International Journal of Primatology

Do fruit nutrients affect subgrouping patterns in wild spider monkeys (Ateles geoffroyi)?

--Manuscript Draft--

Manuscript Number:	IJOP-D-16-00119R1
Full Title:	Do fruit nutrients affect subgrouping patterns in wild spider monkeys (Ateles geoffroyi)?
Article Type:	Original Article
Keywords:	fission-fusion dynamics; feeding competition; food abundance; nutrient quality; Ateles
Corresponding Author:	Laura Busia Universidad Veracruzana Xalapa, VER MEXICO
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Universidad Veracruzana
Corresponding Author's Secondary Institution:	
First Author:	Laura Busia
First Author Secondary Information:	
Order of Authors:	Laura Busia
	Colleen M. Schaffner
	Jessica M. Rothman
	Filippo Aureli
Order of Authors Secondary Information:	
Manuscript Region of Origin:	MEXICO
Funding Information:	
Abstract:	One of the main costs of group living is feeding competition. Fission-fusion dynamics are thought to be a strategy to avoid overt competition for food resources. We tested whether food abundance and quality affected such dynamics in a species characterized by a high degree of fission-fusion dynamics. We collected data on 22 adult and subadult spider monkeys (Ateles geoffroyi) living in a large community in the protected area of Otoch Ma'ax Yetel Kooh, Yucatan, Mexico. We recorded subgroup size and fission events as well as fruit abundance during 12 months and carried out nutritional analyses on the fruit species that the study subjects consumed most. We found no effect of fruit abundance or nutritional quality of recently visited food patches on individual fission decisions, but the amount of protein in the food patches visited over the course of the day was a good predictor of subgroup size. While the absence of support for a relationship between fruit characteristics and fission decisions may be due to the short temporal scale of the analysis, our findings relating subgroup size to the amount of protein in the visited food patches over the course of the day may be explained by individual spider monkeys attempting to obtain sufficient protein intake from their fruit-based diet.

Do fruit nutrients affect subgrouping patterns in wild spider monkeys (*Ateles geoffroyi*)?

Laura Busia[1], Colleen M. Schaffner[1], Jessica M. Rothman[2], Filippo Aureli[1,3]

[1]Instituto de Neuroetologia, Universidad Veracruzana, Xalapa, Veracruz, Mexico

[2]Department of Anthropology, Hunter College of the City University of New York, New York, NY, USA

[3]Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moore University, Liverpool, UK

Abstract

One of the main costs of group living is feeding competition. Fission-fusion dynamics are thought to be a strategy to avoid overt competition for food resources. We tested whether food abundance and quality affected such dynamics in a species characterized by a high degree of fission-fusion dynamics. We collected data on 22 adult and subadult spider monkeys (*Ateles geoffroyi*) living in a large community in the protected area of Otoch Ma'ax Yetel Kooh, Yucatan, Mexico. We recorded subgroup size and fission events as well as fruit abundance during 12 months and carried out nutritional analyses on the fruit species that the study subjects consumed most. We found no effect of fruit abundance or nutritional quality of recently visited food patches on individual fission decisions, but the amount of protein in the food patches visited over the course of the day was a good predictor of subgroup size. While the absence of support for a relationship between fruit characteristics and fission decisions may be due to the short temporal scale of the analysis, our findings relating subgroup size to the amount of protein in the visited food patches over the course of the day may be explained by individual spider monkeys attempting to obtain sufficient protein intake from their fruit-based diet.

Keywords: fission-fusion dynamics, feeding competition, food abundance, nutrient quality, *Ateles*

Introduction

Feeding competition is widely acknowledged to be one of the main costs of group living in primates (Chapman 1990; Chapman and Chapman 2000; Janson and Goldsmith 1995; Janson and van Schaik 1988; Koenig 2002; Krause and Ruxton 2002; Terborgh and Janson 1986; Wrangham 1980). When group members compete with each other, an increase in group size usually leads to a decrease in individual foraging efficiency (Janson 1988; Janson and Goldsmith 1995; van Schaik and van Hooff 1983; Williamson and Dunbar 1999). According to socioecological theory, food abundance and its associated costs (e.g. travel length) may be the limiting factor for group size (Chapman et al. 1995; Chapman and Chapman 2000; Milton 1984). For example, food abundance affects male chimpanzee (*Pan troglodytes*) association (i.e. being in the same subgroup) if no receptive female is present (Anderson et al. 2002). An increase in red colobus monkey (*P. rufomitratus*) group size occurred at different spatial scales in relation to the increased availability of important food species (Gogarten et al. 2015). Furthermore, food abundance may influence primate abundance. For example, the abundance of food species affects primate density at a small spatial scale (red colobus monkeys, *Procolobus tephrosceles,* Chapman and Chapman 1999; Southern Bornean gibbon, *Hylobates albibarbis*, Hamard et al. 2010). Seasonality in food abundance affects primate biomass in New and Old World monkeys (Hanya et al., 2011).

Fission-fusion dynamics are one strategy to offset the cost of feeding competition. Species with a high degree of fission–fusion dynamics live in communities characterized by large temporal variation in interindividual cohesion, subgroup composition and subgroup size (Aureli et al. 2008; Kummer 1971). Studies of several species show a relationship between fission-fusion dynamics and feeding competition.

For example, chimpanzee subgroups are smaller during the season with low fruit abundance than during the season with high fruit abundance (e.g. Basabose 2004; Chancellor et al. 2012; Itoh and Nishida 2007). Similarly, the mean subgroup size of spider monkeys is larger when food is more abundant (Asensio et al. 2009; Chapman et al. 1995; Klein and Klein 1977; Smith-Aguilar et al. 2016; Symington 1988) and before than after hurricanes that depleted the fruit supply for several months (Schaffner et al. 2012). Food abundance is also the main factor affecting grouping patterns of other primate (Sumatran orangutans, *Pongo abelii*, van Schaik 1999) and non-primate species (bottlenose dolphins, *Tursiops troncatus*, Heithaus and Dill 2002; spotted hyaenas, *Crocuta crocuta*, Smith et al. 2008). A reduction in chimpanzee community size, likely resulting in reduced feeding competition among community members, affects fission-fusion dynamics, with an increase in subgroup size and duration (Boesch and Boesch-Achermann 2000; Lehmann and Boesch 2004).

The relationship between food abundance and primate group or subgroup size is not always straightforward (e.g. red colobus monkey, *P. badius*, Gillespie and Chapman 2001; chimpanzees, *Pan troglodytes,* Anderson et al. 2002; Hashimoto et al. 2001; Hashimoto et al. 2003; Newton-Fisher et al. 2000; Pennant's red colobus, *P. pennantii,* and black and white colobus monkeys, *Colobus guereza*, Onderdonk and Chapman 2000; blue monkeys, *Cercopithecus mitis,* Worman and Chapman 2006), suggesting that abundance might not be the only food-related factor in determining primate abundance and group size. For example, food nutritional quality affects density and group size of some primate species (black and white colobus monkeys, red colobus monkeys, *Piliocolobus trephosceles,* Chapman et al. 2004; Fashing et al. 2007; Japanese macaques, *Macaca fuscata*, Hanya et al. 2006; Hanya and Chapman 2013). Another example of the importance of a food-related factor other than abundance is given by the extraordinary large group size of a group of black-and-white colobus monkeys. The typical group size is 2-20 individuals, but in an area with much higher leaf quality the group reached up to 300 individuals (Fimbel et al. 2001).

The definition of food quality varies depending on the species' diet and its digestive capabilities. For example, for highly folivorous primates food quality may be defined as the balance between structural fibers and protein of mature leaves in a habitat (Wasserman and Chapman 2003, Chapman et al. 2004; Fashing et al. 2007, but see Chapman et al. 2012; Johnson et al. 2015), whereas for highly frugivorous Atelines the total energy intake is often considered as a food quality index (Rosenberger and Strier 1989; Strier 1992; Di Fiore and Rodman 2001). Several studies of spider monkey diet support this view as individuals select fruits rich in lipids and nonstructural carbohydrates, which can quickly be metabolized into energy (Castellanos 1995; Dew 2005; Di Fiore et al. 2008). However, Peruvian spider monkeys (*A. chamek*) maintain a stable protein intake while energy intake varies depending on the composition of food items (Felton et al. 2009a). There is thus no consensus whether it is energy or protein that has the dominant influence on spider monkey food choice and therefore may have the strongest influence on their subgrouping patterns.

The temporal scale used to measure food abundance and quality might also play a role in subgroup size changes. For example, a monthly scale may not provide sufficiently precise information about the relationship between food abundance and quality and subgroup size because fissioning reduces within-group feeding competition at a specific moment, and thus a shorter temporal scale is recommended (Asensio et al. 2009). Thus, it is plausible that feeding competition depends not only on food abundance but also on food nutritional quality and on the temporal scale used.

Spider monkeys represent an excellent candidate species to investigate the role of fruit abundance and quality on fission decisions for two main reasons. First, spider monkeys' high degree of fission–fusion dynamics provides the opportunity to evaluate the effects of fruit abundance and quality on individual association, as subgroup size changes frequently throughout the day (Chapman 1990; Fedigan and Baxter 1984). Second, spider monkeys are mainly frugivorous, as fruits constitute a large component of their diet (mean: 77%; range: 55-90%, Di Fiore et al. 2008), making a plausible estimation of food abundance easier.

Our aim was to evaluate the role of feeding competition on grouping patterns of spider monkeys, measuring fruit abundance and nutritional quality on a short temporal scale. We evaluated fruit nutritional quality in two ways: non-protein energy (NPE) (i.e. energy (kcal) obtained from lipids and non-structural carbohydrates) and protein in grams. If fissions are a strategy to avoid within-group feeding competition, we predicted that fruit abundance and quality would affect individual association with other community members. We tested this scenario using two approaches. First, we examined whether the characteristics (i.e. fruit abundance and nutritional quality) of recently visited food patches affected individual fission decisions. We predicted more fission events when fruit abundance and quality were lower. Second, we examined whether the characteristics of the visited food patches affected mean daily subgroup size. We expected that a reduction in fruit abundance would lead to a smaller mean daily subgroup size. We predicted that a lower NPE in visited food patches was associated with a smaller mean daily subgroup size. We similarly predicted that lower protein in visited food patches was associated with a smaller mean daily subgroup size.

Methods

Field site and study subjects

The field site is located in the forest surrounding the Punta Laguna lake, within the natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula, Mexico (20°38' N, 87°38' W). The natural protected area measures 5367 ha and includes a mosaic of old-growth, semi-evergreen medium forest, with trees up to 25 m in height, and 30–50-year-old successional forest (Ramos-Fernandez and Ayala-Orozco 2003).

We studied 22 individuals of a well-habituated community of Geoffroy's spider monkeys living in the protected area (6 adult males, 10 adult females, 1 subadult male, 5 subadult females, for age classification see Shimooka et al. 2008). These subjects have been part of a continuous long-term project since 1997 and each monkey was individually recognized by unique facial features and differences in fur coloration.

Data collection

We observed monkeys in 4- or 8-hour shifts throughout the daylight hours. The first author and 2 or 3 field assistants followed subgroups about 5.5 hours a day for 129 days, for a total observation time of about 700 hours. From October 2013 to September 2014, we updated the subgroup membership continuously by identifying each member of the subgroup initially encountered each day and recording all membership changes due to fission and fusion events. We followed the first subgroup met during the day. After a fission event, we followed the subgroup including individuals for which we had fewer focal samples. Subgroup membership was established following a chain rule based on inter-individual distances (Croft et al. 2008). We considered an individual part of the followed subgroup if it was <30 m from any subgroup member; the critical distance of 30 m was empirically established at the study site (Ramos-Fernandez 2005). We recorded fission events when one or more individuals were not seen within 30 m of a subgroup member for 30 min. We recorded fusion events when one or more individuals came within 30 m from any member of the followed subgroup (Rebecchini et al. 2011). We chose the interval of 30 min for recording a fission based on an analysis of data on subgroup membership changes collected independently from this study.

To assess food abundance, we collected data on the fruit phenology of the food patch (i.e. one or more trees of the same species) where subgroup members were observed feeding for longer than 5 minutes. We estimated fruit abundance using a logarithmic scale: 1-10 items, 11-100 items; 101-1000 items and 1001-10000 items (Asensio et al. 2009; Chapman et al. 1992).

To determine food quality we collected fruit samples of the most consumed tree species, i.e. those consumed for at least 20% of the time the followed subgroup spent foraging during the first 15 days of each month, from the same food patches where we observed the monkeys feed a few days earlier. We counted the number of fruits and extracted the seeds for all species but figs, as spider monkeys extracted seeds before ingesting fruits most of the time. We weighed the mass and dried the pulp with a Nesco dehydrator (American Harvest FD-80) at less than 60^{O}C on the same day of sample collection to obtain a minimum of 20 g of dry fruit matter. Considering the potential alteration of nutritional content due to over drying (Hosamani and Desai 2013) and potential differences between species in the duration of the process, we weighed samples every three hours during fruit drying. We considered a sample dried when the weight was equal to the previously measured weight. We put dried samples in a plastic bag containing the relevant information including date, area of collection, fruit species, and a unique alphanumeric code and we stored them in a dark box containing silica to prevent potential damage from humidity. Before analyses, we milled dried samples to 1mm particle size using a Wiley mill (Rothman et al. 2012).

Nutritional analysis

We determined protein, nonstructural carbohydrates and lipid concentrations of fruits in the Nutritional Ecology Laboratory of Hunter College at the City University of New York, according to standard methods (Rothman et al. 2012). We obtained the quantity of nitrogen through combustion, and we multiplied nitrogen by 6.25 to estimate the crude protein concentration. We used this conversion factor to conform with other studies and as a crude measure, although some of this crude protein may not be digestible (Rothman et al., 2008), as it could be bound to fiber or a component of secondary compounds (Milton and Dintzis 1981; Conklin Brittain et al. 1999; Rothman et al. 2012). We obtained the quantity of lipid through petroleum ether extraction using an ANKOM XT15 Fat Analyzer (ANKOM, Macedon, NY). We determined the neutral detergent fiber (NDF) through the detergent method (van Soest et al. 1991) without sodium sulfite and with α amylase using an A200 fiber analyzer (ANKOM, Macedon, NY). We estimated ash by burning the sample at 550C. We estimated the total nonstructural carbohydrates (TNC) by subtracting NDF, lipid, crude protein and ash from 100% (NRC 2003; Rothman et al. 2012).

Data analyses

To test our predictions we ran a generalized linear mixed model (GLMM) and a linear mixed model (LMM) using the “lme4” and “nlme” packages (Bates et al. 2014; Pinheiro et al. 2014) in R (version 3.1.2 R-Core Team, 2014). We set an alpha level of 0.05 for all tests. In the GLMM the occurrence of fission within half an hour of the beginning of a foraging event was considered as the dependent variable (binomial: yes or no). Fission events that did not occur within a half hour of the beginning of a foraging event were excluded from the analyses. We considered a foraging event to take place when at least 75% of subgroup members fed on a food patch. We examined 142 foraging events, 46 followed by fission within half an hour and 96 without fission. The biomass of the food patch was estimated by multiplying the dried mass of each fruit (calculated by dividing the dry mass of the sample by the number of items in the sample) by a value representing the fruit abundance of each visited patch. For each category of fruit abundance we used the following values: 5 for the category 1-10 items, 50 for the category 11-100 items, 500 for the category 101-1000 items and 5000 for the category 1001-10000 items. We considered the biomass as indicator of food abundance, and we included it as an independent variable. We also included the amount of protein (measured in g) for each food patch as an independent variable. As we knew the number of fruits analyzed, we estimated the grams of protein present in each fruit and multiplied it by the value representing the fruit abundance of the food patch. Finally, we considered the non-protein energy of the food patch as an independent variable. We calculated the non-protein energy (NPE) by summing the energy obtained from total nonstructural carbohydrates (TNC, i.e. TNC amount multiplied by 4) and the energy obtained from lipid (i.e. lipid amount multiplied by 9). We assumed little to no fiber fermentation as spider monkeys have a rapid transit time and an unspecialized gut (Milton 1981).

In the LMMs we considered the mean daily subgroup size as the dependent variable. The mean daily subgroup size was calculated based on all subgroup sizes lasting at least one hour during the observations of each day. We included the mean daily amounts of biomass, protein amounts, and NPE calculated considering each food patch visited over the course of the daily observations as independent variables.

To test for multicollinearity, we used the Variance Inflation Factor (VIF) and all variables had VIF<10 (O'Brien 2007). For all the models we included the month as a random factor and compared them with the null models (Forstmeier and Schielzeth 2011) using a likelihood ratio test with the function "anova" (Dobson and Barlett 2008).

Results

There were 1-3 most consumed fruit species (i.e. those fruit species consumed for at least 20% of the time the followed subgroup spent foraging) per month (Table 1). *Brosimium alicastrum* and *Ficus cotinifolia* were the most consumed fruit species in 4 months each. *Manikara zapota, Ficus ovalis* and other *Ficus* species were also important for the spider monkey diet, as they were recorded as the most consumed fruit species for 3 months each.

[TABLE 1 HERE]

The GLMM with the occurrence of fission within half an hour of the beginning of a foraging event as the dependent variable was not statistically different from the null model (N=142, χ^2=2.01, p=0.57). In the LMM only the daily protein content was significantly associated with the daily subgroup size (Table 2). The mean daily subgroup size was larger when the mean protein content of the food patches visited during the day was higher (Figure 1).

[TABLE 2 HERE]

[FIGURE 1 HERE]

Discussion

We found no support for the prediction that fruit abundance and quality in the visited patch affected the likelihood of fissioning within half an hour. By contrast, we found partial support for the predictions on the factors affecting the mean daily subgroup size. Whereas biomass and non-protein energy had no significant effect, the protein amount was positively associated with subgroup size: the mean daily subgroup was larger when the amount of protein in the food patches visited in the day was higher.

A lack of evidence for a relationship between food abundance and fission decisions was also found in the same spider monkey species when fruit abundance and patch size were compared before and after fission events (Asensio et al. 2009). A possible explanation for the lack of support for our first prediction is that fission decisions are not taken based on fruit availability and quality in a given food patch, but they depend on an individual's overall nutritional state. Several studies demonstrate the importance of an individual's nutritional state and nutritional balancing on its behavior. For example, nutritional state is the most important factor predicting the likelihood that an individual initiates a group movement in three species of macaques (Tonkean macaques, *M. tonkeana*, rhesus macaques, *M. mulatta* and Japanese macaques, *M. fuscata yakui*, Sueur et al. 2013); the same possibly happens in geladas (*Theropithecus gelada*), as pregnant females 'decide' the direction of group movements more often than other group members (Dunbar 1985). This likely occurs because following the individual with the greatest nutritional needs allows other group members to also meet their nutritional needs (Sueur et al. 2010). In addition, nutrient balancing between protein and non-protein energy affects patch departure in black and white colobus monkeys (*Colobus guereza*, Johnson et al. 2015). Groups foraged longer and more frequently when the ratio between protein and non-protein energy was constant, highlighting the importance of a nutrient balancing strategy for group decisions. Thus, it is possible that spider monkeys base their fission decision depending on their nutritional states. In order to test this hypothesis, data on complete dietary intake of each individual and nutritional composition of all eaten items will be needed.

Concerning our second hypothesis, several studies show the importance of food abundance (chimpanzees, Anderson et al. 2002; Chancellor et al. 2012; Chapman et al. 1995; spider monkeys, Asensio et al. 2009; Chapman et al. 1995; Schaffner et al. 2012; Southern muriquis, *Brachyteles arachnoides*, Milton 1984; orangutans, van Schaik 1999; see Chapman and Chapman 2000) and of the combined effect of food abundance and quality (black and white colobus monkeys, Chapman et al. 2004; Fashing et al. 2007; Japanese macaques, Hanya et al. 2006; see Hanya and Chapman 2013) on primate association patterns and subgroup size. Species with a high degree of fission-fusion dynamics are expected to adjust their subgroup size according to food abundance and individual nutritional state (Asensio et al. 2009; Chapman 1990; Chapman et al. 1995; Heitaus and Dill 2002; Smith et al. 2008; Smith-Aguilar et al. 2016; Symington 1990). Our findings showed that daily fruit abundance, measured by the biomass of the food patches visited during the day, was not associated with the mean daily subgroup size. By contrast, the mean daily subgroup size was associated with a measure of food quality: the amount of protein estimated in the food patches visited over the course of the day.

We found that spider monkey subgrouping patterns are related to the amount of protein in the visited food patches over the course of the day, supporting the important role of protein found in an earlier study (Felton et al. 2009a). Felton et al. (2009a) suggested that protein has a leveraging effect in spider monkeys whereby the amount of non-protein energy consumed is affected by the digestible protein content of the diet, similar to humans (Simpson & Raubenheimer 2005). In their study, spider monkeys maintained a constant amount of protein in their diet while non-protein energy fluctuated, regardless of the available food. This finding suggests protein could be a key nutritional factor influencing spider monkey foraging (Felton et al. 2009a,b). However, at least three issues make us exercise caution in the interpretation of our results. First, we never observed patch depletion. Spider monkeys left a food patch when many fruits were still present, and monkeys ate fruits from the same patch during the following days, implying that foraging on the patch was still an efficient strategy. Thus, it is likely that they did not adjust subgroup size depending on the daily protein abundance. Second, spider monkeys are mainly frugivorous, but their diet includes young leaves (Di Fiore et al. 2008; unpublished data). Even if leaves typically contain higher concentrations of secondary compounds, such as tannins, and fiber than fruits (Janson and Chapman 1999), it is plausible that individuals can eat leaves to fulfill their protein needs (Milton 1979). Thus, based on our study we cannot know whether leaves are important only in cases of fruit scarcity, as shown in other studies (Schaffner et al. 2012; Wallace 2005), or if they serve a critical role in providing protein year round. Also, we cannot know whether the consumption of fruit, and subsequently the protein obtained through fruit pulp, is the preferred option to fulfill an individual’s protein needs, and whether individuals would prefer to reduce their subgroup size to obtain protein from fruits if fruits are available instead of feeding on leaves without fissioning. Third, we used the amount of crude protein, not available protein to estimate protein intake. The measurement of crude protein is limited because it estimates any nitrogenous compound in a plant as digestible protein, but we know that some nitrogen is contained within secondary compounds like alkaloids, bound to fiber and/or secondary compounds (i.e. Milton and Dintzis, 1981; Conklin-Brittain et al., 1999;

Rothman et al. 2008; Felton et al., 2009b; Wallis et al., 2012). Consequently the amount of protein that is actually digested is likely to be less than the amount of crude protein in the fruits measured in this study. Although we found a positive relationship between crude protein amount and daily subgroup size, it may therefore be possible that the relationship between available protein and daily subgroup size is different.

Given that the high degree of frugivory of spider monkeys is often interpreted in relation to the importance to obtain energy from lipid and carbohydrates from fruits (Di Fiore and Rodman 2001; Rosenberger and Strier 1989; Strier 1992), we predicted that non-protein energy would be a key factor affecting the mean daily subgroup size. However, we found no such effect. One possible reason for this unexpected result is that although spider monkeys may fission (i.e. decrease their subgroup size) to maximize energy availability per individual, they may fusion (i.e. increase their subgroup size) for other reasons, such as predation risk (van Schaik et al. 1983). Similarly, in chimpanzees large subgroups do not always occur when food is abundant (Hashimoto et al. 2003; Newton-Fisher et al. 2000). Another possible reason is that protein may represent a key factor in feeding competition, and thus individuals regulate their grouping patterns to balance nutrient intake and obtain a constant protein supply (cf. Felton et al. 2009a; Johnson et al. 2015), which would be an interesting avenue of research to pursue.

In summary, our findings only partially explain fission-fusion dynamics as a function of food characteristics. Neither abundance nor quality of a food patch affected the likelihood of individuals to fission at the scale of single foraging events. However, mean daily subgroup size was associated with the amount of protein in visited patches. There is evidence that primate density and group size depend on the availability of food resources at longer temporal scales, such as seasonal and monthly (e.g. Asensio et al. 2009; Chapman and Chapman 1999; Hanya and Chapman 2013; Hanya et al. 2006). It may be possible therefore that food availability and food quality affect subgrouping patterns at longer temporal scales, but not at the level of single fission events. Indeed, a study on the same spider monkey community found an increase in individual gregariousness during seasons of high fruit abundance (Smith-Aguilar et al., 2016). Short-term fission decisions instead may be the result of other factors, such as the physiological state based on individual nutritional state (Sueur et al. 2013), the presence of fertile mates (Anderson et al. 2002) and the quality of social relationships between community members (Busia et al. in prep).

Acknowledgements

We thank Anthony R. Denice for his outstanding contribution in data collection, Augusto Canul, Eulogio Canul, Juan Canul and Macedonio Canul for their valuable assistance during fieldwork and tree climbers Octaviano “Tavo” Ciau Dzul and Benito Yam Cocom for their essential assistance during fruit sample collection. We are deeply grateful to Joanna M. Setchell, Annika Felton and a anonymous reviewer for valuable comments on previous versions of the manuscript. We are grateful to Sandra Smith for her overall support and to Gabriel Ramos-Fernandez and Laura G. Vick for sharing the management of the long-term project. We are also indebted to Chester Zoo and The National Geographic Society for financially supporting the long-term project, the Primate Society of Great Britain for a research grant and the Consejo Nacional por la Ciencia y la Tecnologia (CONACyT) for LB’s PhD studentship (CVU n° 490429) and for equipment (n°I0101/152/2014 C-133/2014). We conducted this research with permission from CONANP and SEMARNAT (SGPA/DGVS/00910/13, SGPA/DGVS/02716/14 and SGPA-DGGFS-712-2801-14).

Conflict of Interest: The authors declare that they have no conflict of interest.

Reference

Anderson, D. P., Nordheim, E. V., Boesch, C., & Moermond, T. C. (2002). Factors influencing fission-fusion grouping in chimpanzees in the Taï National Park, Côte d’Ivoire. In Boesch, C., Hohmann G., & Marchant, L. F. (Eds), *Behavioural diversity in chimpanzees and bonobos* (pp. 90-101). Cambridge University Press, Cambridge

Asensio, N., Korstjens, A. H., & Aureli, F. (2009). Fissioning minimizes ranging costs in spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*, 63, 649-659

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R. I. M., Henzi, S. P., Holekamp, K., Korstjens, A. H., Layton, R., Lee, P., Lehmann, J., Manson, J. H., Ramos-Fernandez, G., Strier. K. B., & van Schaik, C. P. (2008). Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49, 627-654

Basabose, A. K. (2004). Fruit availability and chimpanzee party size at Kahuzi Montane Forest, Democratic Republic of Congo. *Primates*, 45, 211–219

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-7. *http://CRAN. R-project. org/package= lme4*

Boesch, C., & Boesch-Achermann, H. (2000). The chimpanzees of the Taï forest: behavioural ecology and evolution. Oxford University Press, Oxford

Chancellor, R. L., Rundus, A. S., & Nyandwi, S. (2012). The influence of seasonal variation on chimpanzee (*Pan troglodytes schweinfurthii*) fallback food consumption, nest group size, and habitat use in Gishwati, a montane rain forest fragment in Rwanda. *International Journal of Primatology*, 33, 115-133

Chapman, C. A. (1990). Ecological constraints on group size in three species of neotropical primates. *Folia Primatologica*, 55, 1–9

Chapman, C. A., & Chapman, L. J. (1999). Implications of small scale variation in ecological conditions for the diet and density of red colobus monkeys. *Primates*, 40, 215-231

Chapman, C. A., & Chapman, L. J. (2000). Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber P (Eds), *On the move: how and why animals travel in groups* (pp. 24–42). University of Chicago Press, Chicago

Chapman, C. A., Chapman, L. J., Naughton-Treves, L., Lawes, M. J., McDowell, L. R. **(**2004). Predicting folivorous primate abundance: Validation of a nutritional model. *American Journal of Primatology*, 62, 55–69

Chapman, C. A., Chapman, L. J., Wangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, 24, 527-531

Chapman, C. A., Rothman, J. M., & Lambert, J. E. (2012). Food as a selective force in primates. In Mitani, J. C., Call, J., Kappeler, P. M., Palombit, R. A., & Silk, J. B. (Eds.). *The evolution of primate societies* (pp. 149- 168). University of Chicago Press, Chicago

Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, 36, 59–70

Conklin-Brittain, N. L., Dierenfeld, E. S., Wrangham, R. W., Norconk, M., & Silver, S. C. (1999). Chemical protein analysis: a comparison of Kjeldahl crude protein and total ninhydrin protein from wild, tropical vegetation. *Journal of Chemical Ecology*, 25, 2601–2622

Croft, D. P., James, R., & Krause, J. (2008). Exploring Animal Social Networks. Princeton University Press, Princeton

Dew, J. L. (2005). Foraging, food choice, and food processing by sympatric ripe-fruit specialists: *Lagothrix lagotricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology*, 26, 1107–1135

Di Fiore, A., Link, A., & Dew, J. L. (2008). Diets of wild spider monkeys. In Campbell, C (Ed.), *Spider monkeys: The biology, behavior and ecology of the genus Ateles* (pp 55-81). Cambridge University Press, New York

Di Fiore, A., & Rodman, P. S. (2001). Time allocation patterns of lowland woolly monkeys (*Lagothrix lagotricha poeppigii*) in a neotropical terra firma forest. *International Journal of Primatology*, 22, 449–480

Dobson, A. J., & Barnett, A. G. (2008). An introduction to generalized linear models. Chapman & Hall/CRC, Boca Raton, Florida

Dunbar, R. I. M. (1985). *Reproductive decisions: an economic analysis of gelada baboon social strategies*. Princeton University Press, Princeton, New Jersey

Fashing, P. J., Dierenfeld, E., & Mowry, C. B. (2007). Influence of plant and soil chemistry on food selection, ranging patterns, and biomass of Colobus guereza in Kakamega Forest, Kenya. *International Journal of Primatology*, 28, 673–703

Fedigan, L. M., & Baxter, M. J. (1984). Sex differences and social organization in free-ranging spider monkeys (*Ateles geoffroyi*). *Primates*, 25, 279–294

Felton, A. M., Felton, A., Raubenheimer, D., Simpson, S. J., Foley, W. J., Wood, J. T., Wallis, I. R., & Lindenmayer, D. B. (2009a). Protein content of diets dictates the daily energy intake of a free-ranging primate. *Behavioral Ecology*, 20, 685-670.

Felton, A. M., Felton, A., Lindenmayer, D. B., & Foley, W. J. (2009b). Nutritional goals of wild primates. *Functional Ecology*, 23, 70-78.

Fimbel, C., Vedder, A., Dierenfeld, E., & Mulindahabi, F. (2001). An ecological basis for large group size in Colobus angolensis in the Nyungwe Forest, Rwanda. *African Journal of Ecology*, 39, 83-92

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology*, 65, 47-55

Gillespie, T. R., & Chapman, C. A. (2001). Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. *Behavioral Ecology and Sociobiology*, 50, 329-338

Gogarten, J. F., Jacob, A. L., Ghai, R. R., Rothman, J. M., Twinomugisha, D., Wasserman, M. D., & Chapman, C. A. (2015). Group size dynamics over 15+ years in an African forest primate community. *Biotropica*, 47, 101-112

Hamard, M., Cheyne, S. M., & Nijman, V. (2010). Vegetation correlates of gibbon density in the peat - swamp forest of the Sabangau catchment, Central Kalimantan, Indonesia. *American Journal of Primatology*, 72, 607-616

Hanya, G., & Chapman, C. A. (2013). Linking feeding ecology and population abundance: a review of food resource limitation on primates. *Ecological Research*, 28, 183-190

Hanya, G., Kiyono, M., Yamada, A., Suzuki, K., Furukawa, M., Yoshida, Y., & Chijiiwa, A. (2006). Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. *Primates*, 47, 275-278

Hanya, G., Stevenson, P., van Noordwijk, M., Te Wong, S., Kanamori, T., Kuze, N., Aiba, S., Chapman, C. A., & van Schaik, C. (2011). Seasonality in fruit availability affects frugivorous primate biomass and species richness. *Ecography*, 34, 1009-1017

Hashimoto, C., Furuichi, T., & Tashiro, Y. (2001). What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *International Journal of Primatology*, 22, 947-959

Hashimoto, C., Suzuki, S., Takenoshita, Y., Yamagiwa, J., Basabose, A. K., Furuichi, T. (2003). How fruit abundance affects the chimpanzee party size: a comparison between four study sites. *Primates*, 44, 77-81

Heithaus, M. R., & Dill, L. M. (2002). Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology*, 83, 480–491

Hosamani, R., & Desai, S. R. (2013). Solar Based Temperature Controlled Fruit Drying System. *International Journal of Research in Instrumentation Engineering*, 2, 4-7

Janson, C. H. (1988). Intra-specific food competition and primate social structure: a synthesis. *Behaviour*, 105, 1–17

Janson, C. H., & Chapman, C. A. (1999). Resources and primate community structure. In Fleagle, J. G., Janson, C. H., & Reed, K. (Eds.), *Primate communities* (pp. 237- 267). Cambridge University Press, Cambridge

Janson, C. H., & Goldsmith, M. L. (1995). Predicting group size in primates: foraging costs and predation risks. *Behavioral Ecology*, 6, 326–336

Janson, C. H., & van Schaik, C. P. (1988). Recognizing the many faces of primate food competition: methods. *Behaviour*, 105, 165–186

Johnson, C. A., Raubenheimer, D., Chapman, C. A., Tombak, K. J., Reid, A. J., & Rothman, J. M. (2015). Macronutrient balancing affects patch departure by guerezas (*Colobus guereza*). *American Journal of Primatology*. doi: 10.1002/ajp.22495

Klein, L. L., & Klein, D. B. (1977). Feeding behaviour of the Colombian spider monkey. In Clutton-Brock, T. H. (Ed), *Primate ecology: studies of feeding and ranging behaviour in lemurs, monkeys and apes* (pp. 153-181). Accademic Press Inc., London

Koenig, A. (2002). Competition for resources and its behavioral consequences among female primates. *International Journal of Primatology*, 23,759-783

Krause, J., & Ruxton, G. D. (2002). *Living in groups*. Oxford University Press, New York

Kummer, H. (1971). Primate societies: group techniques of ecological adaptation. Aldine, Chicago

Itoh, N., & Nishida, T. (2007). Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. *Primates*, 48, 87–96

Lee, D. J., & Putnam, G. B. (1973). The response of rainbow trout to varying protein/energy ratios in a test diet. *The Journal of Nutrition*, 103, 916-922

Lehmann, J.,& Boesch, C. **(**2004). To fission or to fusion: effects of community size on wild chimpanzee (*Pan troglodytes verus*) social organisation. *Behavioral Ecology and Sociobiol*ogy, 56, 207-216

Milton, K. (1979). Factors influencing leaf choice by howler monkeys: A test of some hypotheses of food selection by generalist herbivores. *American Naturalist*, 114, 362-378

Milton, K. (1981). Food choice and digestive strategies of two sympatric primate species. *American Naturalist*, 117, 496-505

Milton, K. (1984). Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroyi 1806). *International Journal of Primatology*, 5, 491–514

Milton, K, & Dintzis, F. (1981). Nitrogen-to-protein conversion factors for tropical plant samples. *Biotropica*, 12, 177-181

National Research Council. (2003). Nutrient requirements of nonhuman primates. Washington, DC: National Academies Press

Newton-Fisher, N. E., Reynolds, V., & Plumptre A. J. (2000). Food supply and chimpanzee (*Pan troglodytes schweinfurthii*) party size in the Budongo Forest Reserve, Uganda. *International Journal of Primatology*, 21, 613-628

O’Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity*, 41, 673-690

Onderdonk, D. A., & Chapman, C. A. (2000). Coping with forest fragmentation: the primates of Kibale National Park, Uganda. *International Journal of Primatology*, 21, 587-611

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2014). R Core Team (2014). nlme: linear and nonlinear mixed effects models. R package version 3.1–117.*URL: http://cran. r-project. org/web/packages/nlme/index.html*

Ramos-Fernandez, G. (2005). Vocal communication in a fission-fusion society: do spider monkeys stay in touch with close associates? *International Journal of Primatology*, 26, 1077- 1092

Ramos-Fernandez, G., & Ayala Orozco, B. (2003). Population size and habitat use of spider monkeys at Punta Laguna, Mexico. — In Marsh, L.K. (Ed.), *Primates in fragments* (pp. 191-209). Kluwer Academic/ Plenum Press, New York

Rebecchini, L., Schaffner, C. M., & Aureli, F. (2011). Risk is a component of social relationships in spider monkeys. *Ethology*, 117, 691-699

Rosenberger, A. L., & Strier, K. B. (1989). Adaptive radiation of the ateline primates. *Journal of Human Evolution*, 18, 717–750

Rothman, J. M., Chapman C. A., & Pell, A. N.. (2008). Fiber - bound nitrogen in gorilla diets: implications for estimating dietary protein intake of primates. *American Journal of Primatology*, 70, 690-694

Rothman, J. M., Chapman, C. A., & Van Soest, P. J. (2012). Methods in primate nutritional ecology: a user's guide. *International Journal of Primatology*, 33, 542-566

Schaffner, C. M., Rebecchini, L., Ramos-Fernandez, G., Vick, L. G., & Aureli, F. (2012). Spider monkeys (*Ateles geoffroyi yucatenensis*) cope with the negative consequences of hurricanes through changes in diet, activity budget, and fission–fusion dynamics. *International Journal of Primatology*, 33, 922-936

Shimooka, Y., Campbell, C. J., Di Fiore, A., Felton, A. M., Izawa, K., Link, A., Nishimura, A., Ramos-Fernandez, G., & Wallace, R. (2008). Demography and group composition of Ateles. In Campbell, C. (Ed.), *Spider monkeys: behavior, ecology & evolution of the genus Ateles* (pp. 329-348). Cambridge University Press, Cambridge

Smith, J. E., Kolowski, J. M., Graham, S. E. D., Holekamp, K. E. (2008). Social and ecological determinants of fission–fusion dynamics in the spotted hyena. *Animal Behavior*, 76, 619–636

Smith-Aguilar, S. E., Ramos-Fernández, G., & Getz, W. M. (2016). Seasonal changes in socio-spatial structure in a group of free-living spider monkeys (*Ateles geoffroyi*). *PloS One,* 11, e0157228

Strier, K. B. (1992). Atelinae adaptations - behavioral strategies and ecological constraints. *American Journal of Physical Anthropology*, 88, 515–524

Sueur, C., Deneubourg, J. L., Petit, O., & Couzin, I. D. (2010). Differences in nutrient requirements imply a non-linear emergence of leaders in animal groups. *PLoS Computational Biology*, 6, e1000917.

Sueur, C., MacIntosh, A. J., Jacobs, A. T., Watanabe, K., & Petit, O. (2013). Predicting leadership using nutrient requirements and dominance rank of group members. *Behavioral Ecology and Sociobiology*, 67, 457-470

Symington, M. M. (1988). Food competition and foraging party size in the black spider monkey (*Ateles paniscus chamek*). *Behaviour*, 105, 117–134

Symington, M. M. (1990). Fission-fusion social organization in *Ateles* and *Pan*. *International Journal of Primatology*, 11, 47-61

Tabachnick, B. G. & Fidell L. S. (2007). *Using multivariate statistics. 6th edition*. Allyn & Bacon, Chicago

Terborgh, J., & Janson, C. H. (1986). The socioecology of primate groups. *Annual Review of Ecology and Systematics*, 17, 111–135

van Schaik, C. P. (1999). The socioecology of fission-fusion sociality in orangutans. *Primates*, 40, 69-86

van Schaik, C. P., & van Hooff, J. A. R. A. M. (1983). On the ultimate causes of primate social systems. *Behaviour*, 85, 91–117

van Schaik, C. P., van Noordwijk, M. A., Wersono, B., & Sutriono E. (1983). Party size and early detection of predators. *Primates*, 24, 211–221

van Soest, P. J., Robertson, J. B., & Lewis, B. A. (1991). Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of Dairy Science*, 74, 3583-3597

Wallace, R. B. (2005). Seasonal variations in diet and foraging behavior of Ateles chamek in a southern Amazonian tropical forest. *International Journal of Primatology*, 26, 1053-1075

Wallace, R. B. (2008). The influence of feeding patch size and relative fruit density on the foraging behavior of the black spider monkey *Ateles chamek*. *Biotropica*, 40, 501-506

Wallis, I. R., Edwards, M. J., Windley, H., Krockenberger, A. K., Felton, A., Quenzer, M., Ganzhorn, J.U., & Foley, W. J. (2012). Food for folivores: nutritional explanations linking diets to population density. *Oecologia*, 169, 281-291.

Williamson, D. K., & Dunbar, R. (1999). Energetics, time budgets and group size. In Lee, P. C. (Ed.) *Comparative primate socioecology* (pp. 320-338), Cambridge University Press, Cambridge

Worman, C. O. D., & Chapman, C. A. (2006). Densities of two frugivorous primates with respect to forest and fragment tree species composition and fruit availability. *International Journal of Primatology,* 27, 203-225

Wrangham, R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262–300

Fig. 1: Mean (±SE) amount of protein in the food patches visited during the day depending on three classes of mean daily subgroup size of spider monkeys in the protected area of Otoch Ma’ax Yetel Kooh, Mexico, October 2013 – September 2014.

Do fruit nutrients affect subgrouping patterns in wild spider monkeys (*Ateles geoffroyi*)?

Laura Busia[1], Colleen M. Schaffner[1], Jessica M. Rothman[2], Filippo Aureli[1,3]

[1]Instituto de Neuroetologia, Universidad Veracruzana, Xalapa, Veracruz, Mexico

[2]Department of Anthropology, Hunter College of the City University of New York, New York, NY, USA

[3]Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moore University, Liverpool, UK

Table 1: Nutritional composition of the fruits eaten most frequently by spider monkeys in the protected area of Otoch Ma'ax Yetel Kooh, Mexico, October 2013 – September 2014.

Month	Species	NDF	Crude Protein	Lipid	TNC	NPE
October	*Ficus ovalis*	60.1	11.2	6.0	15.1	114.4
	Spondias mombim	17.9	4.6	3.9	70.6	317.5
November	*Brosimium alicastrum*	58.4	23.0	7.6	3.0	80.4
	Other *Ficus* sp.	56.7	8.7	5.6	21.1	134.8
December	*Brosimium alicastrum*	37.5	20.8	7.6	3.0	80.4
	Other *Ficus* sp.	59.1	9.7	7.1	16.3	129.1
January	*Diospryros cuneata*	43.8	4.4	2.4	33.1	154.0
	Ficus cotinifolia	50.2	6.4	5.0	33.5	179.0
February	*Ficus cotinifolia*	53.0	6.8	3.3	31.1	154.1
	Ficus ovalis	61.3	7.8	3.7	19.4	110.9

	Other *Ficus* sp.	49.2	6.5	6.9	30.5	184.1
March	*Guazuma ulmifolia*	62.1	6.0	3.6	22.1	120.8
	Manikara zapota	42.6	3.0	7.2	44.8	244.0
	Sideroxylon foetidissimum	24.4	13.0	10.3	37.3	241.9
April	*Ficus cotinifolia*	44.3	5.7	5.0	39.7	203.8
	Manikara zapota	48.6	3.7	5.7	37.9	202.9
May	*Enterolobium cyclocarpum*	24.2	15.5	1.7	55.2	236.1
	Manikara zapota	36.9	2.3	4.7	53.2	255.1
June	*Ficus cotinifolia*	43.4	5.8	5.8	40.0	212.2
	Ficus ovalis	46.8	7.4	6.4	30.3	178.8
August	*Brosimium alicastrum*	19.9	9.0	3.1	62.9	279.5
September	*Brosimium alicastrum*	33.2	14.3	3.3	41.9	197.3
	Spondias mombin	20.1	5.6	3.3	67.3	298.9

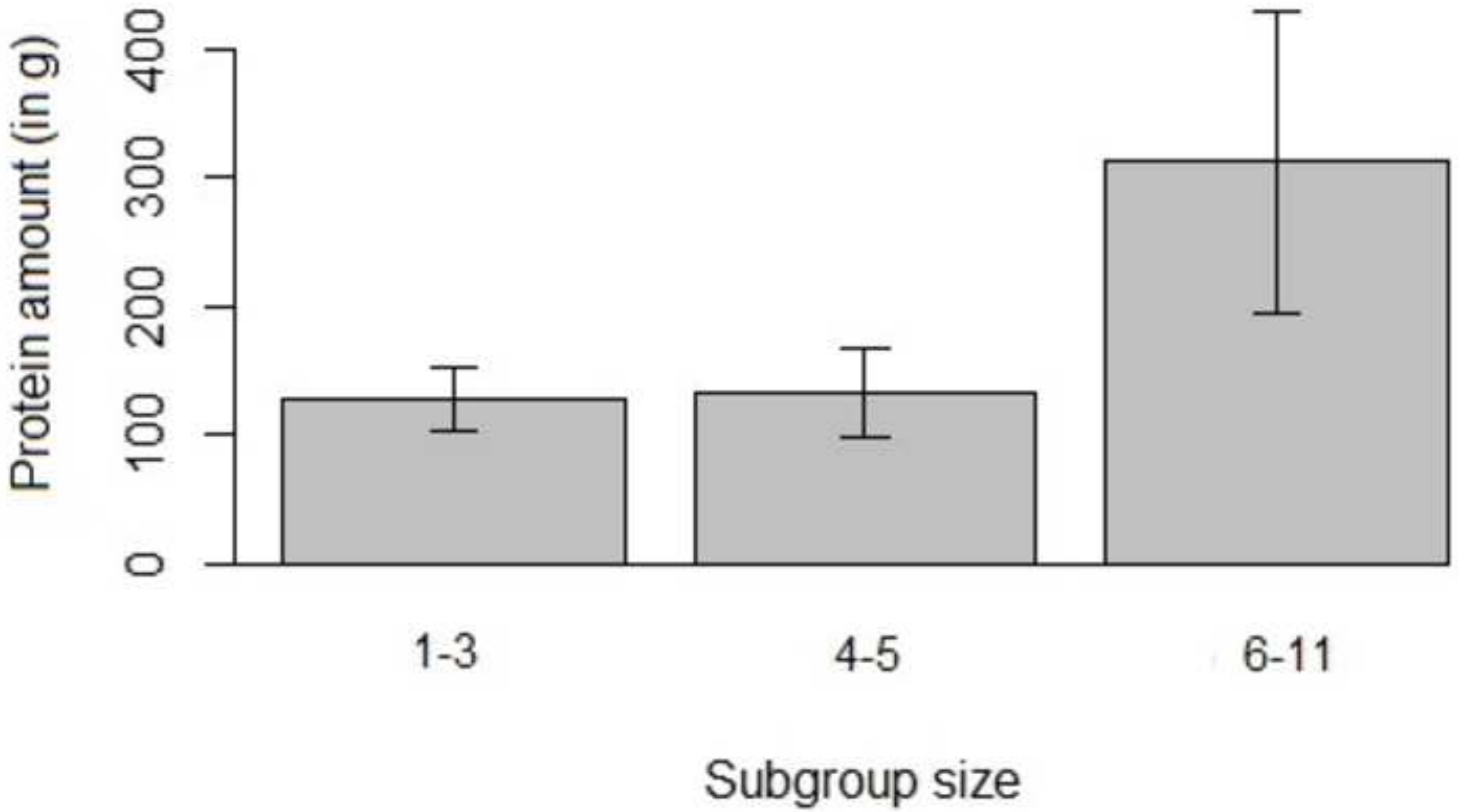
NDF=neutral detergent fibers; TNC=total nonstructural carbohydrates; NPE=non-protein energy. All nutrients are expressed as % of dry matter, apart from NPE that is expressed in kcal per 100 g of dry matter.

In July the most consumed fruit species was *Talisia olivaeformis*, a fruit containing a small portion of aqueous pulp. To obtain 20 grams of dry matter, we would have depleted the fruit patches used by the monkeys. Thus, we preferred not to collect the fruit samples, excluding July from the analyses.

Table 2: Results of linear mixed model testing the influence of biomass, protein content and non-protein energy (NPE) of a food patch on the daily subgroup size of spider monkeys in the protected area of Otoch Ma'ax Yetel Kooh, Mexico, October 2013 – September 2014.

	ß	SE	t	P
Intercept	3.869	0.358	10.806	<0.001
Biomass	<-0.001	<0.001	-0.426	0.672
Protein content	0.005	0.002	3.061	0.003
NPE	<-0.001	<-0.001	-0.354	0.724

The model was statistically different from the null model (likelihood ratio test: N= 68, χ^2=19.9, P=0.012)


Protein amount (in g)
0
100
200
300
400
1-3
4-5
6-11
Subgroup size