE=0.4917), gum (B= +18.493SE= 38.8800), insects (B= +25.933 SE= 19.2735), flowers (B= -36.145 SE= 16.25) and leaves (B= 46.45 SE= 13.94). The interaction between sex and season had an effect on ADF (B= +0.994 SE= 0.305), flowers (B= +27.88 SE= 10.0839) and leaves (B= -19.999 SE= 8.6488) (Table 3).

DISCUSSION

Characterizing the diet of the Javan slow lorises

Our data indicate that the Javan slow loris consumes a narrow range of food items found within the study area (table 1). As a note of caution, we acknowledge that the nature of our field site, with crops and planted trees and bushes with economic value, may provide different sources of food and nutrients from Javan slow lorises found in primary forests. Plant diversity, nutrient intake and phenology could vary significantly, potentially resulting in different results than observed here. However, since our studied slow loris population is breeding regularly and thus is likely to receive an adequate nutrition we believe that our results represent a valid contribution for future comparisons with other *Nycticebus* studies. Although the field site was largely affected by anthropogenic disturbances, our results may be indicative of slow loris evolutionary adaptations rather than a mere result of disturbance. For example, fruit and other food items (flowers and leaves) were available year round and yet the individuals chose to ingest gum as a majority food item. All other studied slow loris species (studied in secondary or primary forests) also reported an exudate and insect based natural diet (Starr and Nekaris, 2013; Das et al. 2015; Wiens et al. 2006). Future studies in secondary or primary forest areas are necessary to obtain more robust conclusions in support of the observed trend.

As expected, gum was the staple food of this exudativorous primate ranging from 38 to 60% of diet intake, being exploited in both the wet and dry season (fig. 1). The Javan slow loris exhibited the same gouging feeding behaviors as described in Nekaris (2014), which is similar to all *Nycticebus* taxa studied thus far. The slow lorises would anchor their lower mandible into the cambium and use the upper maxilla to bite into the tree and remove pieces of cambium. This process is repeated until the desired size and depth has been reached to stimulate gum production. Along with gum, we also recorded insect feeding during the majority of observation periods. Nectar from the flowers of *Calliandra calothyrsus* was seasonally consumed, as the flowers mostly bloom during the wet season, although a small amount was also present in the diet during the dry season.

We observed the slow lorises ingesting a variety of plant parts rarely reported as part of the slow loris diet. They targeted the young leaves of only one of three bamboo species available, *Gigantochloa* cf. *ater* as well as the flowers of *Eucalyptus* spp.; both of which contained high levels of NDF (> 40 %). Following the Jarman-Bell rule (Gaulin, 1974), the larger size of *N. javanicus* would allow it to subsist on a diet that contains more fermentable food items when compared to the smaller *N. pygmaeus,* which has a higher amount of insects within its diet (Starr and Nekaris, 2013). The total amount of potentially fermentable plant food items (gum, leaves, flowers) is still lower in proportion than what was observed for the largest *N. bengalensis*, which theoretically should have the largest fermentation capacity of the slow lorises due to its large size (Das et al., 2014). With an average weight of 900 g, *N. javanicus* may have similar fermentation capabilities as the 1 kg white-footed sportive lemur (*Lepilemur leucopus*), which is entirely folivorous, as both genera exhibit complex large intestines with a well-developed cecum (Droscher et al., 2016). However differences in gut microflora, surface area and presence of diverticula will impact fiber digestibility. A complete diet necessitating fermentation is predicted to be energetically sustainable only for a primate with a mass is greater than 700 g (Kay, 1984). Javan slow lorises are at the cusp of reaching the metabolic weight where it would be very difficult for them to consume enough insects to meet their energetic requirements (Rothman et al., 2014). Both Kay (1984) and Rothman et al. (2014) do not factor in the reduced metabolic rates of strepsirrhine primates, that at this weight, may potentially allow them to flow between a more fermentable diet or a more insect based diet to meet their needs. This potential flexibility is consistent with our observations as the intake of insects ranged from 12 % of intake during the dry season to 27 % during the wet season.

Lastly, we observed fruit feeding rarely within our field site. Only two fruits were ingested, the domesticated persimmon (*D. kaki)* and jackfruit (*A. heterophyllus*). Jackfruit was available year round but we only observed one instance of feeding, and persimmon was heavily abundant between late dry seasons until early wet season, yet we only saw four feeding bouts of this food item (fig. 2). Other domestic fruits widely available but never seen to be consumed by Javan slow lorises included banana, mango, avocado, guava, custard apple, snake fruit, and rambutan. Indeed the avoidance of these abundant fruits further reinforces the current body of evidence that *Nycticebus* are not frugivores. Although gum is overall a low quality food item and may fit the description of a fallback food for many species (see Smith, 2010), it comprises the majority of the diet of *N. javanicus* even when other food items were available, providing evidence that gum is an obligate food source for the Javan slow loris. Being the only venomous primate, slow lorises are hypothesized to ingest specific compounds from one or more of their food items and metabolically alter it to bolster their biologically produced venom (Nekaris et al., 2013). Gum or noxious insects may potentially contain the necessary compound(s), perhaps making gum even more important than solely for nutrition. Future analyses are necessary to clarify this aspect.

Seasonal feeding ecology

The Javan slow lorises employed two different nutritional strategies between the abundant wet season where protein energy was easier to obtain, and leaner dry season that necessitated a more important non-protein energy income. The varying seasonal availability of food items such as leaves, flowers, nectar and insects meant that the slow lorises had to alter their feeding intake in order to balance their needs between seasons (fig. 3). Although energy amounts may seem low in respects to representing average daily amounts, Figure 3 corresponds to intake ratios, similar to Johnson et al. (2015), who also observed some small amounts and did not control for outliers. The dry season has lower food abundance than the wet season; however it was not as drastic as lean seasons described for other primates (Curtis 2004; Felton et al., 2009; Rothman et al., 2006) since it allowed for the slow lorises to maintain their overall energy intake. During the dry season, NPE:PE shows a shift towards non-protein energy, whereas during the wet season, protein energy becomes favored. The wet season has an abundance of all food types, which would allow the free-ranging slow lorises to select their intake from a larger variety of food items. The main source of protein for this population of *N. javanicus* is insects, whose ingested amounts are significantly affected by season, i.e. much higher in the wet season (table 3). Feeding on insects during the wet seasons apparently led to both a relatively constant proportion of energy from fat and a higher protein intake than during the dry season, when energy needs drove a higher carbohydrate (gum) intake. High NPE foods such as nectar, flowers and leaves, whose average daily-ingested amounts were also affected by season, are also exploited more during the wet season.

Diet switching is a strategy used by slow lorises seems to be a response to variations in food availability. This trend was also observed by the generalist *Propithecus* (Pichon and Simmen, 2015; Sato et al., 2015). *Eulemur* spp.*,* fruit specialists, did not employ diet switching, but instead resorted to a cathemeral lifestyle and increase total foraging time (Sato et al., 2015). This option is not available to the nocturnal slow loris, as our data-loggers indicate an essential lack of activity during the day. Mountain gorillas (*Gorilla beringei)* over-eat protein to reach carbohydrate energy requirements, which is a strategy that would not apply for slow lorises considering their main food items are exclusively high in either carbohydrates (gum) or in fat and protein (insects) (Rothman et al., 2011). The overall strategy of diet switching, however, is still possible. Exudativorous primates such as the slow loris should be able to find tune their nutrient intake throughout the seasons by balancing the intake of different food items, which is supported by our data. *Nycticebus javanicus* were thus able to manage their nutrient intake during temporary shifts of availability using nutritional strategies similar to generalist leaf-eating primates.

The analysis of the proportion of energy ingested from fat, carbohydrates (TNC and 40% of NDF) and protein in a right-angle mixture triangle depicted a tightly controlled response to seasonal food availability (Raubenheimer et al., 2015). Fat energy intake is relatively constant throughout the year while protein and carbohydrates are used somewhat interchangeably without regards for seasonal food availability (fig. 4). This strategy is different than what has been observed in *Colobus guereza* where carbohydrates and fats are used interchangeably, both of which are the major energy providing macronutrients (Johnson et al., 2013). Chimpanzees exhibit a trend similar to slow lorises, decreasing protein during the lean season, substituting it with carbohydrate energy also being able to adjust between them (Conklin-Brittain et al., 1998). The main source of fat for the slow lorises is insects, and the stable and relatively low proportion of fat energy of the diet suggests the slow lorises are controlling their intake. The main source of carbohydrates was from gum, which must be consumed as the main source of available energy. The intake of gum and insects seem to be finely balanced throughout the year. Young leaf specialist *Avahi meridionalis* branched out into broader folivory during the lean season, selecting from a large array of lower quality leaves. During this time they must cope with a higher fiber and lower protein intake, also increasing their structural carbohydrate intake during their lean season (Norscia et al., 2011). In this study, gum intake was significantly affected by season, which supports these observations (table 3). Although gum is available year round, reliance on it as a food item and source of energy increases during the dry season hence NPE energy intake is more prominent during the dry season. The variation between energy proportions of this triangle mixture may be largely due to the seasonal intake of the nutrient dense insects (also significantly affected by season in the GLMM). During the abundant wet season, insects are easily available and their intake balanced alongside flowers, leaves and gum which may explain variations observed in total NPE:PE ratio. The frugivorous atelines preferred to over-eat food items, therefore over-consuming carbohydrates and fat in order to reach their protein requirements (Felton et al., 2009) whereas *N. javanicus* can interchangeably use the proportions of foods eaten in order to ensure minimal requirements. Further evidence that *Nycticebus* spp. are employing a mix of strategies to cope with varying seasonal food availability are necessary; again, however, their strategies appear to be more akin to folivores than frugivores.

The effect of sex on nutrient selection

Crude protein, ADF, gum fruit and insect intake were all shown to be significantly affected by sex of the slow loris (table 3). Males and females form pairs where both individuals have their own superimposed territories; hence, it would appear that the seasonal abundances within each individual's territory can explain some amount of these differences or we would have observed similar patterns amongst the sexes from varying territories (Nekaris, 2014). Although males and females are comparable in mass, the energetic costs of reproduction may place a burden, which requires a larger demand for females, as shown by O'Mara and Hickey (2014) where female *L. catta* became much more efficient and selective during periods of lactation (and higher energy/nutrient needs). Acid detergent fibers are composed mainly of lignin and cellulose found in all plant food items except gum. Our results in Table 1 include a value for ADF although theoretically this component should not be present. Both ADF and NDF represent variable and complex carbohydrates; although analyses were properly conducted; different soluble fibre fractions may also be measured in these assays, depending on the sample matrix (Hall, 2003; 2007). Both females and males increased their protein intake during the wet period; this increase is expected since they included more insects in their diet during the wet period, this is expected since insects were a larger proportion of their diet during the wet season. While the response of a male may vary, female strepsirrhines in general tend to increase their protein intake seasonally more so than males (Gould et al., 1999; Gould et al. 2011; LaFleur and Gould, 2009; Meyers and Wright, 1993; Overdorff, 1993; Rasamimanana and Rafidinarivo, 1993; Sauther, 1994; Yamashita et al. 2015; Vasey, 2002). Fruit intake was similar between seasons yet we observed females consuming more fruit than males (4 bouts versus 1), possibly due to their higher energetic needs, especially during the dry season. They increase NPE intake by increasing gum intake, of which a larger amount was ingested during the dry season. Although not ingested in particularly large amounts, the seasonal intake of flowers and leaves may also be a significant source of fermentable fiber energy for females as its intake was affected by an interaction between sex and season. Although small overall amounts, we cannot dismiss them as unimportant. Being a potentially available source of energy, leaves, flowers, and gums may have provided essential energy and fiber as well as other micronutrients not measured here (i.e. vitamins, minerals). The results from the GLMM were all supported by our data and observations.

The exudativorous *N. javanicus* seems to follow a foraging strategy more closely resembling a generalist folivore, rather than a frugivore. At our field site, the lean season was characterized by a qualitative decrease of food items (flowers, leaves, insects and nectar) (Ganzhorn, 1992). Generalist frugivores should preferentially ingest fruit when it is available yet broaden their range of food items ingested during the lean season (Norscia et al., 2006). These diets are expected to result in an overall decrease in protein and digestible carbohydrate intake during the lean season but will recover in the following season, possibly causing seasonal fattening. These food choices are based on nutritional composition. Calculations for dietary energy value estimates are based on many assumptions, often extrapolated from chemical analyses of unique feeds (for which the assays may not be explicitly validated), as well as digestibility/metabolizability data based on the most suitable physiological models, in this case, both human and non-human primates. Until more detailed experimental data are specifically derived describing digestibility and fermentation in the slow loris, these estimated values represent our best efforts to document and clarify nutrient utilization by exudativorous primates.

Slow lorises were able to manage their nutrient intake meticulously and maintain constant contributions of fat energy while using carbohydrate and protein interchangeably. NPE was prioritized during the dry season probably due to their higher gum intake, similar to the energy and protein maximization rule described in Altmann (2006). Leaf eating primates will prioritize protein only if protein is limiting in their environment (Ganzhorn et al., 2016). The only significant source of protein for our slow lorises was insects, with their availability decreasing in the lean season. The slow lorises were able to continue ingesting protein to meet their requirements. Their protein intake became more consistent in its proportion with crude fat and carbohydrates when protein was difficult to find. This behavior is also consistent with the behavior of a generalist leaf eating primate. The slow lorises were able to control their NPE:PE as thoroughly as some generalist species (Johnson et al., 2012; 2015), which is consistent with slow lorises following an energy and nutrient maximization strategy.

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