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

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1 **Relationship quality affects fission decisions**

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

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4

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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

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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*)**

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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

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309

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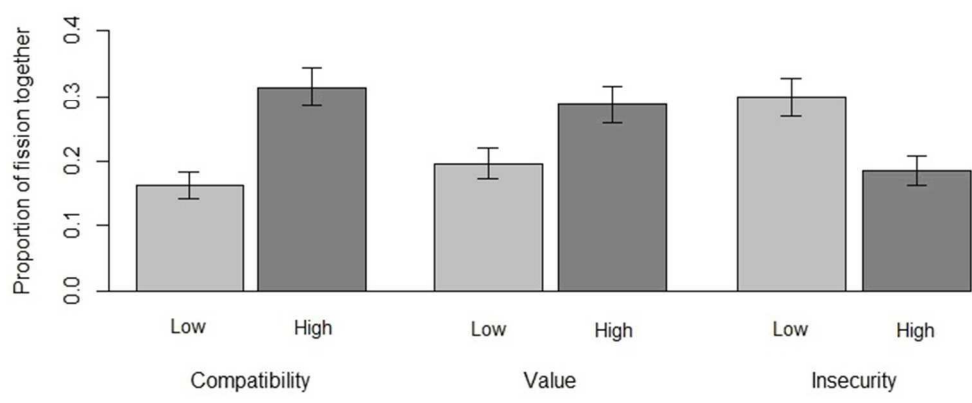
471 **Figure 1:** The mean (\pm SE) proportion of fissioning together for dyads of low and high
472 levels of compatibility, value and insecurity. Low levels are those lower than the
473 median, whereas high levels are those higher than the median of the three extracted
474 components.

475

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.

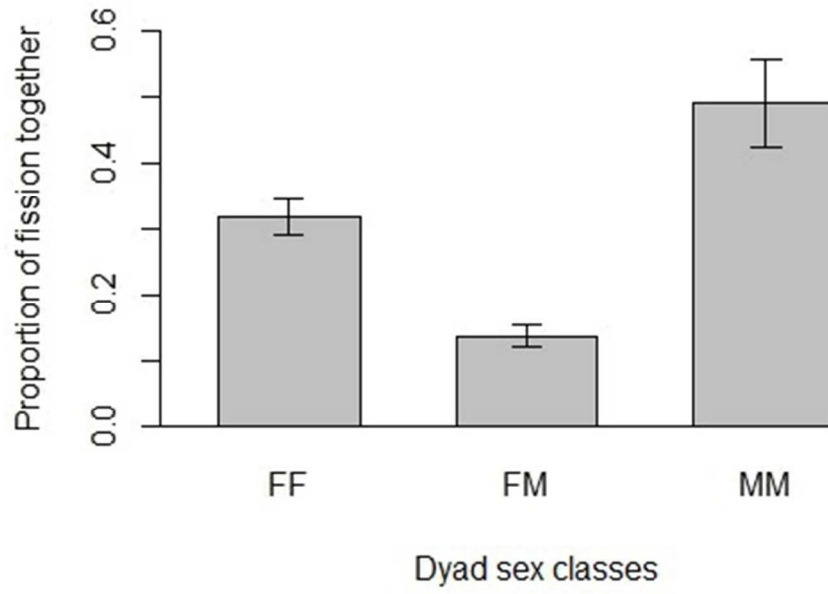
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