



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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Abstract

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

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

Introduction

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

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

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

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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).

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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]**

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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.

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Results

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

[Table 2 here]

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

[Figure 1 here]

[Figure 2 here]

[Table 3 here]

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

[Table 4 here]

Discussion

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

Rates or duration of social interactions may be affected by an unbalanced data collection across subjects, which is basically inevitable in species with a high degree of

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.

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

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323 **References**

- 324 Altmann, J. 1974. Observational studies of behavior: sampling methods. *Behaviour* 49,
325 227-267.
- 326 Altmann, J. 1980. Baboon mothers and infants. Cambridge, MA: Harvard University
327 Press.
- 328 Asensio, N., Korstjens, A.H. & Aureli, F. 2009. Fissioning minimizes ranging costs in
329 spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*
330 63, 649-659.
- 331 Asensio, N., Korstjens, A. H., Schaffner, C. M. & Aureli, F. 2008. Intragroup
332 aggression, fission fusion dynamics and feeding competition in spider monkeys.
333 *Behaviour* 145, 983-1001.
- 334 Aureli, F., Fraser, O.N., Schaffner, C.M. & Schino, G. 2012. The regulation of social
335 relationship. In: *Evolution of Primate Societies*. J. Mitani, J. Call, P. Kappeler, R.
336 Palombit, J. Silk (eds) University of Chicago Press, pp. 531-551
- 337 Aureli, F. & Schaffner, C.M. 2008. Social interactions, social relationships and the
338 social system of spider monkeys. In: *Spider Monkeys: Behavior, Ecology and*
339 *Evolution of the Genus Ateles*. Campbell C.J. ed. Cambridge University Press,
340 Cambridge, pp. 236-265.
- 341 Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., et al.
342 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49,
343 627-654.
- 344 Aureli, F., Schaffner, C.M., Verpooten, J., Slater, K. & Ramos-Fernandez, G. 2006.
345 Raiding parties of male spider monkeys: insights into human warfare? *American*
346 *Journal of Physical Anthropology* 131, 486-497.

- 347 Busia, L., Schaffner, C.M., Rothman, J.M., & Aureli, F. (2016). Do fruit nutrients affect
348 subgrouping patterns in wild spider monkeys (*Ateles geoffroyi*)? International Journal
349 of Primatology 37, 738-751.
- 350 Chapman, C. A. 1990. Association patterns of spider monkeys: the influence of ecology
351 and sex on social organization. Behavioral Ecology and Sociobiology 26, 409-414.
- 352 Chapman, C. A., & Chapman, L. J. 1999. Implications of small scale variation in
353 ecological conditions for the diet and density of red colobus monkeys. Primates 40,
354 215-231.
- 355 Chapman, C.A., Chapman, L.J. & Wrangham, R.W. 1995. Ecological constraints on
356 group size: an analysis of spider monkey and chimpanzee subgroups. Behavioral
357 Ecology and Sociobiology 36, 59-70.
- 358 Chapman, C. A., Fedigan, L. M., Fedigan, L. & Chapman, L. J. 1989. Post-weaning
359 resource competition and sex ratios in spider monkeys. Oikos 54, 315-319.
- 360 Conradt L. & Roper T.J. 2000. Activity synchrony and social cohesion: a
361 fission–fusion model. Proceedings of the Royal Society B: Biological Science 267,
362 2213–2218.
- 363 Cords, M. & Aureli, F. 2000. Reconciliation and relationship quality. In: Natural
364 conflict resolution. Aureli, F. and de Waal, F. B.M. (eds) University of California
365 Press. Berkeley Los Angeles London, pp- 177-198.
- 366 Croft, D.P., James, R. & Krause, J. 2008. Exploring animal social networks. Princeton
367 University Press, Princeton, New Jersey.
- 368 Dobson, A.J. & Barnett, A.G. 2008. An introduction to generalized linear models.
369 Chapman & Hall/CRC, Boca Raton, Florida.
- 370 Fedigan, L.M. & Baxter, M.J. 1984. Sex difference and social organization in
371 free-ranging spider monkeys (*Ateles geoffroyi*). Primates 25, 279-294.

- 372 Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby,
373 I. C., et al. 2015. Social bonds in the dispersing sex: partner preferences among adult
374 female chimpanzees. *Animal Behaviour* 105, 139-152.
- 375 Forstmeier, W. & Schielzeth, H. 2011. Cryptic multiple hypotheses testing in
376 linear models: overestimated effect sizes and the winner's curse. *Behavioral Ecology*
377 and *Sociobiology* 65, 47–55.
- 378 Fraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal*
379 *Behaviour* 79, 927-933.
- 380 Fraser, O. N., Schino, G. & Aureli, F. 2008. Components of relationship quality in
381 chimpanzees. *Ethology* 114, 834-843.
- 382 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. 2010.
383 Social and genetic interactions drive fitness variation in a free-living dolphin
384 population. *Proceedings of the National Academy of Science* 107, 19949-19954.
- 385 Hartwell, K. S., Notman, H., Bonenfant, C. & Pavelka, M. S. 2014. Assessing the
386 occurrence of sexual segregation in spider monkeys (*Ateles geoffroyi yucatanensis*),
387 its mechanisms and function. *International Journal of Primatology* 35, 425-444.
- 388 Hinde, R.A. 1979. *Towards Understanding Relationships*. London Academic
389 Press.
- 390 Hrdy S.B. 2009. *Mothers and others: the evolutionary origins of mutual understanding*.
391 Cambridge, Massachusetts: The Belknap Press of Harvard University Press
- 392 Kummer, H. 1971. *Primate societies: group techniques of ecological adaptation*.
393 Chicago: Aldine.
- 394 Kummer, H. 1978. On the value of social relationships to non-human primates. *Social*
395 *Science Information* 17, 687–705.

- 396 Lusseau, D. 2007. Why are male social relationships complex in the Doubtful Sound
397 bottlenose dolphin population. PLoS One 2, 348
- 398 Majolo, B., Ventura, R. & Schino, G. 2010. Asymmetry and dimensions of relationship
399 quality in the Japanese macaque (*Macaca fuscata yakui*). International Journal of
400 Primatology 31, 736-750.
- 401 Mitani, J.C. & Amstler S.J. 2003. Social and spatial aspects of male subgrouping in a
402 community of wild chimpanzees. Behaviour 140, 869-884.
- 403 Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall,
404 J., et al.. 2014. Early social exposure in wild chimpanzees: Mothers with sons are
405 more gregarious than mothers with daughters. Proceedings of the National Academy
406 of Science 111, 18189-18194.
- 407 Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2014. R Core Team (2014). nlme:
408 linear and nonlinear mixed effects models. R package version 3.1-117. URL:
409 <http://cran.r-project.org/web/packages/nlme/index.html>
- 410 Quinn, G. P. & Keough, M. J. 2002. Experimental design and data analysis for
411 biologists. Cambridge University Press, Cambridge.
- 412 R Core Team. 2014. R: a language and environment for statistical computing,
413 <http://www.R-project.org/>.
- 414 Ramos-Fernandez, G. 2005. Vocal communication in a fission-fusion society: do spider
415 monkeys stay in touch with close associates? International Journal of Primatology
416 26, 1077- 1092.
- 417 Ramos-Fernández, G. & Morales, J. M. 2014. Unravelling fission-fusion dynamics:
418 how subgroup properties and dyadic interactions influence individual
419 decisions. Behavioral Ecology and Sociobiology 68, 1225-1235.

- 420 Rebecchini, L., Schaffner, C.M. & Aureli, F. 2011. Risk is a component of social
421 relationships in spider monkeys. *Ethology* 117, 691-699.
- 422 Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. 2010. Social bonds enhance
423 reproductive success in male macaques. *Current Biology* 20, 2207-2210
- 424 Silk, J. B. 2007. Social components of fitness in primate groups. *Science* 317, 1347-
425 1351.
- 426 Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance
427 infant survival. *Science* 302, 1231-1234.
- 428 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R.,
429 et al. 2009. The benefits of social capital: close social bonds among female baboons
430 enhance offspring survival. *Proceedings of the Royal Society B: Biological Science*
431 276, 3099-3104.
- 432 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R.,
433 et al. 2010. Strong and consistent social bonds enhance the longevity of female
434 baboons. *Current Biology* 20, 1359-1361.
- 435 Shimooka, Y., Campbell, C. J., Di Fiore, A., Felton, A. M., Izawa, K., Link, A., et al.
436 2008. Demography and group composition of *Ateles*. In: *Spider Monkeys: Behavior,*
437 *Ecology & Evolution of the Genus Ateles* Campbell ed. Cambridge University Press,
438 Cambridge, pp 329-348.
- 439 Slater, K. Y., Schaffner, C. M. & Aureli, F. 2007. Embraces for infant handling in
440 spider monkeys: evidence for a biological market?. *Animal Behaviour* 74, 455-461.
- 441 Slater, K. Y., Schaffner, C. M. & Aureli, F. 2009. Sex differences in the social behavior
442 of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of*
443 *Primatology* 71, 21-29.

- 444 Smith, J.E., Memenis, S.K. & Holekamp, K. E. 2007. Rank-related partner choice in the
 445 fission–fusion society of the spotted hyena (*Crocuta crocuta*). Behavioral Ecology
 446 and Sociobiology 61, 753-765.
- 447 Smith-Aguilar, S.E., Ramos-Fernández, G., & Getz, W.M. 2016. Seasonal changes in
 448 socio-spatial structure in a group of free-living spider monkeys (*Ateles*
 449 *geoffroyi*). PloS one 11, e0157228.
- 450 Sueur, C., Petit O. & Deneubourg, J. L. 2010. Short-term group fission processes in
 451 macaques: a social networking approach. Journal of Experimental Biology 213,
 452 1338-1346.
- 453 Symington. M.M. 1990. Fission-fusion social organization in *Ateles* and *Pan*.
 454 International Journal of Primatology 11, 47-61.
- 455 Tabachnick, B. G. & Fidell, L. S. 2001. Using multivariate statistics.
 456 www.dandelion.com
- 457 Te Boekhorst, I.J. & Hogeweg, P. 1994. Self-structuring in artificial “chimps” offers
 458 new hypotheses for male grouping in chimpanzees. Behaviour 130, 229- 252.
- 459 Tokuda, M., Boubli, J. P., Izar, P. & Strier, K. B. 2012. Social cliques in male northern
 460 muriquis *Brachyteles hypoxanthus*. Current Zoology 58, 342-352.
- 461 Wallace, R. B. 2008. Towing the party line: territoriality, risky boundaries and male
 462 group size in spider monkey fission–fusion societies. American Journal Primatology
 463 70, 271-281.
- 464 Williams, J. M., Liu, H. Y. & Pusey, A. E. 2002. Costs and benefits of grouping for
 465 female chimpanzees at Gombe. In: Behavioural diversity in chimpanzees and
 466 bonobos. Boesch, C., Hohmann, G. & Marchant L.F. eds. Cambridge University
 467 Press, Cambridge, pp 192-203.
- 468

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 Kooh, 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,

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

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

[Table 3 here]

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

[Table 4 here]

Discussion

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

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323

324 **References**

- 325 Altmann, J. 1974. Observational studies of behavior: sampling methods. *Behaviour* 49,
326 227-267.
- 327 Altmann, J. 1980. Baboon mothers and infants. Cambridge, MA: Harvard University
328 Press.
- 329 Asensio, N., Korstjens, A.H. & Aureli, F. 2009. Fissioning minimizes ranging costs in
330 spider monkeys: a multiple-level approach. *Behavioral Ecology and Sociobiology*
331 63, 649-659.
- 332 Asensio, N., Korstjens, A. H., Schaffner, C. M. & Aureli, F. 2008. Intragroup
333 aggression, fission fusion dynamics and feeding competition in spider monkeys.
334 *Behaviour* 145, 983-1001.
- 335 Aureli, F., Fraser, O.N., Schaffner, C.M. & Schino, G. 2012. The regulation of social
336 relationship. In: *Evolution of Primate Societies*. J. Mitani, J. Call, P. Kappeler, R.
337 Palombit, J. Silk (eds) University of Chicago Press, pp. 531-551
- 338 Aureli, F. & Schaffner, C.M. 2008. Social interactions, social relationships and the
339 social system of spider monkeys. In: *Spider Monkeys: Behavior, Ecology and*
340 *Evolution of the Genus Ateles*. Campbell C.J. ed. Cambridge University Press,
341 Cambridge, pp. 236-265.
- 342 Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., et al.
343 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology* 49,
344 627-654.
- 345 Aureli, F., Schaffner, C.M., Verpooten, J., Slater, K. & Ramos-Fernandez, G. 2006.
346 Raiding parties of male spider monkeys: insights into human warfare? *American*
347 *Journal of Physical Anthropology* 131, 486-497.

- 348 Busia, L., Schaffner, C.M., Rothman, J.M., & Aureli, F. (2016). Do fruit nutrients affect
349 subgrouping patterns in wild spider monkeys (*Ateles geoffroyi*)? International Journal
350 of Primatology 37, 738-751.
- 351 Chapman, C. A. 1990. Association patterns of spider monkeys: the influence of ecology
352 and sex on social organization. Behavioral Ecology and Sociobiology 26, 409-414.
- 353 Chapman, C. A., & Chapman, L. J. 1999. Implications of small scale variation in
354 ecological conditions for the diet and density of red colobus monkeys. Primates 40,
355 215-231.
- 356 Chapman, C.A., Chapman, L.J. & Wrangham, R.W. 1995. Ecological constraints on
357 group size: an analysis of spider monkey and chimpanzee subgroups. Behavioral
358 Ecology and Sociobiology 36, 59-70.
- 359 Chapman, C. A., Fedigan, L. M., Fedigan, L. & Chapman, L. J. 1989. Post-weaning
360 resource competition and sex ratios in spider monkeys. Oikos 54, 315-319.
- 361 Conradt L. & Roper T.J. 2000. Activity synchrony and social cohesion: a
362 fission–fusion model. Proceedings of the Royal Society B: Biological Science 267,
363 2213–2218.
- 364 Cords, M. & Aureli, F. 2000. Reconciliation and relationship quality. In: Natural
365 conflict resolution. Aureli, F. and de Waal, F. B.M. (eds) University of California
366 Press. Berkeley Los Angeles London, pp- 177-198.
- 367 Croft, D.P., James, R. & Krause, J. 2008. Exploring animal social networks. Princeton
368 University Press, Princeton, New Jersey.
- 369 **Dobson, A.J. & Barnett, A.G. 2008. An introduction to generalized linear models.**
370 **Chapman & Hall/CRC, Boca Raton, Florida.**
- 371 Fedigan, L.M. & Baxter, M.J. 1984. Sex difference and social organization in
372 free-ranging spider monkeys (*Ateles geoffroyi*). Primates 25, 279-294.

- 373 Foerster, S., McLellan, K., Schroepfer-Walker, K., Murray, C. M., Krupenye, C., Gilby,
 374 I. C., et al. 2015. Social bonds in the dispersing sex: partner preferences among adult
 375 female chimpanzees. *Animal Behaviour* 105, 139-152.
- 376 **Forstmeier, W. & Schielzeth, H. 2011. Cryptic multiple hypotheses testing in**
 377 **linear models: overestimated effect sizes and the winner's curse. *Behavioral***
 378 ***Ecology and Sociobiology* 65, 47–55.**
- 379 Fraser, O. N. & Bugnyar, T. 2010. The quality of social relationships in ravens. *Animal*
 380 *Behaviour* 79, 927-933.
- 381 Fraser, O. N., Schino, G. & Aureli, F. 2008. Components of relationship quality in
 382 chimpanzees. *Ethology* 114, 834-843.
- 383 Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. & Sherwin, W. B. 2010.
 384 Social and genetic interactions drive fitness variation in a free-living dolphin
 385 population. *Proceedings of the National Academy of Science* 107, 19949-19954.
- 386 Hartwell, K. S., Notman, H., Bonenfant, C. & Pavelka, M. S. 2014. Assessing the
 387 occurrence of sexual segregation in spider monkeys (*Ateles geoffroyi yucatanensis*),
 388 its mechanisms and function. *International Journal of Primatology* 35, 425-444.
- 389 Hinde, R.A. 1979. *Towards Understanding Relationships*. London Academic
 390 Press.
- 391 Hrdy S.B. 2009. *Mothers and others: the evolutionary origins of mutual understanding*.
 392 Cambridge, Massachusetts: The Belknap Press of Harvard University Press
- 393 Kummer, H. 1971. *Primate societies: group techniques of ecological adaptation*.
 394 Chicago: Aldine.
- 395 Kummer, H. 1978. On the value of social relationships to non-human primates. *Social*
 396 *Science Information* 17, 687–705.

- 397 Lusseau, D. 2007. Why are male social relationships complex in the Doubtful Sound
398 bottlenose dolphin population. PLoS One 2, 348
- 399 Majolo, B., Ventura, R. & Schino, G. 2010. Asymmetry and dimensions of relationship
400 quality in the Japanese macaque (*Macaca fuscata yakui*). International Journal of
401 Primatology 31, 736-750.
- 402 Mitani, J.C. & Amstler S.J. 2003. Social and spatial aspects of male subgrouping in a
403 community of wild chimpanzees. Behaviour 140, 869-884.
- 404 Murray, C. M., Lonsdorf, E. V., Stanton, M. A., Wellens, K. R., Miller, J. A., Goodall,
405 J., et al.. 2014. Early social exposure in wild chimpanzees: Mothers with sons are
406 more gregarious than mothers with daughters. Proceedings of the National Academy
407 of Science 111, 18189-18194.
- 408 Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. 2014. R Core Team (2014). nlme:
409 linear and nonlinear mixed effects models. R package version 3.1-117. URL:
410 <http://cran.r-project.org/web/packages/nlme/index.html>
- 411 Quinn, G. P. & Keough, M. J. 2002. Experimental design and data analysis for
412 biologists. Cambridge University Press, Cambridge.
- 413 R Core Team. 2014. R: a language and environment for statistical computing,
414 <http://www.R-project.org/>.
- 415 Ramos-Fernandez, G. 2005. Vocal communication in a fission-fusion society: do spider
416 monkeys stay in touch with close associates? International Journal of Primatology
417 26, 1077- 1092.
- 418 Ramos-Fernández, G. & Morales, J. M. 2014. Unravelling fission-fusion dynamics:
419 how subgroup properties and dyadic interactions influence individual
420 decisions. Behavioral Ecology and Sociobiology 68, 1225-1235.

- 421 Rebecchini, L., Schaffner, C.M. & Aureli, F. 2011. Risk is a component of social
422 relationships in spider monkeys. *Ethology* 117, 691-699.
- 423 Schülke, O., Bhagavatula, J., Vigilant, L. & Ostner, J. 2010. Social bonds enhance
424 reproductive success in male macaques. *Current Biology* 20, 2207-2210
- 425 Silk, J. B. 2007. Social components of fitness in primate groups. *Science* 317, 1347-
426 1351.
- 427 Silk, J. B., Alberts, S. C. & Altmann, J. 2003. Social bonds of female baboons enhance
428 infant survival. *Science* 302, 1231-1234.
- 429 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R.,
430 et al. 2009. The benefits of social capital: close social bonds among female baboons
431 enhance offspring survival. *Proceedings of the Royal Society B: Biological Science*
432 276, 3099-3104.
- 433 Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R.,
434 et al. 2010. Strong and consistent social bonds enhance the longevity of female
435 baboons. *Current Biology* 20, 1359-1361.
- 436 Shimooka, Y., Campbell, C. J., Di Fiore, A., Felton, A. M., Izawa, K., Link, A., et al.
437 2008. Demography and group composition of *Ateles*. In: *Spider Monkeys: Behavior,*
438 *Ecology & Evolution of the Genus Ateles* Campbell ed. Cambridge University Press,
439 Cambridge, pp 329-348.
- 440 Slater, K. Y., Schaffner, C. M. & Aureli, F. 2007. Embraces for infant handling in
441 spider monkeys: evidence for a biological market?. *Animal Behaviour* 74, 455-461.
- 442 Slater, K. Y., Schaffner, C. M. & Aureli, F. 2009. Sex differences in the social behavior
443 of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of*
444 *Primatology* 71, 21-29.

- 445 Smith, J.E., Memenis, S.K. & Holekamp, K. E. 2007. Rank-related partner choice in the
 446 fission–fusion society of the spotted hyena (*Crocuta crocuta*). Behavioral Ecology
 447 and Sociobiology 61, 753-765.
- 448 Smith-Aguilar, S.E., Ramos-Fernández, G., & Getz, W.M. 2016. Seasonal changes in
 449 socio-spatial structure in a group of free-living spider monkeys (*Ateles*
 450 *geoffroyi*). PloS one 11, e0157228.
- 451 Sueur, C., Petit O. & Deneubourg, J. L. 2010. Short-term group fission processes in
 452 macaques: a social networking approach. Journal of Experimental Biology 213,
 453 1338-1346.
- 454 Symington. M.M. 1990. Fission-fusion social organization in *Ateles* and *Pan*.
 455 International Journal of Primatology 11, 47-61.
- 456 Tabachnick, B. G. & Fidell, L. S. 2001. Using multivariate statistics.
 457 www.dandelion.com
- 458 Te Boekhorst, I.J. & Hogeweg, P. 1994. Self-structuring in artificial “chimps” offers
 459 new hypotheses for male grouping in chimpanzees. Behaviour 130, 229- 252.
- 460 Tokuda, M., Boubli, J. P., Izar, P. & Strier, K. B. 2012. Social cliques in male northern
 461 muriquis *Brachyteles hypoxanthus*. Current Zoology 58, 342-352.
- 462 Wallace, R. B. 2008. Towing the party line: territoriality, risky boundaries and male
 463 group size in spider monkey fission–fusion societies. American Journal Primatology
 464 70, 271-281.
- 465 Williams, J. M., Liu, H. Y. & Pusey, A. E. 2002. Costs and benefits of grouping for
 466 female chimpanzees at Gombe. In: Behavioural diversity in chimpanzees and
 467 bonobos. Boesch, C., Hohmann, G. & Marchant L.F. eds. Cambridge University
 468 Press, Cambridge, pp 192-203.
- 469

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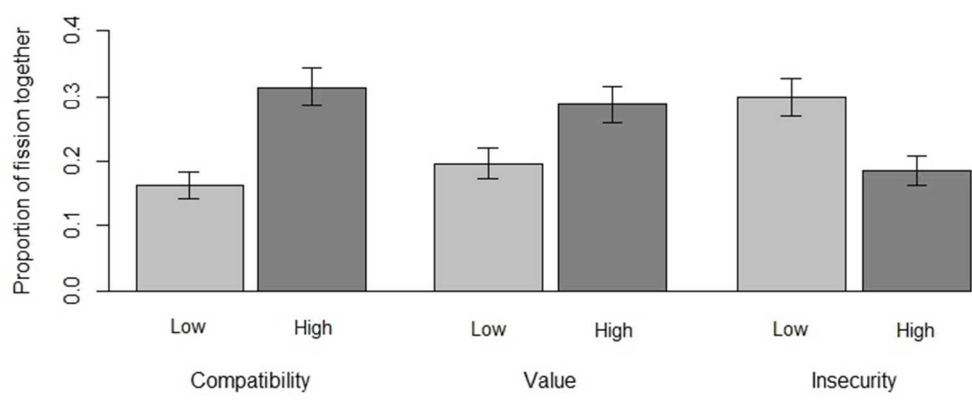
471 **Figure 1:** The mean (\pm SE) proportion of fissioning together for dyads of low and high
472 levels of compatibility, value and insecurity. Low levels are those lower than the
473 median, whereas high levels are those higher than the median of the three extracted
474 components.

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.

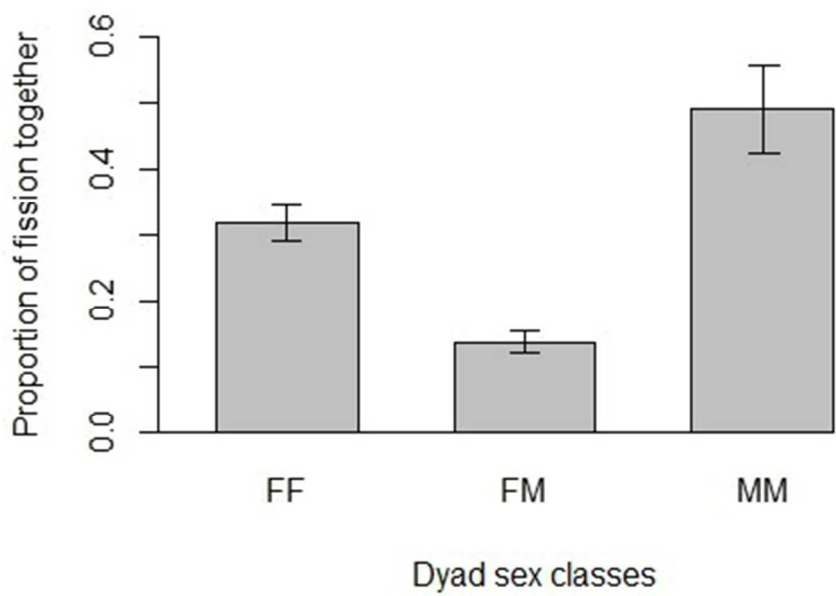
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