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NUTRITIONAL GEOMETRY OF FEMALE CHIMPANZEES (*PAN TROGLODYTES*)

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Abstract

Primate foraging is influenced by the spatial and temporal distribution of foods, which may facilitate or constrain optimal nutrient intakes. Chimpanzees are frugivorous primates that mainly subsist on ripe fruit that is typically low in available protein (AP) and high in easily digestible carbohydrates. Because chimpanzees prefer ripe fruit and often eat it in large quantities compared to other foods, we hypothesized that protein intake would be tightly regulated while non-protein energy (NPE) would vary with fruit intake. To test this hypothesis, we conducted all day follows on female chimpanzees, recorded all types of food consumed (i.e., drupes, figs and non-fruit foods), estimated the nutritional contributions of these foods to daily NPE and AP intake and investigated how the ratio of NPE to AP varied due to changes in the types of foods consumed. Although the proportions of drupes, figs and non-fruit foods varied in their diets, female chimpanzees maintained a relatively stable intake of AP while intake of NPE varied depending on the daily diet, demonstrating that like other frugivorous primates studied to date, chimpanzees prioritize protein. The mean daily ratio of NPE to AP was 7:1, which is similar to that of other frugivorous primates studied. Our results support the hypothesis that frugivorous animals may generally prioritize AP, while maximizing NPE intake within that constraint, and could shed light on aspects of human dietary evolution.

Keywords

diet composition; macronutrient balancing; nutritional geometry; eastern chimpanzees

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DATA AVAILABILITY
The data that support the findings of this study are available from the corresponding author with permission from Prof. Richard Wrangham upon reasonable request.

INTRODUCTION

Wild primates are frequently faced with the challenge of meeting their nutrient requirements in the face of seasonal and long-term fluctuating food resources (Conklin-Brittain, Knott, & Wrangham, 2006; Knott, 1998; Masi et al., 2015; Rothman, Dierenfeld, Hintz, & Pell, 2008; Vogel et al., 2017; Wallace, 2005). This challenge is exacerbated because foods available to primates are typically imbalanced in the nutrients they provide and no single food or food category (e.g., leaves, fruits, stems) can meet all primate nutritional needs (Conklin-Brittain, Wrangham, & Hunt, 1998; Milton, 1999). To overcome this, primates employ a diverse array of strategies. For instance they may adjust their densities, group size, spacing patterns and ranging patterns (Chapman, Chapman, Bjorndal, & Onderdonk, 2002; Ganzhorn, 1992, 2002; Hemingway & Bynum, 2005). Primates may also switch to low-quality foods when high-quality foods are scarce (Marshall & Wrangham, 2007; Vogel, Haag, Mitra-Setia, van Schaik, & Dominy, 2009; Watts, Potts, Lwanga, & Mitani, 2012). While several of these feeding strategies have been studied with respect to food compositions, there is a dearth of information on what is arguably the most important issue of all, how primates meet their nutritional needs under these differing constraints.

The dietary choices employed by different primate species to overcome nutrient reductions following fluctuations in food availability are largely geared towards acquiring food combinations that balance the intake of non-protein energy (carbohydrates and lipids) (NPE) and available protein (AP) (Lambert & Rothman, 2015; Raubenheimer, Machovsky-Capuska, Chapman, & Rothman, 2015; Simpson & Raubenheimer, 2012). These categories of nutrients fulfil specific physiological roles and are not functionally interchangeable. Non-protein energy is important for basal metabolic functions, muscular activity, tissue formation, reproduction and lactation, while protein and its constituent amino acids are vital for growth and maintenance of body tissues (National Research Council, 2003). Many studies have shown that an animal’s fitness is influenced by the specific mix of macronutrients eaten (Jensen et al., 2012; Simpson, Sibly, Lee, Behmer, & Raubenheimer, 2004), and not just the overall energetic intake as often assumed under optimal foraging models (Stephens & Krebs, 1986).

Periodic reduction in nutrient intake resulting from fluctuations in the availability of high-quality foods (foods rich in digestible energy or protein) could have fitness implications, and may adversely influence reproduction (Koenig, Borries, Chalise, & Winkler, 1997). Unlike males, female reproductive success is more strongly constrained by access to food resources (Wrangham, 1980), hence seasonal changes in high-quality food availability can result in decreases in energy intake thereby limiting reproduction. For example, the availability of sugar-rich foods has been associated with increased rates of sexual swellings and conceptions in female chimpanzees (*Pan troglodytes schweinfurthii*) (Emery Thompson & Wrangham, 2008) and Hanuman langurs (*Preshytis entellus*) (Koenig et al., 1997). In blue monkeys (*Cercopithecus mitis*), a shift in diet to low-quality or fallback foods (foods which are poor in digestible energy and protein) is associated with an increase in energetic stress which is negatively correlated with the individual’s fitness (Foerster, Cords, & Monfort, 2012).

The geometric framework of nutrition is an approach for modelling animal nutrition in a multidimensional, mixture context (Raubenheimer & Simpson, 1993; Raubenheimer, 2011; Simpson & Raubenheimer, 2012). Studies using the geometric framework have shown that the nutritional goal of foraging is to achieve a specific amount and balance of particular nutrients, termed the “intake target”, which in some cases has been shown to be the mixture that maximizes fitness (Jensen et al., 2012; Raubenheimer et al., 2009; Simpson et al., 2004). For example, frugivorous Bolivian spider monkeys (*Ateles chamek*) selectively ingest nutrient combinations that target a NPE:AP intake ratio of 8:1 (Felton et al., 2009a), while more folivorous mountain gorillas (*Gorilla beringei*) have a target NPE:AP ratio of 4:1 (Rothman, Raubenheimer, & Chapman, 2011). However, given the unpredictable fluctuations in food availability, wild primates may not be able to easily reach their intake targets in all seasons or environments. In such cases the animal is forced to trade-off between over-eating and/or under-eating some nutrients (Raubenheimer et al., 2009). This trade-off, also called the “rule of compromise”, is an important part of the foraging strategies of animals which has been found to vary among species (Raubenheimer et al., 2009). For instance, folivorous mountain gorillas in Bwindi Impenetrable National Park, Uganda consumed more available protein when leaves accounted for a higher proportion of the diet than fruit and maintained a stable intake of non-protein energy, irrespective of the proportion of fruit in their diet (Rothman et al., 2008; Rothman et al., 2011). In contrast, frugivorous spider monkeys maintained a stable daily protein intake while consuming more non-protein energy during fruit-abundant seasons (Felton et al., 2009a). Unlike folivorous gorillas, folivorous diademed sifakas (*Propithecus diadema*) maintained nutrient balance irrespective of the fluctuations in fruit availability, although total macronutrient intake varied (Irwin, Raharison, Raubenheimer, Chapman, & Rothman, 2015). These examples illustrate that the rule of compromise may differ among primate species, and most likely represents adaptation to particular ecological conditions.

Chimpanzees are generally frugivorous; every population that is studied consumes fruits though the proportion of different types of fig and non-fig fruits in their diet varies seasonally and spatially within the various habitats (Abwe et al., 2020; Basabose, 2002; Bryson-Morrison, Matsuzawa, & Humle, 2016; Lindshield, Danielson, Rothman, & Pruetz, 2017; Newton-Fisher, 1999; Tweheyo, Hill, & Obua, 2005; Wrangham, 1977; Wrangham, Conklin-Brittain, Chapman, & Hunt, 1991; Yamagiwa & Basabose, 2009). All chimpanzee populations studied to date consume non-fruit low-quality foods, whether ripe fruits are abundant or not (Wrangham et al., 1991); but the types of low-quality foods vary across locations (reviewed in: Harrison & Marshall, 2011).

The Kanyawara chimpanzees live in Kibale National Park, Uganda and eat forest foods. They are reported to prefer drupe-fruits (hereafter referred to as drupes) rather than figs (Wrangham et al., 1996). Drupes are rich in digestible energy and therefore considered as “high-quality foods” (Uwimbabazi et al., 2019; Wrangham et al., 1993). Unlike fig-fruits (hereafter referred to as figs) which are available and abundant all year round, drupes are rare and availability is unpredictable (Wrangham et al., 1996). During drupe-scarce periods, Kibale chimpanzees increase consumption of figs and non-fruit foods such as young leaves and pith (Uwimbabazi et al., 2019; Wrangham et al., 1996, 1991). This disparity in the types of foods consumed presents an opportunity to explore how female chimpanzees prioritise the intake of different macronutrients in the face of daily variation in diet composition (Raubenheimer & Simpson, 1997).

The aim of this study was to examine the nutritional strategy of the Kanyawara female chimpanzees in Kibale National Park, Uganda to test if chimpanzees follow a protein prioritization model as is observed in other frugivorous primates studied to date. Specifically, we examined how various foods contribute nutritionally to the chimpanzee diet by comparing food proportions in the diet to the proportions of daily nutrients they provide. Because Kanyawara chimpanzees prefer sugary fruit over proteinaceous young leaves and other fibrous non-fruit foods, we expected fruits to provide the most dietary sugar and lipid, while we expected young leaves to provide the most daily protein. Second, we investigated how the balance of NPE and AP varies according to intake of different food sources. We expected AP intake to be less variable than NPE intake. Lastly, we examined whether the mean daily ratio of NPE to AP is similar to the 8:1 mean daily ratio consumed by frugivorous spider monkeys (Felton et al., 2009a).

METHODS

Study site and subjects

Kanyawara is found in Kibale National Park (KNP) which is located in southwestern Uganda (0°13’ to 0°41’N and 30°19’ to 30°32’E) near the foothills of the Rwenzori Mountains. KNP covers an area of 776 km^2 (Chapman, Chapman, Kaufman, & Zanne, 1999) and hosts the largest population of chimpanzees in Uganda (Plumptre et al., 2007). Kanyawara experiences bimodal rainfall distribution with two dry (December to January and June to August) and wet seasons (March to May and September to November). Although peak fruiting periods have been registered at Kanyawara, they vary greatly between years, thus the fruiting period is not strictly linked to certain months or climate season (Chapman, Wrangham, Chapman, Kennard, & Zanne, 1999). Female chimpanzees of the Kanyawara community were observed by MU from January 2014 to June 2015. The Kanyawara chimpanzee community ranges in the northwestern sector of KNP and has been studied since 1983 (Isabirye-Basuta, 1988; Wrangham et al., 1991). At the time of this study, the Kanyawara community comprised 47 to 51 chimpanzees of which 17 were adult females. Fourteen lactating female chimpanzees who were fully habituated were selected as study subjects. Estimated ages at the start of the study were between 13.3 and 54.9 years.

Behavioral data, food sample collection and processing

We used the methods presented in detail in Uwimbabazi et al. (2019) to collect behavioral data and plant foods. These plant foods included ripe fruit, young leaves, seeds, flowers, pith, bark and wood from trees, lianas and other terrestrial herbaceous vegetation (THV). Field data collection was conducted from January 2014 to June 2015 using continuous focal observations (Altmann, 1974). Ideally each focal observation (or “follow”) started at dawn when the focal individual left her nest and ended at dusk when she made her sleeping nest. However, sometimes the focal individual had already left the nest before dawn, or we lost the focal individual before she entered her night nest at dusk. As much as possible, focal females were selected based on a rotating scheme to ensure that all individuals were sampled for a similar amount of time. In each month, focal observations were conducted for a mean of 14±2 days, with each individual sampled for at least one day per month. On average, each individual was subjected to 15±1 days of focal observations.

We defined a feeding bout as a continuous feeding session on a particular food item that is not interrupted by any non-feeding activity. We stopped counting the behavior as a feeding bout on a particular food item until a food switch, or the individual engaged in another behavior. The feeding bout continued until the animal stopped chewing (up to 5 minutes). During each feeding bout, we recorded the start and end time of feeding on the particular food item to the nearest minute, including the plant species, part ingested and its developmental stage (e.g., ripe or unripe fruit, young or mature leaf). We recorded the number of discrete food units (individual items e.g., one fruit, a strip of leaves or bunch of flowers) consumed per minute throughout the feeding bout.

Fresh samples of all the plant foods eaten during focal follows were collected in air tight bags on the same day or within the same week from the exact plant eaten by the chimpanzees or from adjacent plants of the same species. The samples were then processed in the same way the chimpanzee processed them before ingesting the food. For example, if the seed was removed from the fruit before ingesting the fruit, we removed the seed, if the outer part of the stem was removed, we did the same before taking the weights of each unit sample to the nearest 0.01g (wet unit weight). They were then dried to constant weight at ~40°C using a Nesco plant dehydrator and weighed to the nearest 0.01g (dry unit weight) (Rothman, Chapman, & Van Soest, 2012). The mass of these unit measurements were used to calculate the feeding rate of each food item which was later used in the calculation of macronutrient intake.

Laboratory analyses

Laboratory methods are outlined in detail in Uwimbabazi et al. (2019). Briefly we used standard methods, as well as near-infrared reflectance spectroscopy (NIRS) using a Foss XDS Rapid Content Analyzer to estimate macronutrient concentrations. Crude protein (CP) was analyzed using NIRS and calculated by multiplying total nitrogen by 6.25 (Rothman, Chapman, Hansen, Cherney, & Pell, 2009). Available protein (AP) (not bound by cellulose in the plant cell wall) was estimated by subtracting acid detergent insoluble crude protein (ADCP) from CP. We used ADCP values for the same Kibale food species estimated by Conklin-Brittain, Dierenfeld, Wrangham, Norconk, & Silver (1999). For the rest of the macronutrients, we used traditional standardized methods. Lipid content was measured using petroleum ether extraction for four days at room temperature (Conklin-Brittain & Wrangham, 1994). Water-soluble carbohydrates (WSC) were estimated using a modified phenol/sulfuric acid colorimetric assay with a sucrose standard (Conklin-Brittain et al., 1998). Neutral detergent fiber (NDF with α-amylase), acid detergent fiber (ADF), and acid detergent lignin (ADL) were measured through sequential analysis using an A200 fiber analyzer (ANKOM, Macedon, NY) (Rothman et al., 2012). Total nonstructural carbohydrates (TNC) were estimated by subtracting NDF, lipid, AP, and ash from 100%.

We adopted the methods used by Conklin-Brittain, et al. (2006) to determine dry matter, total ash, and organic matter. Nutrients are expressed as a percentage of organic matter (OM) instead of dry matter (DM) because DM contains ash and ash does not contribute energy to a food. A dry-matter correction coefficient (g 105°C DM/g field dried sample) was calculated by drying the field-dried samples in an oven at 105°C for 8 h and weighing them hot. Total ash (g ash/g field-dried sample) was measured by ashing (burning) the same DM sub-sample at 502°C for 8h and then weighing it at 100°C. Organic matter correction coefficient of the sample was calculated as:

$$\text{OM correction coefficient (g OM/g field-dried sample)} = (1 - \text{total ash}) \times \text{ the DM correction coefficient}.$$

These DM and OM correction coefficients were applied to the field-dried DM value to determine the grams of OM in the fresh food:

$$\text{g OM/ g fresh food} = \text{field DM coefficient} \times \text{ final DM correction coefficient} \times \text{ OM correction coefficient}.$$

Food and nutrient intake calculations

We computed the wet weight ingested per minute for each food item as the product of its wet unit weight and the corresponding average number of discrete food units eaten per minute, the detailed formulae are included in Uwimbabazi et al. (2019).

Feeding rate was defined as the dry weight ingested per minute (e.g., in Rothman et al., 2008) and was calculated as:

$$\text{Feeding rate for each food item} = \text{ wet weight ingested per minute} * (\text{dry unit weight} \div \text{wet unit weight} * 100).$$

The daily amount of dry food ingested (g/day) was calculated as:

$$\text{DM}(\text{g}) = \sum (\text{t}_\text{i} * ʎ_\text{i});$$

where t_i=time spent feeding on food item i per day (mins); $ʎ_i$= average feeding rate for item i (g/min).

The daily nutrient intake (DI) (g/day) was calculated as the product of daily amount of dry food ingested per food item and its corresponding mean nutrient content.

Each macronutrient was converted into calories using standard physiological values derived from human diets (conversion factors) (National Research Council, 2003): 4 kcal/g carbohydrates, 4 kcal/g crude protein, 9 kcal/g lipid. The physiological value used for NDF (1.6 kcal/g) was that derived for chimpanzees by Conklin-Brittain, et al. (2006)..

Daily metabolizable energy was then computed as follows:

$$\text{ME (Kcal)} = \text{Lipid (Kcal)} + \text{AP (Kcal)} + \text{NDF (Kcal)} + \text{TNC (Kcal)}$$

Daily non-protein energy *(NPE):*

$$\text{NPE (Kcal)} = \text{TNC (Kcal)} + \text{lipid (Kcal)} + \text{NDF (Kcal)}.$$

Daily available protein:

$$\text{AP (Kcal)} = \sum AP(Kcal)\,per\,day\,.$$

The proportion of daily nutrient intake (PN) from different food items was calculated as:

$$\text{PN}_{\text{y}} = \left(\text{DN}_{\text{iy}} \div \text{ME}\right) * 100,$$

where DN_{iy} is the daily amount of nutrient i from food item y (ripe fruit, young leaves, pith, unripe fruit, flowers, back) and ME is the total daily metabolizable energy intake.

Fruit intake

Since the geometric framework of nutrition models the relationship between variation in actual dietary intakes and nutrient intakes, we considered the daily diet composition (proportions of the respective food types) as the categorical factor for statistical tests. This approach follows other nutrient intake studies of apes that examined the effects of diet composition on nutrient intakes (Rothman et al., 2008; Rothman, Plumptre, Dierenfeld, & Pell, 2007; Vogel et al., 2017). Hence, for each day, we calculated the percent grams of fig ripe fruits, drupe ripe fruits or non-fruit foods (NFF: young leaves, pith, flowers, seeds, bark) consumed. From these data, we determined the dominant food type as the food type that contributed the most to the total weight consumed on that day. The data were then partitioned into three categories according to the food type which dominated the diet on a given day as fig-days, drupe-days and NFF-days.

Statistical analyses

Behavioral data that included complete focal follows (nest to nest) and incomplete focal follows (where the individual was observed for 10 hrs or more) were considered for data analysis. We excluded follows below 10 hrs per day because the average time spent feeding and the dry weight ingested during the <10hr follows were not comparable to nest-to-nest follows (ANOVA: time spent feeding: $F_{2,\,135}$=22.3, P=0.000; dry weight: $F_{2,\,135}$=171.9, P=0.000). On the other hand, there was no significant difference in time spent feeding and dry weight ingested on focal follows which were observed for ≥10 hrs and nest to nest follows (ANOVA: time spent feeding: $F_{2,\,135}$=35.3, P=0.15; dry weight: $F_{2,\,135}$=93.2, P=0.12). To this end we considered 141 focal follows representing 1597 observation hours for analysis. Since the data were largely not normally distributed, we used non-parametric Kruskal wallis test to compare: 1) the nutritional contribution of the different food items to ME; and 2) the nutritional contribution of different food items to ME across days dominated by different the food-type. Pairwise tests corrected with Bonferroni test were conducted to show where the difference lay. One-way ANOVA was used to compare the ingested amount of each nutrient from the different food items. Tukey's post-hoc tests were used to show where the difference really lay. The relative percentage contributions (% of total energy) to the diet in relation to available protein, carbohydrate (digestible NDF+TNC) and lipid were also examined using right angled mixture triangles (Raubenheimer, 2011). To test whether the relative contributions of macronutrients to ME (response variables) were influenced by dominant food-type (fixed factor) we used linear mixed models. Linear mixed effect models were also used to analyse if daily available protein and non-protein energy intake (response variables) were influenced by the dominant food-type. All models included the identity of the individuals and climate-season as random factors. The models were fitted by REML (Restricted Maximum Likelihood criterion) using lme4 package (R Core Team, 2015). All models were validated by checking the residual distribution, plotting residuals against predictors and plotting a Q-Q plot. P-values were obtained by likelihood ratio tests of the full model with the effect in question against the model without the effect in question. Pairwise comparisons corrected with Bonferroni test were conducted to show where the significance lay. R software ver 3.3.2 was used to run all the statistical analyses and the significance level was set at $\alpha = 0.05$.

Ethical statement

All research protocols were reviewed and approved by Uganda Wildlife Authority and the Zoology Department of Makerere University. This research was conducted in accordance with regulations of the Uganda National Council for Science and Technology and Uganda Wildlife Authority. The study also complied with the American Society of Primatologists' Principles for the Ethical Treatment of Non-Human Primates.

RESULTS

Contributions of foods to nutrient intake

Over the study period, the daily diet of chimpanzees was dominated by figs (mean 56 ± SE 2.6%), followed by drupes (mean 17± SE 2.3%), young leaves (mean 15± SE 1.2%) and lastly other non-fruit foods (mean 9 ± SE 2.1%) on a dry weight basis. Based on dry weight ingested, chimpanzees obtained most of their macronutrients from ripe fruits, particularly figs (Table 1). Compared with other food items, figs thus contributed the largest proportion of lipids (Kruskal wallis: H=366.3, df=5, P=0.001), protein (H=302.1, df=5, P<0.0001), TNC (H=346.2, df=5, P<0.0001) and NDF (H=296.6, df=5, P<0.0001) (Table 2) to the diet. Moreover, figs accounted for the largest nutritional contribution to ME, having contributed more lipid, AP, TNC and NDF (Table 3). The nutritional contribution of the non-fruit food items to ME was significantly low (Table 3).

Nutrient Balancing

The mean daily metabolisable energy intake for female chimpanzees was 2479 Kcal, which comprised 7% (0.5–19.0%) lipids, 15% (range 3.9–33.0%) AP, 76% (range:59.2–94.2%) carbohydrates (TNC +NDF) (Figure 1). Carbohydrates (TNC+NDF) contributed more to daily energy (ME) intake when drupes and figs dominated the diet than when non-fruit foods dominated the diet (Kruskal wallis test (H): Drupes and NFF: H=15.4, p=0.04; between figs and NFF:H=13.9, p=0.0006) (Figure 2). The contribution of carbohydrates to ME when drupes dominated the diet did not vary greatly from that when figs dominated the diet (H=1.8, p=0.11) (Figure 2). Conversely, AP contributed more to ME when non-fruit foods dominated the diet than when drupes or figs dominated the diet (Drupes and NFF: H=28.8, p<0.0001; figs and NFF: H=22.1, p<0.0001). However, there was no significant difference between the contribution of AP to ME when drupes dominated the diet and when figs dominated the diet (H=4.4, p=0.30). The contribution of lipids to ME did not vary despite the changes in diet composition (Drupes and figs: H=1.6, p=0.6, Drupes and NFF: H=1.9, p=0.5; figs and NFF: H=0.02, p=1.1) (Figure 2).

Ratio of Non-protein Energy to Available Protein

The daily intake of NPE and AP was: mean 2099 ± SE 66 (Kcal) and mean 355 ± SE 12 (Kcal) respectively. The average NPE:AP ratio was 7:1. On a daily basis, female chimpanzees consumed varying amounts of NPE depending on the diet composition (Figure 3). Larger amounts of NPE were consumed when the diet was dominated by drupes (mean 2384 ± SE 193 Kcal) or figs (mean 2203 ± SE 88 Kcal) than when the diet was dominated by non-fruit-foods (mean 1795 ± SE 103 Kcal) (LMM: $F_{2,138}$=5.7, P=0.001) (Figure 3). In contrast, AP intake remained relatively stable despite diet variation (drupe-days: mean 327 ± SE 46 Kcal; Fig-days: mean 338 ± SE 15 Kcal; NFF-days: mean 395 ± SE 20 Kcal; LMM: $F_{2,127}$=2.6, P=0.08). NPE:AP was higher when the diet was dominated by drupes (mean 9.1 ± SE 1.0) than when the diet was dominated by figs (mean 7.2 ± SE 0.4) and non-fruit foods (mean 4.9 ± SE 0.3) ($F_{2, 138}$=16.7, P=0.001), (Figure 3).

DISCUSSION

This study used nutritional geometry to explore nutritional balancing strategies of female chimpanzees in the face of fluctuating food resources. Our results showed that female chimpanzees ingest a variable amount of digestible carbohydrates and lipids and regulate protein similar to other frugivorous primates studied (Felton et al., 2009b; Takahashi, Rothman, Raubenheimer, & Cords, 2019). .

Female chimpanzees consumed more NPE Kcal on drupe and fig-days. They did not, however, consume more AP Kcal on NFF-abundant days, and consequently AP Kcal intake was relatively stable irrespective of the dominant food type, suggesting that female chimpanzees more closely regulated protein while maximizing NPE Kcal intake when fruits were abundant. This finding is similar to that of spider monkeys (Felton et al., 2009a; Felton et al., 2009b). Although proteinaceous foods such as young leaves are easily available, chimpanzees seem to prefer sugary fruits which have low protein, which they complement with small amounts of young leaves and other non-fruit foods to reach their protein target. Figs contain less protein than drupes, which explains why chimpanzees consumed more young leaves and other non-fruit foods on fig-days than on drupe-days (Uwimbabazi et al., 2019). Although drupes are richer in soluble carbohydrates and AP compared to figs, figs dominated the diet in terms of food intake and macronutrient contribution. This is partly because figs are more abundant and readily available in the Kanyawara habitat (Uwimbabazi et al., 2019; Wrangham et al., 1991, 1993). Our findings concur with evidence from long term data which shows that Kanyawara chimpanzees spend more time feeding on figs compared to young leaves and other non-fruit foods (Wrangham et al., 1996).

In line with our expectation and previous findings (Uwimbabazi et al., 2019), ripe fruits contributed larger proportions of lipids and non-structural carbohydrates to daily energy intake than other food items (Felton et al., 2009b; Masi et al., 2015; Rothman et al., 2011). This partly explains why the contribution of carbohydrates to ME was greater on drupe and fig-days than on non-fruit days; in addition to the fact that female chimpanzees consumed greater proportions of carbohydrate rich foods (ripe fruits) on drupe and fig-days. Contrary to our expectation and despite the relatively high protein concentrations of young leaves (Milton, 1999; Uwimbabazi et al., 2019), they did not account for the largest contribution of either AP or fiber intake (Table 2) because they were eaten in much smaller quantities than ripe fruits (figs & drupes) (Table 1). However, despite the generally low intake of protein rich foods compared to ripe fruit and the stable intake of AP Kcal, the contribution of AP (%) to ME was much higher when non-fruit foods dominated the diet than when drupes or figs dominated the diet. When ripe fruit is scarce, female chimpanzees increase their consumption of higher fiber and/or protein-rich foods, such as leaves and pith (Wrangham et al. 1991).

Furthermore, our analyses showed that chimpanzees achieved similar intakes of NPE Kcal and similar contribution of carbohydrates to ME on drupe and fig-days, suggesting that drupes and figs, are from a similar macronutrient perspective, interchangeable, supplementary foods. This may explain why chimpanzees alternated between figs and drupes irrespective of fruit availability (Uwimbabazi et al., 2019). While the inclusion of either fruit-type in the diet may depend on the nutrient quality, there is a trade-off in searching for a less available high-quality food and the amount of nutrients one is likely to ingest (Wrangham et al., 1991). Hence, it is likely that chimpanzees may forego the search for patchily distributed high-quality drupes (Wrangham et al., 1996) and consume readily available figs since they are able to reach their NPE intake target by consuming either of the fruit categories, as confirmed by the similarity of the NPE:AP ratio for figs and drupes (Figure 3). The other reason why figs are often consumed despite their low carbohydrate and protein content is because they provide other nutritional benefits such as calcium, which is critical for maintenance and reproduction (Wrangham et al., 1993). Therefore, at Kanyawara, figs may not just be staple low-quality foods that are consumed when drupes are scarce as is often reported (Felton, Felton, Wood, & Lindenmayer, 2008; Lambert & Rothman, 2015; Marshall & Wrangham, 2007).

In line with our expectation, the NPE:AP ratio of the diets of female chimpanzees at 7:1 is comparable to that of spider monkeys at 8:1 (Felton et al, 2009a). The similarity in the ratios might be an indication that frugivorous hindgut fermenters use a similar nutritional strategy. Female chimpanzees included different foods in their diet and combined these foods in specific proportions so that the resulting combination provided a targeted amount of NPE:AP ratio. This response has also been observed in spider monkeys (NPE:AP: 8:1) (Felton et al., 2009a) and blue monkeys (NPE:AP: 4:1) (Takahashi et al., 2019). Our findings further show that like other frugivorous primates, female chimpanzees target a relatively high NPE:AP ratio compared with folivorous primates such as gorillas and colobus monkeys (Figure 4).

Interestingly, the total calorie intake of lactating female chimpanzees at 2479 Kcal is close to that of lactating female humans at 2500 Kcal (Kominiarek & Rajan, 2016), and at 15% the mean contribution of available protein to non-protein energy intake likewise falls within the typical range in the human diet (10% – 35%) (Raubenheimer & Simpson, 2019). Even though the range of 10% to 35% is most common for humans, lower protein diets have in several human populations been associated with obesity (Raubenheimer & Simpson, 2019). This is not likely driven by macronutrient ratios per se but by the consumption of highly processed foods, rich in lipids and refined carbohydrates and low in fiber (Martínez Steele, Raubenheimer, Simpson, Baraldi, & Monteiro, 2018). Those populations with a typical diet that is low in protein relative to lipids and non-structural carbohydrates, but also high in fiber, such as the traditional Okinawan and Blue Zone Mediterranean diets, are notable for healthy metabolic profiles and long life spans (Le Couteur et al., 2016; Raubenheimer & Simpson, 2019). There is thus an interesting parallel between the diets selected by chimpanzees in the current study and diets associated with good health in human populations. Further, the protein prioritization pattern of macronutrient regulation that we observed for chimpanzees (Figure 3) has also been established in several independent studies in humans (reviewed in Raubenheimer & Simpson, 2019), and is the same pattern associated with energy over-consumption and obesity in industrialized food systems (Gosby, Conigrave, Raubenheimer, & Simpson, 2014; Martínez Steele et al., 2018; Simpson & Raubenheimer, 2005). These observations suggest that free-ranging chimpanzees might provide a useful model system for examining evolutionary hypotheses of human nutrition, and might help to inform debates around human dietary adaptation. Our results contribute an important addition to the comparative database of how primates, including humans, respond to variation in nutritional balance, and provide insights on how chimpanzees are able to survive in a range of habitats (including degraded forests) and how they are able to adapt to changes in the environment (McLennan, 2008, 2013).

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RESEARCH HIGHLIGHTS

- Female chimpanzees regulate protein intake while maximizing non-protein energy during periods of high fruit intake.
- Female chimpanzees access and exploit different food types (food generalism) to offset macronutrient imbalances following variations in diet composition.
- Female chimpanzees eat a balance of protein to non-protein energy that is similar to other frugivorous primates, such as spider monkeys.

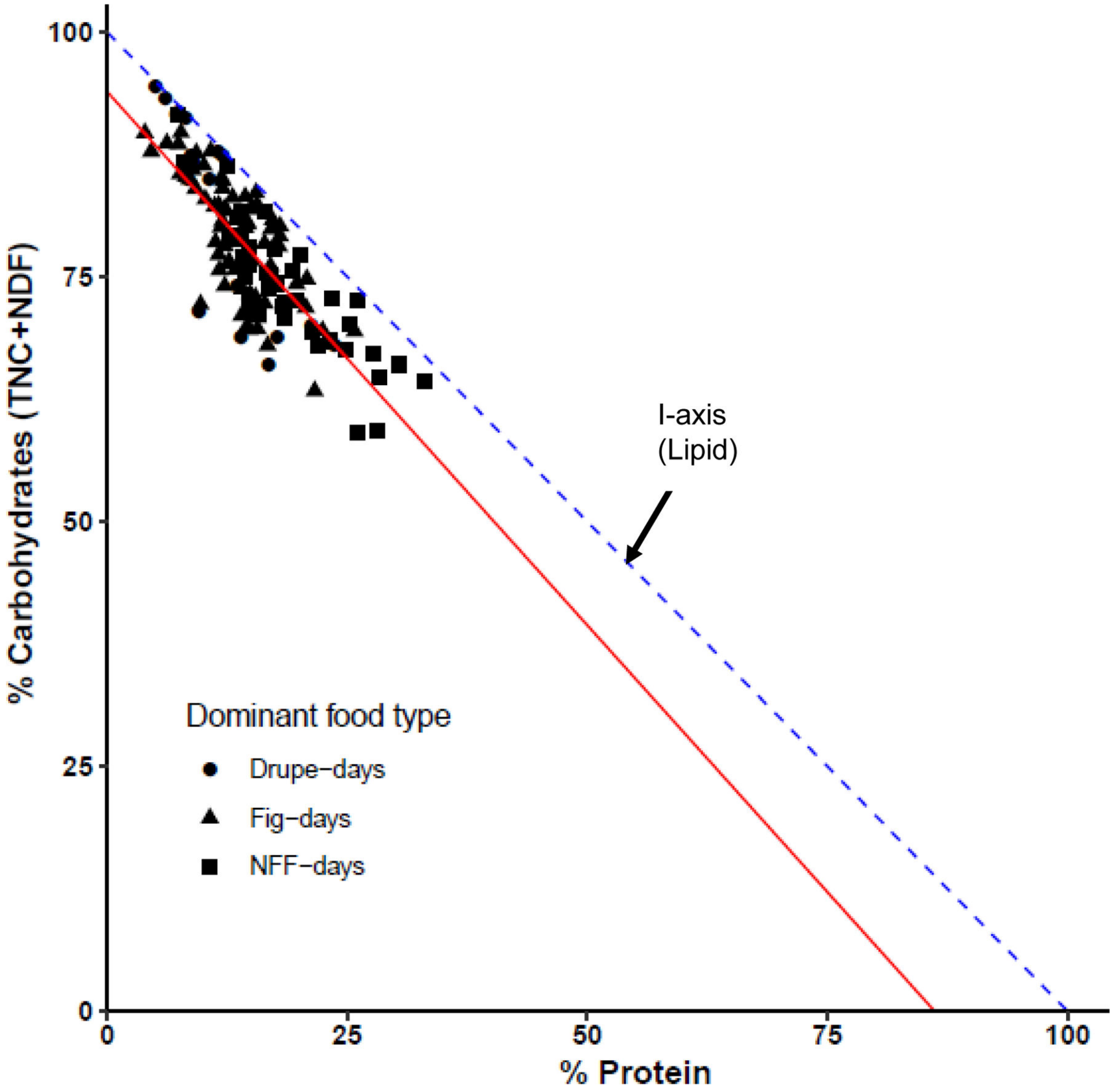

Figure 1:

Right-Angled Mixture Triangle (RMT) showing the contribution of macronutrients to daily energy intake (ME) across days when the diet was dominated by different food types. X-axis: is % ME from protein, Y-axis: % ME from carbohydrates (Total non-structural carbohydrates (TNC)+Neutral Detergent Fibre (NDF)). The dashed blue line represents the I-axis (implicit axis: lipid): r^2 of 0.65, slope is −1.09. The solid red line is regression line for carbohydrates and protein. The nutrient contributions to daily ME for each point sum to 100. $N_{Drupe\text{-}days}$=22 days, $N_{Fig\text{-}days}$=76 days, $N_{NFF\text{-}days}$=77 days

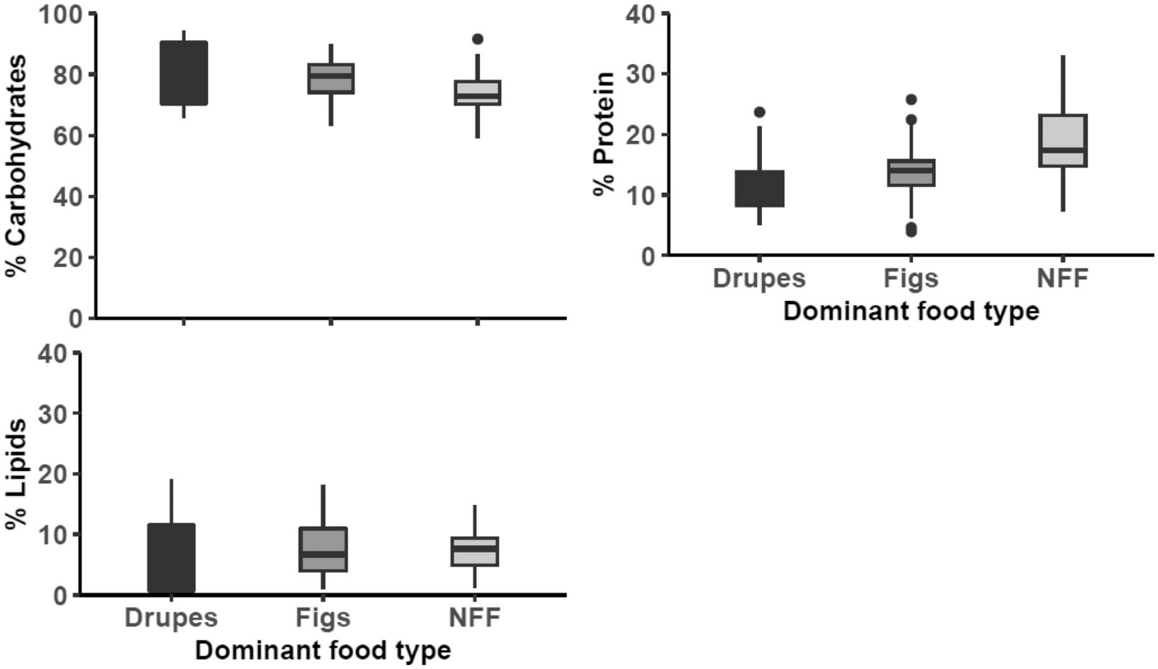

Figure 2:

Contribution of macronutrients to daily energy intake (ME) across days dominated by different food types. *$N_{Drupe\text{-}days}$=22 days, $N_{Fig\text{-}days}$=76 days, $N_{NFF\text{-}days}$=77 days*

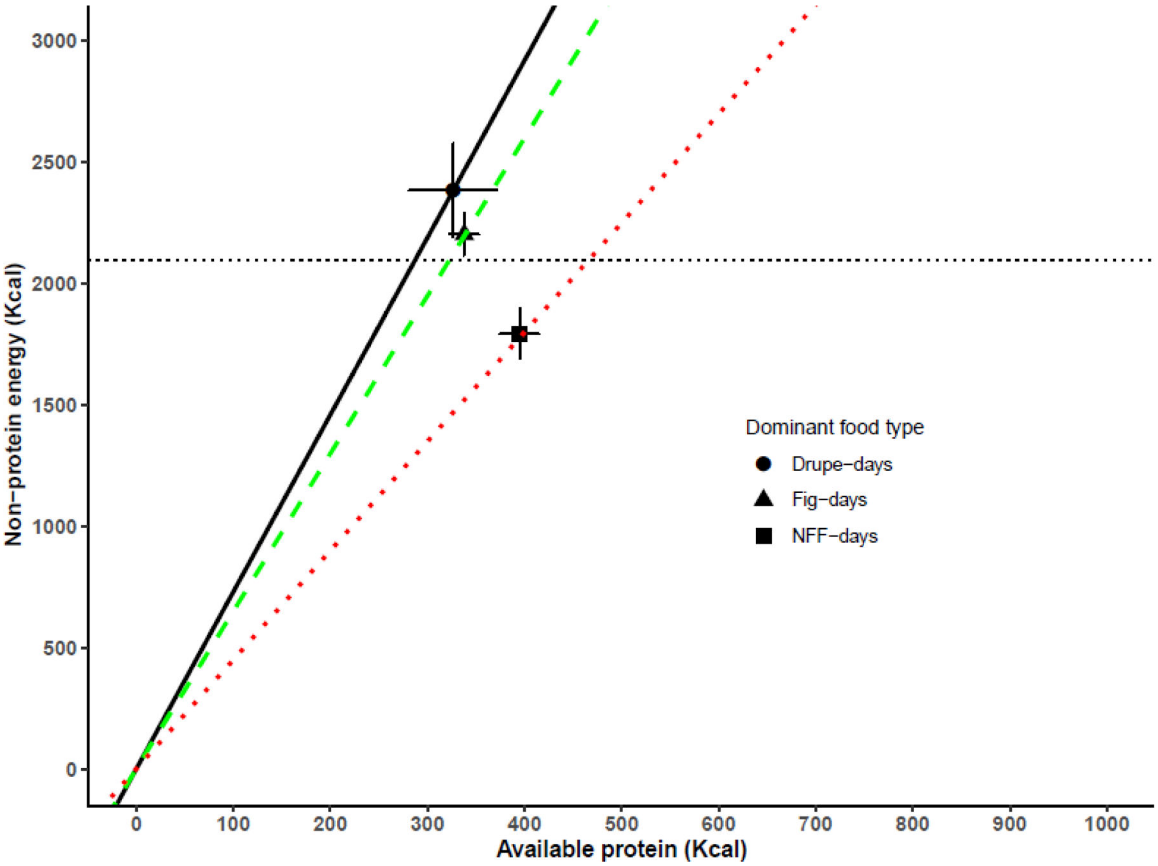

Figure 3:

A geometric plot of mean daily intake (±SE) of non-protein energy (NPE) vs available protein (AP) following variation in fruit intake. The solid, dashed and dotted lines are the nutritional rails which represent the ratio of NPE:AP for Drupe-days, Fig-days and Non-fruit food (NFF)-days respectively. Diet compositions are represented as Cartesian points (proportions of AP and NPE in the diet) and the nutritional rails (vectors passing through the origin) represent the AP: NPE balance for the diet consumed on different days.

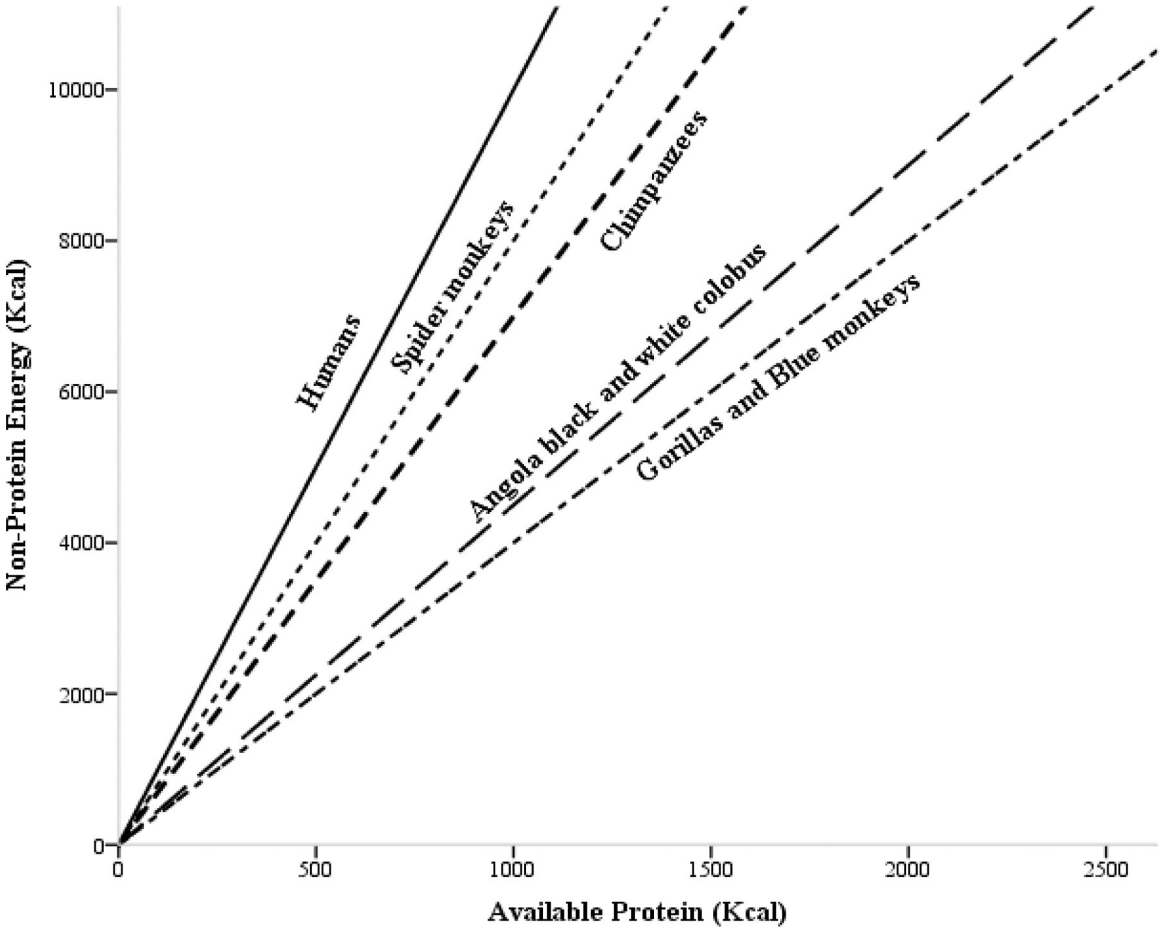

Figure 4:

The balance of non-protein energy to protein (kcal) in six primate species. Data are from: Dunham & Rodriguez-Saona, 2018; Felton, et al., 2009b; Kominiarek & Rajan, 2016; Rothman et al., 2011; Takahashi et al., 2019.

Table 1:

Weight based averages of daily grams of nutrients from different food items.

Food item	**Lipid (g)** **($F_{8,468}$=49.8, P=0.001)**	**AP (g)** **($F_{8,468}$=37.2, P<0.0001)**	**NDF(g)** **($F_{8,468}$=98.3, P<0.0001)**	**TNC(g)** **($F_{8,468}$=99.2, P<0.0001)**
Ripe drupes (78)	10.3±1.8	19.8±2.4	101.5±14.3	137.2±16.0
Ripe figs (128)	20.8±1.3	34.0±2.0	269.7±14.0	206.8±12.3
Young leaves (127)	0.3±0.0	33.7±3.0	49.4±3.3	32.4±2.0
Pith (103)	0.0±0.0	4.9±0.5	36.5±3.5	16.0±1.3
Seed (22)	4.8±1.8	18.1±4.3	26.3±12.6	9.5±4.2
Flowers (15)	3.1±1.5	19.8±3.6	41.4±9.2	11.1±3.9
Bark (9)	0.0±0.0	9.7±3.1	43.5±13.2	1.2±0.4

Cells represent mean ± SE. The number in parentheses represents the number of days when that food item was consumed by female chimpanzees during the study period. Both drupes and figs are ripe fruits. The statistic in parentheses is derived from a one-way ANOVA.

Table 2:

Mean contribution of the different food items to daily nutrient intake

Food item	**Lipid (%)** (H=366.3, df=5, P<0.0001)	**AP (%)** (H=302.1, df=5, P<0.0001)	**NDF (%)** (H=296.6, df=5, P<0.0001)	**TNC (%)** (H=346.2, df=5, P<0.0001)
Ripe drupes	32.8±3.5	23.7±2.4	26.1±3.1	38.0±3.5
Ripe figs	69.5±2.4	40.9±2.0	63.0±2.1	64.2±2.3
Young leaves	5.4±0.6	36.7±1.8	11.1±0.9	12.4±0.9
Pith	1.9±0.2	6.5±0.7	9.9±0.9	6.2±0.5
Seed	15.3±2.8	18.0±3.0	6.6±1.6	2.7±0.5
Flowers	13.9±5.9	23.5±3.8	11.9±2.7	4.6±6.4
Bark	0.0±0.0	14.7±4.5	13.9±4.1	0.7±0.2

Cells represent mean ±SE.

Percentage of macronutrients is the % of the total daily nutrient intake. For example, on days when ripe figs were eaten, they contributed 69.5% of lipid intake, 40.9% of AP intake, 63% of NDF intake and 64.2% of TNC intake. Kruskal Wallis test (in parentheses) shows the comparison of proportion of each macronutrient from different food items to daily nutrient intake.

Table 3:

Nutritional contributions of foods to daily energy intake (ME)

Food item	**Lipid (%)** ***(H=309.2, P<0.0001)***	**AP (%)** ***(H=193.7, P<0.0001)***	**NDF (%)** ***(H=146.8, P<0.0001)***	**TNC (%)** ***(H=214.3, P<0.0001)***
Ripe drupes	3.2±0.5	2.9±0.3	6.3±0.8	20.9±2.1
Ripe figs	7.2±0.4	5.3±0.3	16.9±0.7	31.1±1.3
Young leaves	0.4±0.0	5.7±0.4	3.2±0.3	5.1±0.4
Pith	0.1±0.0	0.8±0.1	2.7±0.3	3.0±0.3
Seed	1.5±0.3	2.9±0.5	1.5±0.4	1.2±0.2
Flower	1.5±0.6	4.0±0.7	3.1±0.6	1.9±0.7
Bark	0.0±0.0	2.3±0.7	4.2±1.2	0.3±0.0

Cells represent the mean ± SE

Macronutrient % is the % of the mean ME intake, for example, 7.2% of lipid, 5.3% of AP, 16.9% of NDF and 31.1 % of TNC in daily energy intake is from ripe figs on days when they are eaten. Statistic in parentheses is the Kruskal Wallis test.