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

1   **Do fruit nutrients affect subgrouping patterns in wild spider monkeys (*Ateles***

2   ***geoffroyi*)?**

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26 **Abstract**

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28 are thought to be a strategy to avoid overt competition for food resources. We tested

29 whether food abundance and quality affected such dynamics in a species characterized

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31 spider monkeys (*Ateles geoffroyi*) living in a large community in the protected area of

32 Otoch Ma'ax Yetel Kooh, Yucatan, Mexico. We recorded subgroup size and fission

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34 on the fruit species that the study subjects consumed most. We found no effect of fruit

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36 decisions, but the amount of protein in the food patches visited over the course of the

37 day was a good predictor of subgroup size. While the absence of support for a

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39 temporal scale of the analysis, our findings relating subgroup size to the amount of

40 protein in the visited food patches over the course of the day may be explained by

41 individual spider monkeys attempting to obtain sufficient protein intake from their fruit-

42 based diet.

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

45 quality, *Ateles*

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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.

76   For example, chimpanzee subgroups are smaller during the season with low fruit

77   abundance than during the season with high fruit abundance (e.g. Basabose 2004;

78   Chancellor et al. 2012; Itoh and Nishida 2007). Similarly, the mean subgroup size of

79   spider monkeys is larger when food is more abundant (Asensio et al. 2009; Chapman et

80   al. 1995; Klein and Klein 1977; Smith-Aguilar et al. 2016; Symington 1988) and before

81   than after hurricanes that depleted the fruit supply for several months (Schaffner et al.

82   2012). Food abundance is also the main factor affecting grouping patterns of other

83   primate (Sumatran orangutans, *Pongo abelii*, van Schaik 1999) and non-primate species

84   (bottlenose dolphins, *Tursiops troncatus*, Heithaus and Dill 2002; spotted hyaenas,

85   *Crocuta crocuta*, Smith et al. 2008). A reduction in chimpanzee community size, likely

86   resulting in reduced feeding competition among community members, affects fission-

87   fusion dynamics, with an increase in subgroup size and duration (Boesch and Boesch-

88   Achermann 2000; Lehmann and Boesch 2004).

89   The relationship between food abundance and primate group or subgroup size is

90   not always straightforward (e.g. red colobus monkey, *P. badius*, Gillespie and Chapman

91   2001; chimpanzees, *Pan troglodytes*, Anderson et al. 2002; Hashimoto et al. 2001;

92   Hashimoto et al. 2003; Newton-Fisher et al. 2000; Pennant's red colobus, *P. pennantii,*

93   and black and white colobus monkeys, *Colobus guereza*, Onderdonk and Chapman

94   2000; blue monkeys, *Cercopithecus mitis,* Worman and Chapman 2006), suggesting

95   that abundance might not be the only food-related factor in determining primate

96   abundance and group size. For example, food nutritional quality affects density and

97   group size of some primate species (black and white colobus monkeys, red colobus

98   monkeys, *Piliocolobus trephosceles*, Chapman et al. 2004; Fashing et al. 2007; Japanese

99   macaques, *Macaca fuscata*, Hanya et al. 2006; Hanya and Chapman 2013). Another

100   example of the importance of a food-related factor other than abundance is given by the

101 extraordinary large group size of a group of black-and-white colobus monkeys. The

102 typical group size is 2-20 individuals, but in an area with much higher leaf quality the

103 group reached up to 300 individuals (Fimbel et al. 2001).

104   The definition of food quality varies depending on the species' diet and its

105 digestive capabilities. For example, for highly folivorous primates food quality may be

106 defined as the balance between structural fibers and protein of mature leaves in a habitat

107 (Wasserman and Chapman 2003, Chapman et al. 2004; Fashing et al. 2007, but see

108 Chapman et al. 2012; Johnson et al. 2015), whereas for highly frugivorous Atelines the

109 total energy intake is often considered as a food quality index (Rosenberger and Strier

110 1989; Strier 1992; Di Fiore and Rodman 2001). Several studies of spider monkey diet

111 support this view as individuals select fruits rich in lipids and nonstructural

112 carbohydrates, which can quickly be metabolized into energy (Castellanos 1995; Dew

113 2005; Di Fiore et al. 2008). However, Peruvian spider monkeys (*A. chamek*) maintain a

114 stable protein intake while energy intake varies depending on the composition of food

115 items (Felton et al. 2009a). There is thus no consensus whether it is energy or protein

116 that has the dominant influence on spider monkey food choice and therefore may have

117 the strongest influence on their subgrouping patterns.

118   The temporal scale used to measure food abundance and quality might also play

119 a role in subgroup size changes. For example, a monthly scale may not provide

120 sufficiently precise information about the relationship between food abundance and

121 quality and subgroup size because fissioning reduces within-group feeding competition

122 at a specific moment, and thus a shorter temporal scale is recommended (Asensio et al.

123 2009). Thus, it is plausible that feeding competition depends not only on food

124 abundance but also on food nutritional quality and on the temporal scale used.

125   Spider monkeys represent an excellent candidate species to investigate the role

126   of fruit abundance and quality on fission decisions for two main reasons. First, spider

127   monkeys' high degree of fission–fusion dynamics provides the opportunity to evaluate

128   the effects of fruit abundance and quality on individual association, as subgroup size

129   changes frequently throughout the day (Chapman 1990; Fedigan and Baxter 1984).

130   Second, spider monkeys are mainly frugivorous, as fruits constitute a large component

131   of their diet (mean: 77%; range: 55-90%, Di Fiore et al. 2008), making a plausible

132   estimation of food abundance easier.

133   Our aim was to evaluate the role of feeding competition on grouping patterns of

134   spider monkeys, measuring fruit abundance and nutritional quality on a short temporal

135   scale. We evaluated fruit nutritional quality in two ways: non-protein energy (NPE) (i.e.

136   energy (kcal) obtained from lipids and non-structural carbohydrates) and protein in

137   grams. If fissions are a strategy to avoid within-group feeding competition, we predicted

138   that fruit abundance and quality would affect individual association with other

139   community members. We tested this scenario using two approaches. First, we examined

140   whether the characteristics (i.e. fruit abundance and nutritional quality) of recently

141   visited food patches affected individual fission decisions. We predicted more fission

142   events when fruit abundance and quality were lower. Second, we examined whether the

143   characteristics of the visited food patches affected mean daily subgroup size. We

144   expected that a reduction in fruit abundance would lead to a smaller mean daily

145   subgroup size. We predicted that a lower NPE in visited food patches was associated

146   with a smaller mean daily subgroup size. We similarly predicted that lower protein in

147   visited food patches was associated with a smaller mean daily subgroup size.

148

149   **Methods**

Field site and study subjects

151 The field site is located in the forest surrounding the Punta Laguna lake, within the

152 natural protected area of Otoch Ma'ax Yetel Kooh, Yucatan Peninsula, Mexico (20°38'

153 N, 87°38' W). The natural protected area measures 5367 ha and includes a mosaic of

154 old-growth, semi-evergreen medium forest, with trees up to 25 m in height, and 30–50-

155 year-old successional forest (Ramos-Fernandez and Ayala-Orozco 2003).

156 We studied 22 individuals of a well-habituated community of Geoffroy's spider

157 monkeys living in the protected area (6 adult males, 10 adult females, 1 subadult male,

158 5 subadult females, for age classification see Shimooka et al. 2008). These subjects

159 have been part of a continuous long-term project since 1997 and each monkey was

160 individually recognized by unique facial features and differences in fur coloration.

161

162 *Data collection*

163 We observed monkeys in 4- or 8-hour shifts throughout the daylight hours. The

164 first author and 2 or 3 field assistants followed subgroups about 5.5 hours a day for 129

165 days, for a total observation time of about 700 hours. From October 2013 to September

166 2014, we updated the subgroup membership continuously by identifying each member

167 of the subgroup initially encountered each day and recording all membership changes

168 due to fission and fusion events. We followed the first subgroup met during the day.

169 After a fission event, we followed the subgroup including individuals for which we had

170 fewer focal samples. Subgroup membership was established following a chain rule

171 based on inter-individual distances (Croft et al. 2008). We considered an individual part

172 of the followed subgroup if it was <30 m from any subgroup member; the critical

173 distance of 30 m was empirically established at the study site (Ramos-Fernandez 2005).

174 We recorded fission events when one or more individuals were not seen within 30 m of

175   a subgroup member for 30 min. We recorded fusion events when one or more

176   individuals came within 30 m from any member of the followed subgroup (Rebecchini

177   et al. 2011). We chose the interval of 30 min for recording a fission based on an analysis

178   of data on subgroup membership changes collected independently from this study.

179   To assess food abundance, we collected data on the fruit phenology of the food

180   patch (i.e. one or more trees of the same species) where subgroup members were

181   observed feeding for longer than 5 minutes. We estimated fruit abundance using a

182   logarithmic scale: 1-10 items, 11-100 items; 101-1000 items and 1001-10000 items

183   (Asensio et al. 2009; Chapman et al. 1992).

184   To determine food quality we collected fruit samples of the most consumed tree

185   species, i.e. those consumed for at least 20% of the time the followed subgroup spent

186   foraging during the first 15 days of each month, from the same food patches where we

187   observed the monkeys feed a few days earlier. We counted the number of fruits and

188   extracted the seeds for all species but figs, as spider monkeys extracted seeds before

189   ingesting fruits most of the time. We weighed the mass and dried the pulp with a Nesco

190   dehydrator (American Harvest FD-80) at less than $60^{O}C$ on the same day of sample

191   collection to obtain a minimum of 20 g of dry fruit matter. Considering the potential

192   alteration of nutritional content due to over drying (Hosamani and Desai 2013) and

193   potential differences between species in the duration of the process, we weighed

194   samples every three hours during fruit drying. We considered a sample dried when the

195   weight was equal to the previously measured weight. We put dried samples in a plastic

196   bag containing the relevant information including date, area of collection, fruit species,

197   and a unique alphanumeric code and we stored them in a dark box containing silica to

198   prevent potential damage from humidity. Before analyses, we milled dried samples to

199   1mm particle size using a Wiley mill (Rothman et al. 2012).

200

Nutritional analysis

202   We determined protein, nonstructural carbohydrates and lipid concentrations of

203 fruits in the Nutritional Ecology Laboratory of Hunter College at the City University of

204 New York, according to standard methods (Rothman et al. 2012). We obtained the

205 quantity of nitrogen through combustion, and we multiplied nitrogen by 6.25 to estimate

206 the crude protein concentration. We used this conversion factor to conform with other

207 studies and as a crude measure, although some of this crude protein may not be

208 digestible (Rothman et al., 2008), as it could be bound to fiber or a component of

209 secondary compounds (Milton and Dintzis 1981; Conklin Brittain et al. 1999; Rothman

210 et al. 2012). We obtained the quantity of lipid through petroleum ether extraction using

211 an ANKOM XT15 Fat Analyzer (ANKOM, Macedon, NY). We determined the neutral

212 detergent fiber (NDF) through the detergent method (van Soest et al. 1991) without

213 sodium sulfite and with α amylase using an A200 fiber analyzer (ANKOM, Macedon,

214 NY). We estimated ash by burning the sample at 550C. We estimated the total

215 nonstructural carbohydrates (TNC) by subtracting NDF, lipid, crude protein and ash

216 from 100% (NRC 2003; Rothman et al. 2012).

217

Data analyses

219   To test our predictions we ran a generalized linear mixed model (GLMM) and a

220 linear mixed model (LMM) using the "lme4" and "nlme" packages (Bates et al. 2014;

221 Pinheiro et al. 2014) in R (version 3.1.2 R-Core Team, 2014). We set an alpha level of

222 0.05 for all tests. In the GLMM the occurrence of fission within half an hour of the

223 beginning of a foraging event was considered as the dependent variable (binomial: yes

224 or no). Fission events that did not occur within a half hour of the beginning of a

225 foraging event were excluded from the analyses. We considered a foraging event to take

226 place when at least 75% of subgroup members fed on a food patch. We examined 142

227 foraging events, 46 followed by fission within half an hour and 96 without fission. The

228 biomass of the food patch was estimated by multiplying the dried mass of each fruit

229 (calculated by dividing the dry mass of the sample by the number of items in the

230 sample) by a value representing the fruit abundance of each visited patch. For each

231 category of fruit abundance we used the following values: 5 for the category 1-10 items,

232 50 for the category 11-100 items, 500 for the category 101-1000 items and 5000 for the

233 category 1001-10000 items. We considered the biomass as indicator of food abundance,

234 and we included it as an independent variable. We also included the amount of protein

235 (measured in g) for each food patch as an independent variable. As we knew the number

236 of fruits analyzed, we estimated the grams of protein present in each fruit and multiplied

237 it by the value representing the fruit abundance of the food patch. Finally, we

238 considered the non-protein energy of the food patch as an independent variable. We

239 calculated the non-protein energy (NPE) by summing the energy obtained from total

240 nonstructural carbohydrates (TNC, i.e. TNC amount multiplied by 4) and the energy

241 obtained from lipid (i.e. lipid amount multiplied by 9). We assumed little to no fiber

242 fermentation as spider monkeys have a rapid transit time and an unspecialized gut

243 (Milton 1981).

244   In the LMMs we considered the mean daily subgroup size as the dependent

245 variable. The mean daily subgroup size was calculated based on all subgroup sizes

246 lasting at least one hour during the observations of each day. We included the mean

247 daily amounts of biomass, protein amounts, and NPE calculated considering each food

248 patch visited over the course of the daily observations as independent variables.

249

250   To test for multicollinearity, we used the Variance Inflation Factor (VIF) and all

251   variables had VIF<10 (O'Brien 2007). For all the models we included the month as a

252   random factor and compared them with the null models (Forstmeier and Schielzeth

253   2011) using a likelihood ratio test with the function "anova" (Dobson and Barlett 2008).

254

255   **Results**

256   There were 1-3 most consumed fruit species (i.e. those fruit species consumed for at

257   least 20% of the time the followed subgroup spent foraging) per month (Table 1).

258   *Brosimium alicastrum* and *Ficus cotinifolia* were the most consumed fruit species in 4

259   months each. *Manikara zapota*, *Ficus ovalis* and other *Ficus* species were also

260   important for the spider monkey diet, as they were recorded as the most consumed fruit

261   species for 3 months each.

262

263   [TABLE 1 HERE]

264

265   The GLMM with the occurrence of fission within half an hour of the beginning of a

266   foraging event as the dependent variable was not statistically different from the null

267   model (N=142, χ^2=2.01, p=0.57). In the LMM only the daily protein content was

268   significantly associated with the daily subgroup size (Table 2). The mean daily

269   subgroup size was larger when the mean protein content of the food patches visited

270   during the day was higher (Figure 1).

271

272   [TABLE 2 HERE]

273   [FIGURE 1 HERE]

274

Discussion

275

276 We found no support for the prediction that fruit abundance and quality in the visited

277 patch affected the likelihood of fissioning within half an hour. By contrast, we found

278 partial support for the predictions on the factors affecting the mean daily subgroup size.

279 Whereas biomass and non-protein energy had no significant effect, the protein amount

280 was positively associated with subgroup size: the mean daily subgroup was larger when

281 the amount of protein in the food patches visited in the day was higher.

282   A lack of evidence for a relationship between food abundance and fission

283 decisions was also found in the same spider monkey species when fruit abundance and

284 patch size were compared before and after fission events (Asensio et al. 2009). A

285 possible explanation for the lack of support for our first prediction is that fission

286 decisions are not taken based on fruit availability and quality in a given food patch, but

287 they depend on an individual's overall nutritional state. Several studies demonstrate the

288 importance of an individual's nutritional state and nutritional balancing on its behavior.

289 For example, nutritional state is the most important factor predicting the likelihood that

290 an individual initiates a group movement in three species of macaques (Tonkean

291 macaques, *M. tonkeana*, rhesus macaques, *M. mulatta* and Japanese macaques, *M.*

292 *fuscata yakui*, Sueur et al. 2013); the same possibly happens in geladas (*Theropithecus*

293 *gelada*), as pregnant females 'decide' the direction of group movements more often than

294 other group members (Dunbar 1985). This likely occurs because following the

295 individual with the greatest nutritional needs allows other group members to also meet

296 their nutritional needs (Sueur et al. 2010). In addition, nutrient balancing between

297 protein and non-protein energy affects patch departure in black and white colobus

298 monkeys (*Colobus guereza*, Johnson et al. 2015). Groups foraged longer and more

299 frequently when the ratio between protein and non-protein energy was constant,

300 highlighting the importance of a nutrient balancing strategy for group decisions. Thus, it

301 is possible that spider monkeys base their fission decision depending on their nutritional

302 states. In order to test this hypothesis, data on complete dietary intake of each individual

303 and nutritional composition of all eaten items will be needed.

304   Concerning our second hypothesis, several studies show the importance of food

305 abundance (chimpanzees, Anderson et al. 2002; Chancellor et al. 2012; Chapman et al.

306 1995; spider monkeys, Asensio et al. 2009; Chapman et al. 1995; Schaffner et al. 2012;

307 Southern muriquis, *Brachyteles arachnoides,* Milton 1984; orangutans, van Schaik

308 1999; see Chapman and Chapman 2000) and of the combined effect of food abundance

309 and quality (black and white colobus monkeys, Chapman et al. 2004; Fashing et al.

310 2007; Japanese macaques, Hanya et al. 2006; see Hanya and Chapman 2013) on primate

311 association patterns and subgroup size. Species with a high degree of fission-fusion

312 dynamics are expected to adjust their subgroup size according to food abundance and

313 individual nutritional state (Asensio et al. 2009; Chapman 1990; Chapman et al. 1995;

314 Heitaus and Dill 2002; Smith et al. 2008; Smith-Aguilar et al. 2016; Symington 1990).

315 Our findings showed that daily fruit abundance, measured by the biomass of the food

316 patches visited during the day, was not associated with the mean daily subgroup size.

317 By contrast, the mean daily subgroup size was associated with a measure of food

318 quality: the amount of protein estimated in the food patches visited over the course of

319 the day.

320   We found that spider monkey subgrouping patterns are related to the amount of

321 protein in the visited food patches over the course of the day, supporting the important

322 role of protein found in an earlier study (Felton et al. 2009a). Felton et al. (2009a)

323 suggested that protein has a leveraging effect in spider monkeys whereby the amount of

324 non-protein energy consumed is affected by the digestible protein content of the diet,

13

325   similar to humans (Simpson & Raubenheimer 2005). In their study, spider monkeys

326   maintained a constant amount of protein in their diet while non-protein energy

327   fluctuated, regardless of the available food. This finding suggests protein could be a key

328   nutritional factor influencing spider monkey foraging (Felton et al. 2009a,b). However,

329   at least three issues make us exercise caution in the interpretation of our results. First,

330   we never observed patch depletion. Spider monkeys left a food patch when many fruits

331   were still present, and monkeys ate fruits from the same patch during the following

332   days, implying that foraging on the patch was still an efficient strategy. Thus, it is likely

333   that they did not adjust subgroup size depending on the daily protein abundance.

334   Second, spider monkeys are mainly frugivorous, but their diet includes young leaves

335   (Di Fiore et al. 2008; unpublished data). Even if leaves typically contain higher

336   concentrations of secondary compounds, such as tannins, and fiber than fruits (Janson

337   and Chapman 1999), it is plausible that individuals can eat leaves to fulfill their protein

338   needs (Milton 1979). Thus, based on our study we cannot know whether leaves are

339   important only in cases of fruit scarcity, as shown in other studies (Schaffner et al.

340   2012; Wallace 2005), or if they serve a critical role in providing protein year round.

341   Also, we cannot know whether the consumption of fruit, and subsequently the protein

342   obtained through fruit pulp, is the preferred option to fulfill an individual's protein

343   needs, and whether individuals would prefer to reduce their subgroup size to obtain

344   protein from fruits if fruits are available instead of feeding on leaves without fissioning.

345   Third, we used the amount of crude protein, not available protein to estimate protein

346   intake. The measurement of crude protein is limited because it estimates any

347   nitrogenous compound in a plant as digestible protein, but we know that some nitrogen

348   is contained within secondary compounds like alkaloids, bound to fiber and/or

349   secondary compounds (i.e. Milton and Dintzis, 1981; Conklin-Brittain et al., 1999;

14

350   Rothman et al. 2008; Felton et al., 2009b; Wallis et al., 2012). Consequently the amount

351   of protein that is actually digested is likely to be less than the amount of crude protein in

352   the fruits measured in this study. Although we found a positive relationship between

353   crude protein amount and daily subgroup size, it may therefore be possible that the

354   relationship between available protein and daily subgroup size is different.

355   Given that the high degree of frugivory of spider monkeys is often interpreted in

356   relation to the importance to obtain energy from lipid and carbohydrates from fruits (Di

357   Fiore and Rodman 2001; Rosenberger and Strier 1989; Strier 1992), we predicted that

358   non-protein energy would be a key factor affecting the mean daily subgroup size.

359   However, we found no such effect. One possible reason for this unexpected result is that

360   although spider monkeys may fission (i.e. decrease their subgroup size) to maximize

361   energy availability per individual, they may fusion (i.e. increase their subgroup size) for

362   other reasons, such as predation risk (van Schaik et al. 1983). Similarly, in chimpanzees

363   large subgroups do not always occur when food is abundant (Hashimoto et al. 2003;

364   Newton-Fisher et al. 2000). Another possible reason is that protein may represent a key

365   factor in feeding competition, and thus individuals regulate their grouping patterns to

366   balance nutrient intake and obtain a constant protein supply (cf. Felton et al. 2009a;

367   Johnson et al. 2015), which would be an interesting avenue of research to pursue.

368   In summary, our findings only partially explain fission-fusion dynamics as a

369   function of food characteristics. Neither abundance nor quality of a food patch affected

370   the likelihood of individuals to fission at the scale of single foraging events. However,

371   mean daily subgroup size was associated with the amount of protein in visited patches.

372   There is evidence that primate density and group size depend on the availability of food

373   resources at longer temporal scales, such as seasonal and monthly (e.g. Asensio et al.

374   2009; Chapman and Chapman 1999; Hanya and Chapman 2013; Hanya et al. 2006). It

375 may be possible therefore that food availability and food quality affect subgrouping

376 patterns at longer temporal scales, but not at the level of single fission events. Indeed, a

377 study on the same spider monkey community found an increase in individual

378 gregariousness during seasons of high fruit abundance (Smith-Aguilar et al., 2016).

379 Short-term fission decisions instead may be the result of other factors, such as the

380 physiological state based on individual nutritional state (Sueur et al. 2013), the presence

381 of fertile mates (Anderson et al. 2002) and the quality of social relationships between

382 community members (Busia et al. in prep).

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

401

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717 **Fig. 1**: Mean (±SE) amount of protein in the food patches visited during the day
718 depending on three classes of mean daily subgroup size of spider monkeys in the
719 protected area of Otoch Ma'ax Yetel Kooh, Mexico, October 2013 – September 2014.
720

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

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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)