



## Relationship quality affects fission decisions in wild spider monkeys (*Ateles geoffroyi*)

Journal:	<i>Ethology</i>
Manuscript ID	ETH-17-0022.R1
Manuscript Type:	Research Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Busia, Laura; Universidad Veracruzana, Instituto de Neuroetologia Schaffner, Colleen M.; Universidad Veracruzana, Instituto de Neuroetologia Aureli, Filippo; Universidad Veracruzana, Instituto de Neuroetologia; School of Biological and Earth Sciences. Liverpool John Moores University, Research Centre in Evolutionary Anthropology and Palaeoecology
keywords:	fission-fusion dynamics, relationship quality components, sex classes, partner preference, Ateles

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1 **Relationship quality affects fission decisions**

2 **in wild spider monkeys (*Ateles geoffroyi*)**

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11 Total words: 4518

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## 26 **Abstract**

27 Fission-fusion dynamics are thought to be mainly a response to differential availability  
28 of food resources. However, social factors may also play a role. Here we examined  
29 whether the quality of social relationships between group members affects fission  
30 decisions. During 21 months we collected data on social interactions and fission events  
31 of 22 spider monkeys (*Ateles geoffroyi*) living in a community in the protected area of  
32 Otoch Ma'ax Yetel Kooch, Yucatan, Mexico. By entering seven indexes of social  
33 interactions into a principal component analysis we obtained three components of  
34 relationship quality, which we labelled "compatibility", "value" and "insecurity" given  
35 the relative loadings of the indexes. Our results showed that individuals were more  
36 likely to fission into the same subgroup with community members with whom they  
37 shared higher levels of compatibility and value and lower levels of insecurity. In  
38 addition, individuals preferred to fission into the same subgroup with same-sex group  
39 members, as expected based on what is known for the species. Our findings highlight  
40 the role of social factors in fission decisions. Adjustments in subgroup size are based on  
41 multifaceted social preferences, incorporating previously unexamined aspects of  
42 relationship quality, which are independent from overall levels of affiliative  
43 interactions.

44

45 **Keywords:** fission-fusion dynamics, relationship quality components, sex classes,  
46 partner preference, *Ateles*.

47

## 48 **Introduction**

49 The expression "fission-fusion dynamics" describes the extent of variation in  
50 cohesion and individual membership in a group over time (Aureli et al., 2008; Kummer,

51 1971). Any social system can then be characterized by its degree of fission-fusion  
52 dynamics (Aureli et al., 2008). Fission-fusion dynamics, and thus fission decisions, are  
53 thought to be driven mainly by ecological factors, such as the adjustment of subgroup  
54 size depending on food availability to reduce within-group feeding competition  
55 (Asensio et al., 2009; Aureli & Schaffner, 2008; Chapman, 1990; Chapman et al., 1995;  
56 Kummer, 1971; Symington, 1990). Recently, social factors also started to be taken into  
57 account. For example, association in subgroups is related to the pattern of proximity and  
58 affiliative interactions between individuals (bottlenose dolphins, *Tursiops* sp. Lusseau,  
59 2007; chimpanzees, *Pan troglodytes*, Mitani & Amstler, 2003; Tonkean and rhesus  
60 macaques, *Macaca tonkeana* and *M. mulata*, Sueur et al., 2010; northern muriquis,  
61 *Brachyteles hypoxantus*, Tokuda et al., 2012). These preferences are not what would be  
62 expected if subgroup size adjustments were solely a means to regulate the number of  
63 subgroup members without taking into account the quality of their social relationships  
64 (Ramos-Fernandez & Morales, 2014; te Boekhorst & Hogeweg, 1994).

65 Social relationships are emergent properties reflecting the unique history of  
66 interactions between two individuals (Aureli et al., 2012; Hinde, 1979). Furthermore,  
67 social relationships can be considered an investment (Kummer, 1978), as individuals  
68 gain fitness benefits (Frère et al., 2010; Schülke et al., 2010; Silk et al., 2003, 2009,  
69 2010; see Silk, 2007 for a review). Variation in the patterns of social interactions  
70 between group members results in social relationships that differ in their quality.  
71 According to Cords and Aureli (2000), there are at least three measurable components  
72 of relationship quality: value, compatibility and security. Value is a measure of the  
73 benefits that an individual gains from the relationship with the partner. Compatibility  
74 refers to the general tenor of social interactions between two individuals and reflects the

75 overall degree of tolerance between two individuals. Security is a measure of the  
76 consistency of a partner's responses during social interactions over time.

77 Spider monkeys represent a useful model to study the role of social factors in  
78 fission decisions. They live in communities, but individuals are found mainly in  
79 subgroups that may change size and composition several times a day (Aureli &  
80 Schaffner, 2008). Their high degree of fission-fusion dynamics makes it possible to  
81 evaluate an individual's social preferences about subgroup members multiple times a  
82 day during fission events. The individual is the basic unit in spider monkeys' fission-  
83 fusion dynamics, as each individual other than infants and juveniles, who are always  
84 with their mothers, may fission from or fuse with any other subgroup member (cf.  
85 Aureli et al., 2008). In addition, as males are the philopatric sex and females usually  
86 disperse, male-male relationships are considered of higher quality than female-male and  
87 female-female relationships (Aureli & Schaffner, 2008; Chapman et al., 1989; Fedigan  
88 & Baxter, 1984; Slater et al., 2009). Males may prefer to be in subgroups with other  
89 males, given the need for territorial defence (Wallace, 2008), whereas females may  
90 prefer to be in subgroups with other females, given the need for infant socialization  
91 (Williams et al., 2002) and the overall female attraction to other female's infants  
92 (Altmann, 1980; Hrdy, 2009; Slater et al., 2007).

93 The aim of our study was to evaluate whether relationship quality affected the  
94 choice of subgroup members during fission events in Geoffroy's spider monkeys (*Ateles*  
95 *geoffroyi*). First, we expected spider monkeys to select subgroups with individuals with  
96 whom they share high levels of tolerance, i.e. highly compatible partners. Second, if  
97 their social preferences were multifaceted, we also expected spider monkeys to select  
98 subgroups with highly valuable and predictable individuals. Third, we expected males  
99 and females to prefer fissioning with same-sex individuals.

100

101 **Methods**102 *Field Site and Study Subjects*

103 The field site is located in the protected area of Otoch Ma'ax yetel Kooh, Yucatan  
104 Peninsula, Mexico (20°38' N, 87°38' W). During the present study the community was  
105 composed of 28-43 individuals; the changes were due to immigration, birth and  
106 probable emigration. Our study subjects were 22 individuals of a well-habituated  
107 community of Geoffroy's spider monkeys living in the protected area: 6 adult males, 10  
108 adult females, 1 subadult male, 5 subadult females (see Shimooka et al., 2008 for age-  
109 class definitions). Each monkey was individually recognized using differences in facial  
110 features and fur coloration. During a three-month pilot study the first author was trained  
111 to recognize individuals and behavior.

112

113 *Data Collection*

114 Data were collected using focal animal sampling (Altmann, 1974). From January 2013  
115 to September 2014, 1001 15-minute focal samples (mean  $\pm$  SE: 45.1  $\pm$  18.9 per subject)  
116 were collected by the first author and a well-trained field assistant (inter-observer  
117 reliability was high: Pearson coefficients  $>0.9$ ). Focal animals were chosen based on an  
118 *a priori* list in order to have a similar number of focal samples across subjects. No  
119 animal was sampled more than once per hour.

120 During focal samples, we collected all occurrences and durations of social  
121 interactions involving the focal animal, recording the identity of the partner. We  
122 recorded the following social interactions: grooming (manipulation of another  
123 individual's fur with hands or mouth); co-feeding (feeding on the same fruit species  
124 within 1 m from each other); embrace (putting one or two arms around the other's body

125 while facing each other). Every 2 min, we recorded the identity of individuals within 5  
126 m from the focal animal. We also recorded aggressive interactions, including  
127 conspicuous vocalizations, chases and physical contact, with all-occurrence sampling  
128 (Altmann, 1974) and whether other individuals provided support to the aggressor (no  
129 case of support in favour of the victim was witnessed).

130 Subgroup membership was continuously updated as we recorded the identity of  
131 every member of the initially encountered subgroup and all changes due to fission and  
132 fusion events. An individual was considered part of the followed subgroup if it was <30  
133 m from a subgroup member according to a chain rule established for this study site  
134 (Ramos-Fernandez, 2005; see Croft et al., 2008 for the concept of the chain rule).  
135 Fission was defined as individuals from the followed subgroup separating from one  
136 another in different subgroups and was recorded when one or more individuals were not  
137 seen within 30 m from any member of the followed subgroup for 30 min. Fusion was  
138 defined as individuals from two subgroups joining one another to form a larger  
139 subgroup and was recorded when one or more individuals came within 30 m from any  
140 member of the followed subgroup (Rebecchini et al., 2011).

141

#### 142 *Data Analysis*

143 To extract components of relationship quality, seven indexes based on the recorded  
144 social interactions were calculated for every dyad and entered into a principal  
145 component analysis (PCA). For all indexes we controlled for the opportunity each  
146 individual had to interact with any of the other study subjects by considering the time  
147 each dyad spent in the same subgroup. We used the time in which partners in a dyad  
148 were in the same subgroup during their focal samples (individual A's focal time in  
149 which individual B was also in the subgroup + individual B's focal time in which A was

150 also in the subgroup) to calculate the indexes based on data collected with focal samples  
151 (Table 1). For the aggression index, we used the time in which A and B were in the  
152 same subgroup during our subgroup follows. We also calculated a coefficient of  
153 variation (CV) of the time two individuals spent in the same subgroup (i.e. subgroup  
154 association) over the study period, in order to have an index reflecting the degree of  
155 consistency of social interactions over time. We calculated the subgroup association of  
156 each dyad in 3-month periods, and we calculated the CV for the seven resulting periods  
157 for each dyad; a low CV indicates consistency in the time that the two individuals spent  
158 together in the same subgroup, whereas a high CV indicates that the two individuals  
159 were often together in some periods, but they were rarely together in other periods. In  
160 order to avoid circularity, we included the degree of consistency in subgroup association  
161 over time captured by the CV, and not an index simply based on subgroup association,  
162 in the PCA, as we wanted to examine whether relationship components affected fission  
163 decisions, which are directly linked with subgroup association. We used SPSS version  
164 20 to perform the PCA. A varimax rotation was applied (Tabachnick & Fidell, 2001)  
165 and a minimum eigenvalue of 1.0 was considered to select the components. Coefficients  
166 of correlation  $>|0.6|$  were considered as high loadings.

167

168

**[Table 1 here]**

169

170 To test our predictions, we considered only fission events that led to the  
171 formation of two subgroups. Cases in which one of the two subgroups consisted of only  
172 one individual were excluded from the analyses because it was not possible to compare  
173 the relationship quality of members of both subgroups. We used two analytical  
174 approaches by running two generalized linear mixed models (GLMMs) using the



175 “nlme” packages [Pinheiro et al., 2014] in R (version 3.1.2, R Core Team, 2014). We  
176 compared full models with null models, which included only the random factors  
177 (Forstmeier & Schielzeth, 2011), using a likelihood ratio test with the function anova  
178 (Dobson & Barlett, 2008). We set an alpha level of 0.05 for all tests.

179         In the first model the dependent variable was the proportion of times two  
180 individuals fissioned together. An individual was considered to fission together with  
181 another when they were in the same subgroup after the fission event. We used a  
182 binomial model, entering the dependent variable as the number of times two individuals  
183 fissioned together relative to the number of times they were in the same subgroup  
184 before the fission but they did not fission together. We included the components of  
185 relationship quality and the dyad sex class (i.e. female-female, female-male or male-  
186 male) as independent variables. As random factors we included the identities of the  
187 dyad members.

188         In the second binomial model we considered the subgroup type resulting from  
189 the fission event as the dependent variable. We labelled the subgroup the individual  
190 joined after the fission event as the “chosen subgroup” and the subgroup not joined as  
191 the “non-chosen subgroup”, so that every individual contributed two lines for each  
192 fission event, one for the chosen subgroup and one for the non-chosen subgroup. As  
193 independent variables we included the relationship quality components of that  
194 individual with the average subgroup member (calculated for each PCA extracted  
195 component as the mean of the component scores with the subgroup members). As an  
196 additional independent variable we included the interaction between the sex of the  
197 individual and the proportion of males present in the (chosen or non-chosen) subgroup,  
198 in order to test for potential same-sex preference. As random factors we included the  
199 individual identity and the fission event identification number.

200

201 **Results**

202 Three components were extracted with the PCA, which explained 55.4% of the total  
203 variance of the distribution of the seven indexes across the dyads (Table 2). Component  
204 1 had high positive loadings for grooming and proximity and could therefore represent  
205 “Compatibility”. Component 2 was labelled “Value”, having high positive loadings for  
206 support and co-feeding. Component 3 had high positive loadings for aggression and  
207 inconsistency in subgroup association over time, and was therefore labelled  
208 “Insecurity”.

209

210 **[Table 2 here]**

211

212 The proportion of fissioning together was significantly affected by all the three  
213 relationship quality components and dyad sex class (Table 3). As expected, individuals  
214 with a relationship higher in compatibility and value and lower in insecurity were more  
215 likely to fission together (Figure 1). The proportion of fissioning together was lower in  
216 female-male dyads than in female-female and male-male dyads, whereas there was no  
217 difference between female-female and male-male dyads (Figure 2).

218

219 **[Figure 1 here]**

220

221 **[Figure 2 here]**

222

223 **[Table 3 here]**

224



250 fission-fusion dynamics. In this respect we would need to be cautious about the  
251 conclusions we can draw from our seven indexes. If social interaction indexes were  
252 simply due to the unbalanced data collection across subjects (e.g. social interaction rates  
253 depending on the amount of time animals spend in the same subgroup), we would  
254 expect all indexes to be highly correlated with one another. By contrast, the PCA  
255 extracted three components that by definition are not correlated with one another. For  
256 example, only the grooming index loaded highly on a component with the proximity  
257 index, whereas the co-feeding and embrace indexes loaded on two separated  
258 components. Thus, the components we used to characterize the quality of social  
259 relationships appear to be robust to the potential influence of the unbalanced data  
260 collection across subjects.

261       The prediction that relationship quality would affect the choice of subgroup  
262 members during fission events was fully supported using two analytical approaches.  
263 During fission events spider monkeys preferred subgroup members with whom they  
264 shared high levels of compatibility and value, and low levels of insecurity. Similarly,  
265 spider monkeys preferred to fission into subgroups in which they had higher  
266 compatibility and higher security with the average subgroup member. As fission is  
267 expected to occur in order to decrease feeding competition by adjusting subgroup size to  
268 food availability (Asensio et al., 2008; Chapman, 1990; Chapman et al., 1995; Kummer,  
269 1971; Symington, 1990), our findings show that such adjustments follow social  
270 preferences. Although previous studies indicate that subgroup association patterns are  
271 related to affiliative interactions (Lusseau, 2007; Mitani & Amstler, 2003; Sueur et al.,  
272 2010; Tokuda et al., 2012) and relative dominance rank (Smith et al., 2007), our study  
273 goes a step further by providing evidence that the social preferences expressed at fission  
274 are multifaceted. We found that individuals fission with group members with whom

275 they have high grooming and proximity scores, i.e. more compatible partners. More  
276 importantly, our findings reveal that social preferences are also based on the levels of  
277 value and insecurity with other subgroup members, which are independent from the  
278 levels of compatibility. These preferences are qualitatively different from what would  
279 be expected if fission decisions were simply the outcome of a process to reduce the  
280 number of subgroup members without taking into account the extent of variation in the  
281 quality of their social relationships (see Introduction).

282         The prediction concerning dyad sex classes was also supported using both  
283 analytical approaches. During fission events spider monkeys were more likely to fission  
284 with same-sex subgroup members. Similarly, they preferred to fission into subgroups  
285 with a higher proportion of individuals of their own sex. Males may prefer to be in  
286 subgroups with other males because they cooperatively defend the territory (Aureli et  
287 al., 2006; Wallace, 2008), whereas females may prefer to fission with other females to  
288 give the dependent offspring the opportunity to socialize (Foerster et al., 2015; Murray  
289 et al., 2014; Williams et al., 2002). In addition, for both sexes reducing conflict about  
290 decisions may promote preferences for being in the same subgroup with same-sex  
291 individuals (Hartwell et al., 2014), which are likely to have similar needs and therefore  
292 engage in similar activities (Conradt & Roper, 2000).

293         In conclusion, our findings contribute to a better understanding of the  
294 importance of social factors in fission decisions. Fission-fusion dynamics are certainly  
295 driven by ecological factors, and subgroup size likely depends on food availability  
296 (Asensio et al., 2009; Aureli & Schaffner, 2008; Chapman, 1990; Kummer, 1971;  
297 Smith-Aguilar et al., 2016; Symington, 1990) and food quality (Busia et al., 2016).  
298 However, social and ecological factors may play a role on different time scales.  
299 Whereas grouping patterns are affected by food availability on a monthly or seasonal

300 scale (e.g. Asensio et al., 2009; Chapman & Chapman, 1999), individual decisions to  
301 fission according to social preferences occur on a shorter temporal scale. We showed  
302 that these social preferences are multifaceted. Not only do these preferences reflect  
303 overall levels of tolerance (i.e. compatibility), but they also depend on aspects of  
304 relationship quality previously unexamined for fission-fusion dynamics, such as value  
305 and security.

306

307 **Conflict of interest:** authors have no conflict of interest to declare

308

### 309 **Acknowledgements**

310 We thank Anthony R. Denice for his outstanding contribution in data collection,  
311 Augusto Canul, Eulogio Canul, Juan Canul and Macedonio Canul for their valuable  
312 assistance during fieldwork and Sandra Smith for her overall support. We are grateful to  
313 Gabriel Ramos-Fernández and Laura G. Vick for sharing the management of the long-  
314 term project. We are also grateful to Dr. Luis Ebensperger, Dr. Lauren Brent and an  
315 anonymous reviewer for their comments that helped us to improve a previous version of  
316 the manuscript. We are also indebted to Chester Zoo and The National Geographic  
317 Society for financially supporting the long-term project. We thank the Consejo Nacional  
318 por la Ciencia y la Tecnología (CONACyT) for LB's PhD studentship (CVU n°  
319 490429) and for equipment (n°I0101/152/2014 C-133/2014). We conducted this  
320 research with permission from CONANP and SEMARNAT (SGPA/DGVS/00910/13  
321 and SGPA/DGVS/02716/14).

322

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469

470 **Figure 1:** The mean ( $\pm$ SE) proportion of fissioning together for dyads of low and high  
471 levels of compatibility, value and insecurity. Low levels are those lower than the  
472 median, whereas high levels are those higher than the median of the three extracted  
473 components.

474

475 **Figure 2:** The mean ( $\pm$ SE) proportion of fissioning together for the three dyad sex  
476 classes. FF: female-female dyads; FM: female-male dyads; MM: male-male dyads.

477

For Peer Review

1                   **Relationship quality affects fission decisions**  
2                   **in wild spider monkeys (*Ateles geoffroyi*)**

3                   **Laura Busia<sup>a,\*</sup>, Colleen M. Schaffner<sup>a</sup>, Filippo Aureli<sup>a,b</sup>**

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## 26 **Abstract**

27 Fission-fusion dynamics are thought to be mainly a response to differential availability  
28 of food resources. However, social factors may also play a role. Here we examined  
29 whether the quality of social relationships between group members affects fission  
30 decisions. During 21 months we collected data on social interactions and fission events  
31 of 22 spider monkeys (*Ateles geoffroyi*) living in a community in the protected area of  
32 Otoch Ma'ax Yetel Kooch, Yucatan, Mexico. By entering seven indexes of social  
33 interactions into a principal component analysis we obtained three components of  
34 relationship quality, which we labelled "compatibility", "value" and "insecurity" given  
35 the relative loadings of the indexes. Our results showed that individuals were more  
36 likely to fission into the same subgroup with community members with whom they  
37 shared higher levels of compatibility and value and lower levels of insecurity. In  
38 addition, individuals preferred to fission into the same subgroup with same-sex group  
39 members, as expected based on what is known for the species. Our findings highlight  
40 the role of social factors in fission decisions. Adjustments in subgroup size are based on  
41 multifaceted social preferences, incorporating previously unexamined aspects of  
42 relationship quality, which are independent from overall levels of affiliative  
43 interactions.

44

45 **Keywords:** fission-fusion dynamics, relationship quality components, sex classes,  
46 partner preference, *Ateles*.

47

## 48 **Introduction**

49 The expression "fission-fusion dynamics" describes the extent of variation in  
50 cohesion and individual membership in a group over time (Aureli et al., 2008; Kummer,

51 1971). Any social system can then be characterized by its degree of fission-fusion  
52 dynamics (Aureli et al., 2008). Fission-fusion dynamics, and thus fission decisions, are  
53 thought to be driven mainly by ecological factors, such as the adjustment of subgroup  
54 size depending on food availability to reduce within-group feeding competition  
55 (Asensio et al., 2009; Aureli & Schaffner, 2008; Chapman, 1990; Chapman et al., 1995;  
56 Kummer, 1971; Symington, 1990). Recently, social factors also started to be taken into  
57 account. For example, association in subgroups is related to the pattern of proximity and  
58 affiliative interactions between individuals (bottlenose dolphins, *Tursiops* sp. Lusseau,  
59 2007; chimpanzees, *Pan troglodytes*, Mitani & Amstler, 2003; Tonkean and rhesus  
60 macaques, *Macaca tonkeana* and *M. mulata*, Sueur et al., 2010; northern muriquis,  
61 *Brachyteles hypoxantus*, Tokuda et al., 2012). These preferences are not what would be  
62 expected if subgroup size adjustments were solely a means to regulate the number of  
63 subgroup members without taking into account the quality of their social relationships  
64 (Ramos-Fernandez & Morales, 2014; te Boekhorst & Hogeweg, 1994).

65 Social relationships are emergent properties reflecting the unique history of  
66 interactions between two individuals (Aureli et al., 2012; Hinde, 1979). Furthermore,  
67 social relationships can be considered an investment (Kummer, 1978), as individuals  
68 gain fitness benefits (Frère et al., 2010; Schülke et al., 2010; Silk et al., 2003, 2009,  
69 2010; see Silk, 2007 for a review). Variation in the patterns of social interactions  
70 between group members results in social relationships that differ in their quality.  
71 According to Cords and Aureli (2000), there are at least three measurable components  
72 of relationship quality: value, compatibility and security. Value is a measure of the  
73 benefits that an individual gains from the relationship with the partner. Compatibility  
74 refers to the general tenor of social interactions between two individuals and reflects the



75 overall degree of tolerance between two individuals. Security is a measure of the  
76 consistency of a partner's responses during social interactions over time.

77 Spider monkeys represent a useful model to study the role of social factors in  
78 fission decisions. They live in communities, but individuals are found mainly in  
79 subgroups that may change size and composition several times a day (Aureli &  
80 Schaffner, 2008). Their high degree of fission-fusion dynamics makes it possible to  
81 evaluate an individual's social preferences about subgroup members multiple times a  
82 day during fission events. The individual is the basic unit in spider monkeys' fission-  
83 fusion dynamics, as each individual **other than infants and juveniles, who are always**  
84 **with their mothers**, may fission from or fuse with any other subgroup member (cf.  
85 Aureli et al., 2008). In addition, as males are the philopatric sex and females usually  
86 disperse, male-male relationships are considered of higher quality than female-male and  
87 female-female relationships (Aureli & Schaffner, 2008; Chapman et al., 1989; Fedigan  
88 & Baxter, 1984; Slater et al., 2009). Males may prefer to be in subgroups with other  
89 males, given the need for territorial defence (Wallace, 2008), whereas females may  
90 prefer to be in subgroups with other females, given the need for infant socialization  
91 (Williams et al., 2002) and the overall female attraction to other female's infants  
92 (Altmann, 1980; Hrdy, 2009; Slater et al., 2007).

93 The aim of our study was to evaluate whether relationship quality affected the  
94 choice of subgroup members during fission events in Geoffroy's spider monkeys (*Ateles*  
95 *geoffroyi*). First, we expected spider monkeys to select subgroups with individuals with  
96 whom they share high levels of tolerance, i.e. highly compatible partners. Second, if  
97 their social preferences were multifaceted, we also expected spider monkeys to select  
98 subgroups with highly valuable and predictable individuals. Third, we expected males  
99 and females to prefer fissioning with same-sex individuals.

100

101 **Methods**102 *Field Site and Study Subjects*

103 The field site is located in the protected area of Otoch Ma'ax yetel Kooh, Yucatan  
104 Peninsula, Mexico (20°38' N, 87°38' W). During the present study the community was  
105 composed of 28-43 individuals; the changes were due to immigration, birth and  
106 probable emigration. Our study subjects were 22 individuals of a well-habituated  
107 community of Geoffroy's spider monkeys living in the protected area: 6 adult males, 10  
108 adult females, 1 subadult male, 5 subadult females (see Shimooka et al., 2008 for age-  
109 class definitions). Each monkey was individually recognized using differences in facial  
110 features and fur coloration. During a three-month pilot study the first author was trained  
111 to recognize individuals and behavior.

112

113 *Data Collection*

114 Data were collected using focal animal sampling (Altmann, 1974). From January 2013  
115 to September 2014, 1001 15-minute focal samples (mean  $\pm$  SE: 45.1  $\pm$  18.9 per subject)  
116 were collected by the first author and a well-trained field assistant (inter-observer  
117 reliability was high: Pearson coefficients >0.9). Focal animals were chosen based on an  
118 *a priori* list in order to have a similar number of focal samples across subjects. No  
119 animal was sampled more than once per hour.

120 During focal samples, we collected all occurrences and durations of social  
121 interactions involving the focal animal, recording the identity of the partner. We  
122 recorded the following social interactions: grooming (manipulation of another  
123 individual's fur with hands or mouth); co-feeding (feeding on the same fruit species  
124 within 1 m from each other); embrace (putting one or two arms around the other's body

125 while facing each other). Every 2 min, we recorded the identity of individuals within 5  
126 m from the focal animal. We also recorded aggressive interactions, including  
127 conspicuous vocalizations, chases and physical contact, with all-occurrence sampling  
128 (Altmann, 1974) and whether other individuals provided support to the aggressor (no  
129 case of support in favour of the victim was witnessed).

130 Subgroup membership was continuously updated as we recorded the identity of  
131 every member of the initially encountered subgroup and all changes due to fission and  
132 fusion events. An individual was considered part of the followed subgroup if it was <30  
133 m from a subgroup member according to a chain rule established for this study site  
134 (Ramos-Fernandez, 2005; see Croft et al., 2008 for the concept of the chain rule).  
135 Fission was defined as individuals from the followed subgroup separating from one  
136 another in different subgroups and was recorded when one or more individuals were not  
137 seen within 30 m from any member of the followed subgroup for 30 min. Fusion was  
138 defined as individuals from two subgroups joining one another to form a larger  
139 subgroup and was recorded when one or more individuals came within 30 m from any  
140 member of the followed subgroup (Rebecchini et al., 2011).

141

#### 142 *Data Analysis*

143 To extract components of relationship quality, seven indexes based on the recorded  
144 social interactions were calculated for every dyad and entered into a principal  
145 component analysis (PCA). For all indexes we controlled for the opportunity each  
146 individual had to interact with any of the other study subjects by considering the time  
147 each dyad spent in the same subgroup. We used the time in which partners in a dyad  
148 were in the same subgroup during their focal samples (individual A's focal time in  
149 which individual B was also in the subgroup + individual B's focal time in which A was

150 also in the subgroup) to calculate the indexes based on data collected with focal samples  
151 (Table 1). For the aggression index, we used the time in which A and B were in the  
152 same subgroup during our subgroup follows. We also calculated a coefficient of  
153 variation (CV) of the time two individuals spent in the same subgroup (i.e. subgroup  
154 association) over the study period, **in order to have an index reflecting the degree of**  
155 **consistency of social interactions over time.** We calculated the subgroup association  
156 of each dyad in 3-month periods, and we calculated the CV for the seven resulting  
157 periods for each dyad; a low CV indicates consistency in the time that the two  
158 individuals spent together in the same subgroup, whereas a high CV indicates that the  
159 two individuals were often together in some periods, but they were rarely together in  
160 other periods. **In order to avoid circularity, we included the degree of consistency in**  
161 **subgroup association over time captured by the CV, and** not an index simply based  
162 on subgroup association, in the PCA, as we wanted to examine whether relationship  
163 components affected fission decisions, which are directly linked with subgroup  
164 association. We used SPSS version 20 to perform the PCA. A varimax rotation was  
165 applied (Tabachnick & Fidell, 2001) and a minimum eigenvalue of 1.0 was considered  
166 to select the components. Coefficients of correlation  $>|0.6|$  were considered as high  
167 loadings.

168

169

**[Table 1 here]**

170

171 To test our predictions, we considered only fission events that led to the  
172 formation of two subgroups. Cases in which one of the two subgroups consisted of only  
173 one individual were excluded from the analyses because it was not possible to compare  
174 the relationship quality of members of both subgroups. We used two analytical

175 approaches by running two generalized linear mixed models (GLMMs) using the  
176 “nlme” packages [Pinheiro et al., 2014] in R (version 3.1.2, R Core Team, 2014). We  
177 **compared full models with null models, which included only the random factors**  
178 **(Forstmeier & Schielzeth, 2011), using a likelihood ratio test with the function**  
179 **anova (Dobson & Barlett, 2008).** We set an alpha level of 0.05 for all tests.

180         In the first model the dependent variable was the proportion of **times two**  
181 **individuals** fissioned together. An individual was considered to fission together with  
182 another when they were in the same subgroup after the fission event. We **used a**  
183 **binomial model**, entering the dependent variable as the number of times two  
184 individuals fissioned together relative to the number of times they were in the same  
185 subgroup before the fission but they did not fission together. We included the  
186 components of relationship quality and the dyad sex class (i.e. female-female, female-  
187 male or male-male) as independent variables. As random factors we included the  
188 identities of the dyad members.

189         In the second **binomial** model we considered the subgroup type resulting from  
190 the fission event as the dependent variable. We labelled the subgroup the individual  
191 joined after the fission event as the “chosen subgroup” and the subgroup not joined as  
192 the “non-chosen subgroup”, so that every individual contributed two lines for each  
193 fission event, one for the chosen subgroup and one for the non-chosen subgroup. As  
194 independent variables we included the relationship quality components of that  
195 individual with the average subgroup member (calculated for each PCA extracted  
196 component as the mean of the component scores with the subgroup members). As an  
197 additional independent variable we included the interaction between the sex of the  
198 individual and the proportion of males present in the (chosen or non-chosen) subgroup,

199 in order to test for potential same-sex preference. As random factors we included the  
200 individual identity and the fission event identification number.

201

## 202 **Results**

203 Three components were extracted with the PCA, which explained 55.4% of the total  
204 variance of the distribution of the seven indexes across the dyads (Table 2). Component  
205 1 had high positive loadings for grooming and proximity and could therefore represent  
206 “Compatibility”. Component 2 was labelled “Value”, having high positive loadings for  
207 support and co-feeding. Component 3 had high positive loadings for aggression and  
208 inconsistency in subgroup association over time, and was therefore labelled  
209 “Insecurity”.

210

211 **[Table 2 here]**

212

213 The proportion of fissioning together was significantly affected by all the three  
214 relationship quality components and dyad sex class (Table 3). As expected, individuals  
215 with a relationship higher in compatibility and value and lower in insecurity were more  
216 likely to fission together (Figure 1). The proportion of fissioning together was lower in  
217 female-male dyads than in female-female and male-male dyads, whereas there was no  
218 difference between female-female and male-male dyads (Figure 2).

219

220 **[Figure 1 here]**

221

222 **[Figure 2 here]**

223

224 [Table 3 here]

225

226 The second model revealed that compatibility scores with the average subgroup  
227 member were significantly higher and insecurity scores significantly lower in the  
228 chosen subgroup than in the non-chosen subgroup, but there was no difference for value  
229 scores (Table 4). As there was a significant effect of the interaction between the  
230 individual sex and the proportion of males in the subgroup, we reran the model for  
231 males and females separately. In the case of males the proportion of males was lower in  
232 the non-chosen subgroup ( $\beta = -3.80$ ,  $z = -11.29$ ,  $p < 0.001$ ,  $N = 436$ ), whereas in the case  
233 of females the proportion of males was higher in the non-chosen subgroup ( $\beta = 1.58$ ,  $z =$   
234  $3.72$ ,  $p < 0.001$ ,  $N = 314$ ). The two results indicate the preference to fission in same-sex  
235 biased subgroups.

236

237 [Table 4 here]

238

### 239 Discussion

240 The components of social relationships extracted in our study are similar to those  
241 identified in previous studies (Fraser & Bugnyar, 2010; Fraser et al., 2008; Majolo et  
242 al., 2010), which overall correspond to the theoretically proposed components of value,  
243 security and compatibility (Cords & Aureli, 2000). Previous research on the same group  
244 of spider monkeys revealed only two components (Rebecchini et al., 2011); however,  
245 only five indexes were used, and measures for support, co-feeding and consistency of  
246 interaction over time were not included. The methodology used to extract the  
247 components assured that they were independent from one another, which was key for  
248 the purpose of our study (see below).

249 Rates or duration of social interactions may be affected by an unbalanced data  
250 collection across subjects, which is basically inevitable in species with a high degree of  
251 fission-fusion dynamics. In this respect we would need to be cautious about the  
252 conclusions we can draw from our seven indexes. If social interaction indexes were  
253 simply due to the unbalanced data collection across subjects (e.g. social interaction rates  
254 depending on the amount of time animals spend in the same subgroup), we would  
255 expect all indexes to be highly correlated with one another. By contrast, the PCA  
256 extracted three components that by definition are not correlated with one another. For  
257 example, only the grooming index loaded highly on a component with the proximity  
258 index, whereas the co-feeding and embrace indexes loaded on two separated  
259 components. Thus, the components we used to characterize the quality of social  
260 relationships appear to be robust to the potential influence of the unbalanced data  
261 collection across subjects.

262 The prediction that relationship quality would affect the choice of subgroup  
263 members during fission events was fully supported using two analytical approaches.  
264 During fission events spider monkeys preferred subgroup members with whom they  
265 shared high levels of compatibility and value, and low levels of insecurity. Similarly,  
266 spider monkeys preferred to fission into subgroups in which they had higher  
267 compatibility and higher security with the average subgroup member. As fission is  
268 expected to occur in order to decrease feeding competition by adjusting subgroup size to  
269 food availability (Asensio et al., 2008; Chapman, 1990; Chapman et al., 1995; Kummer,  
270 1971; Symington, 1990), our findings show that such adjustments follow social  
271 preferences. Although previous studies indicate that subgroup association patterns are  
272 related to affiliative interactions (Lusseau, 2007; Mitani & Amstler, 2003; Sueur et al.,  
273 2010; Tokuda et al., 2012) and relative dominance rank (Smith et al., 2007), our study



274 goes a step further by providing evidence that the social preferences expressed at fission  
275 are multifaceted. We found that individuals fission with group members with whom  
276 they have high grooming and proximity scores, i.e. more compatible partners. More  
277 importantly, our findings reveal that social preferences are also based on the levels of  
278 value and insecurity with other subgroup members, which are independent from the  
279 levels of compatibility. These preferences are qualitatively different from what would  
280 be expected if fission decisions were simply the outcome of a process to reduce the  
281 number of subgroup members without taking into account the extent of variation in the  
282 quality of their social relationships (see Introduction).

283         The prediction concerning dyad sex classes was also supported using both  
284 analytical approaches. During fission events spider monkeys were more likely to fission  
285 with same-sex subgroup members. Similarly, they preferred to fission into subgroups  
286 with a higher proportion of individuals of their own sex. Males may prefer to be in  
287 subgroups with other males because they cooperatively defend the territory (Aureli et  
288 al., 2006; Wallace, 2008), whereas females may prefer to fission with other females to  
289 give the dependent offspring the opportunity to socialize (Foerster et al., 2015; Murray  
290 et al., 2014; Williams et al., 2002). In addition, for both sexes reducing conflict about  
291 decisions may promote preferences for being in the same subgroup with same-sex  
292 individuals (Hartwell et al., 2014), which are likely to have similar needs and therefore  
293 engage in similar activities (Conradt & Roper, 2000).

294         In conclusion, our findings contribute to a better understanding of the  
295 importance of social factors in fission decisions. Fission-fusion dynamics are certainly  
296 driven by ecological factors, and subgroup size likely depends on food availability  
297 (Asensio et al., 2009; Aureli & Schaffner, 2008; Chapman, 1990; Kummer, 1971;  
298 Smith-Aguilar et al., 2016; Symington, 1990) and food quality (Busia et al., 2016).

299 However, social and ecological factors may play a role on different time scales.  
300 Whereas grouping patterns are affected by food availability on a monthly or seasonal  
301 scale (e.g. Asensio et al., 2009; Chapman & Chapman, 1999), individual decisions to  
302 fission according to social preferences occur on a shorter temporal scale. We showed  
303 that these social preferences are multifaceted. Not only do these preferences reflect  
304 overall levels of tolerance (i.e. compatibility), but they also depend on aspects of  
305 relationship quality previously unexamined for fission-fusion dynamics, such as value  
306 and security.

307

308 **Conflict of interest:** authors have no conflict of interest to declare

309

### 310 **Acknowledgements**

311 We thank Anthony R. Denice for his outstanding contribution in data collection,  
312 Augusto Canul, Eulogio Canul, Juan Canul and Macedonio Canul for their valuable  
313 assistance during fieldwork and Sandra Smith for her overall support. We are grateful to  
314 Gabriel Ramos-Fernández and Laura G. Vick for sharing the management of the long-  
315 term project. We are also grateful to Dr. Luis Ebensperger, Dr. Lauren Brent and an  
316 anonymous reviewer for their comments that helped us to improve a previous version of  
317 the manuscript. We are also indebted to Chester Zoo and The National Geographic  
318 Society for financially supporting the long-term project. We thank the Consejo Nacional  
319 por la Ciencia y la Tecnología (CONACyT) for LB's PhD studentship (CVU n°  
320 490429) and for equipment (n°I0101/152/2014 C-133/2014). We conducted this  
321 research with permission from CONANP and SEMARNAT (SGPA/DGVS/00910/13  
322 and SGPA/DGVS/02716/14).

323

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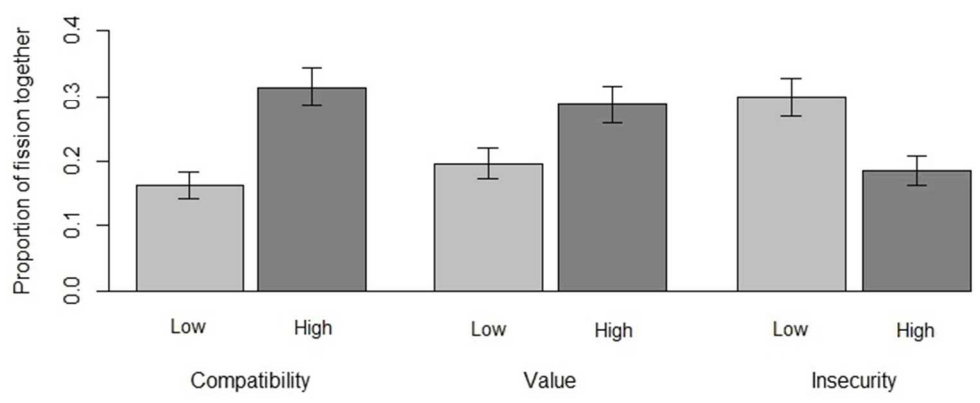
471 **Figure 1:** The mean ( $\pm$ SE) proportion of fissioning together for dyads of low and high  
472 levels of compatibility, value and insecurity. Low levels are those lower than the  
473 median, whereas high levels are those higher than the median of the three extracted  
474 components.

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476 **Figure 2:** The mean ( $\pm$ SE) proportion of fissioning together for the three dyad sex  
477 classes. FF: female-female dyads; FM: female-male dyads; MM: male-male dyads.

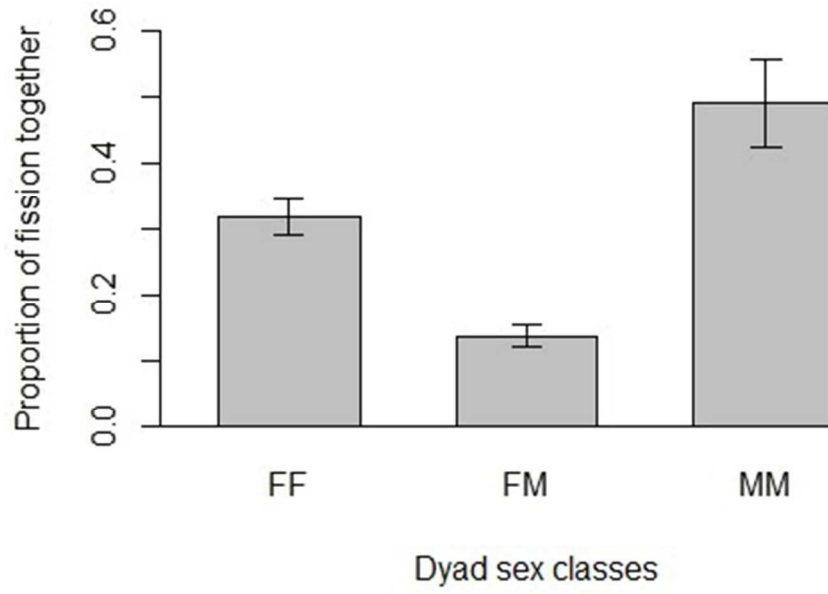
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