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Article

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Relationship quality affects fission decisions 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 Kooh, 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 indviduals (bottlenose dolphins, *Tursiops* sp. Lusseau, 2007; chimpanzees, *Pan troglodytes*, Mitani & Amsler, 2003; Tonkean and reshus macaques, *Macaca tonkeana* and *M. mulata*, Sueur et al., 2010; northen 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 overall degree of tolerance between two individuals. Security is a measure of the consistency of a partner's responses during social interactions over time.

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

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

Methods

Field Site and Study Subjects

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

Data Collection

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

During focal samples, we collected all occurrences and durations of social interactions involving the focal animal, recording the identity of the partner. We recorded the following social interactions: grooming (manipulation of another individual's fur with hands or mouth); co-feeding (feeding on the same fruit species within 1 m from each other); embrace (putting one or two arms around the other’s body while facing each other). Every 2 min, we recorded the identity of individuals within 5 m from the focal animal. We also recorded aggressive interactions, including conspicuous vocalizations, chases and physical contact, with all-occurrence sampling (Altmann, 1974) and whether other individuals provided support to the aggressor (no case of support in favour of the victim was witnessed).

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

Data Analysis

To extract components of relationship quality, seven indexes based on the recorded social interactions were calculated for every dyad and entered into a principal component analysis (PCA). For all indexes we controlled for the opportunity each individual had to interact with any of the other study subjects by considering the time each dyad spent in the same subgroup. We used the time in which partners in a dyad were in the same subgroup during their focal samples (individual A's focal time in which individual B was also in the subgroup + individual B's focal time in which A was also in the subgroup) to calculate the indexes based on data collected with focal samples (Table 1). For the aggression index, we used the time in which A and B were in the same subgroup during our subgroup follows. We also calculated a coefficient of variation (CV) of the time two individuals spent in the same subgroup (i.e. subgroup association) over the study period, in order to have an index reflecting the degree of consistency of social interactions over time. We calculated the subgroup association of each dyad in 3-month periods, and we calculated the CV for the seven resulting periods for each dyad; a low CV indicates consistency in the time that the two individuals spent together in the same subgroup, whereas a high CV indicates that the two individuals were often together in some periods, but they were rarely together in other periods. In order to avoid circularity, we included the degree of consistency in subgroup association over time captured by the CV, and not an index simply based on subgroup association, in the PCA, as we wanted to examine whether relationship components affected fission decisions, which are directly linked with subgroup association. We used SPSS version 20 to perform the PCA. A varimax rotation was applied (Tabachnick & Fidell, 2001) and a minimum eigenvalue of 1.0 was considered to select the components. Coefficients of correlation >|0.6| were considered as high loadings.

[Table 1 here]

To test our predictions, we considered only fission events that led to the formation of two subgroups. Cases in which one of the two subgroups consisted of only one individual were excluded from the analyses because it was not possible to compare the relationship quality of members of both subgroups. We used two analytical approaches by running two generalized linear mixed models (GLMMs) using the “nlme” packages [Pinheiro et al., 2014) in R (version 3.1.2, R Core Team, 2014). We compared full models with null models, which included only the random factors (Forstmeier & Schielzeth, 2011), using a likelihood ratio test with the function anova (Dobson & Barlett, 2008). We set an alpha level of 0.05 for all tests.

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

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

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 ($ß = -3.80$, $z = -11.29$, $p<0.001$, $N=436$), whereas in the case of females the proportion of males was higher in the non-chosen subgroup ($ß = 1.58$, $z = 3.72$, $p<0.001$, $N=314$). 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 fission-fusion dynamics. In this respect we would need to be cautious about the conclusions we can draw from our seven indexes. If social interaction indexes were simply due to the unbalanced data collection across subjects (e.g. social interaction rates depending on the amount of time animals spend in the same subgroup), we would expect all indexes to be highly correlated with one another. By contrast, the PCA extracted three components that by definition are not correlated with one another. For example, only the grooming index loaded highly on a component with the proximity index, whereas the co-feeding and embrace indexes loaded on two separated components. Thus, the components we used to characterize the quality of social relationships appear to be robust to the potential influence of the unbalanced data collection across subjects.

The prediction that relationship quality would affect the choice of subgroup members during fission events was fully supported using two analytical approaches. During fission events spider monkeys preferred subgroup members with whom they shared high levels of compatibility and value, and low levels of insecurity. Similarly, spider monkeys preferred to fission into subgroups in which they had higher compatibility and higher security with the average subgroup member. As fission is expected to occur in order to decrease feeding competition by adjusting subgroup size to food availability (Asensio et al., 2008; Chapman, 1990; Chapman et al., 1995; Kummer, 1971; Symington, 1990), our findings show that such adjustments follow social preferences. Although previous studies indicate that subgroup association patterns are related to affiliative interactions (Lusseau, 2007; Mitani & Amsler, 2003; Sueur et al., 2010; Tokuda et al., 2012) and relative dominance rank (Smith et al., 2007), our study goes a step further by providing evidence that the social preferences expressed at fission are multifaceted. We found that individuals fission with group members with whom they have high grooming and proximity scores, i.e. more compatible partners. More importantly, our findings reveal that social preferences are also based on the levels of value and insecurity with other subgroup members, which are independent from the levels of compatibility. These preferences are qualitatively different from what would be expected if fission decisions were simply the outcome of a process to reduce the number of subgroup members without taking into account the extent of variation in the quality of their social relationships (see Introduction).

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

In conclusion, our findings contribute to a better understanding of the importance of social factors in fission decisions. Fission-fusion dynamics are certainly driven by ecological factors, and subgroup size likely depends on food availability (Asensio et al., 2009; Aureli & Schaffner, 2008; Chapman, 1990; Kummer, 1971; Smith-Aguilar et al., 2016; Symington, 1990) and food quality (Busia et al., 2016). However, social and ecological factors may play a role on different time scales. Whereas grouping patterns are affected by food availability on a monthly or seasonal scale (e.g. Asensio et al., 2009; Chapman & Chapman, 1999), individual decisions to fission according to social preferences occur on a shorter temporal scale. We showed that these social preferences are multifaceted. Not only do these preferences reflect overall levels of tolerance (i.e. compatibility), but they also depend on aspects of relationship quality previously unexamined for fission-fusion dynamics, such as value and security.

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

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

Figure 2: The mean (±SE) proportion of fissioning together for the three dyad sex classes. FF: female-female dyads; FM: female-male dyads; MM: male-male dyads.

Relationship quality affects fission decisions 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 Kooh, 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 indviduals (bottlenose dolphins, *Tursiops* sp. Lusseau, 2007; chimpanzees, *Pan troglodytes*, Mitani & Amsler, 2003; Tonkean and reshus macaques, *Macaca tonkeana* and *M. mulata*, Sueur et al., 2010; northen 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 overall degree of tolerance between two individuals. Security is a measure of the consistency of a partner's responses during social interactions over time.

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

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

Methods

Field Site and Study Subjects

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

Data Collection

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

During focal samples, we collected all occurrences and durations of social interactions involving the focal animal, recording the identity of the partner. We recorded the following social interactions: grooming (manipulation of another individual's fur with hands or mouth); co-feeding (feeding on the same fruit species within 1 m from each other); embrace (putting one or two arms around the other's body while facing each other). Every 2 min, we recorded the identity of individuals within 5 m from the focal animal. We also recorded aggressive interactions, including conspicuous vocalizations, chases and physical contact, with all-occurrence sampling (Altmann, 1974) and whether other individuals provided support to the aggressor (no case of support in favour of the victim was witnessed).

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

Data Analysis

To extract components of relationship quality, seven indexes based on the recorded social interactions were calculated for every dyad and entered into a principal component analysis (PCA). For all indexes we controlled for the opportunity each individual had to interact with any of the other study subjects by considering the time each dyad spent in the same subgroup. We used the time in which partners in a dyad were in the same subgroup during their focal samples (individual A's focal time in which individual B was also in the subgroup + individual B's focal time in which A was also in the subgroup) to calculate the indexes based on data collected with focal samples (Table 1). For the aggression index, we used the time in which A and B were in the same subgroup during our subgroup follows. We also calculated a coefficient of variation (CV) of the time two individuals spent in the same subgroup (i.e. subgroup association) over the study period**, in order to have an index reflecting the degree of consistency of social interactions over time**. We calculated the subgroup association of each dyad in 3-month periods, and we calculated the CV for the seven resulting periods for each dyad; a low CV indicates consistency in the time that the two individuals spent together in the same subgroup, whereas a high CV indicates that the two individuals were often together in some periods, but they were rarely together in other periods. **In order to avoid circularity, we included the degree of consistency in subgroup association over time captured by the CV, and** not an index simply based on subgroup association, in the PCA, as we wanted to examine whether relationship components affected fission decisions, which are directly linked with subgroup association. We used SPSS version 20 to perform the PCA. A varimax rotation was applied (Tabachnick & Fidell, 2001) and a minimum eigenvalue of 1.0 was considered to select the components. Coefficients of correlation >|0.6| were considered as high loadings.

[Table 1 here]

To test our predictions, we considered only fission events that led to the formation of two subgroups. Cases in which one of the two subgroups consisted of only one individual were excluded from the analyses because it was not possible to compare the relationship quality of members of both subgroups. We used two analytical approaches by running two generalized linear mixed models (GLMMs) using the "nlme" packages [Pinheiro et al., 2014) in R (version 3.1.2, R Core Team, 2014). **We compared full models with null models, which included only the random factors (Forstmeier & Schielzeth, 2011), using a likelihood ratio test with the function anova (Dobson & Barlett, 2008).** We set an alpha level of 0.05 for all tests.

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

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

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

The prediction that relationship quality would affect the choice of subgroup members during fission events was fully supported using two analytical approaches. During fission events spider monkeys preferred subgroup members with whom they shared high levels of compatibility and value, and low levels of insecurity. Similarly, spider monkeys preferred to fission into subgroups in which they had higher compatibility and higher security with the average subgroup member. As fission is expected to occur in order to decrease feeding competition by adjusting subgroup size to food availability (Asensio et al., 2008; Chapman, 1990; Chapman et al., 1995; Kummer, 1971; Symington, 1990), our findings show that such adjustments follow social preferences. Although previous studies indicate that subgroup association patterns are related to affiliative interactions (Lusseau, 2007; Mitani & Amsler, 2003; Sueur et al., 2010; Tokuda et al., 2012) and relative dominance rank (Smith et al., 2007), our study goes a step further by providing evidence that the social preferences expressed at fission are multifaceted. We found that individuals fission with group members with whom they have high grooming and proximity scores, i.e. more compatible partners. More importantly, our findings reveal that social preferences are also based on the levels of value and insecurity with other subgroup members, which are independent from the levels of compatibility. These preferences are qualitatively different from what would be expected if fission decisions were simply the outcome of a process to reduce the number of subgroup members without taking into account the extent of variation in the quality of their social relationships (see Introduction).

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

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

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

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

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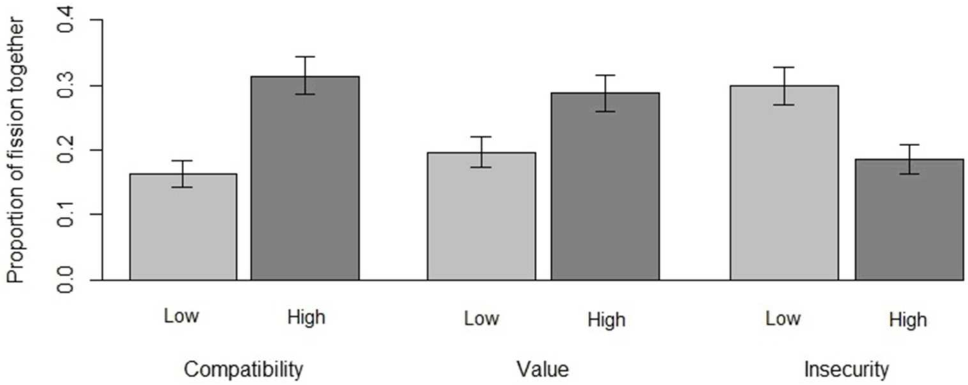
Figure 1: The mean (±SE) proportion of fissioning together for dyads of low and high levels of compatibility, value and insecurity. Low levels are those lower than the median, whereas high levels are those higher than the median of the three extracted components.

Figure 2: The mean (±SE) proportion of fissioning together for the three dyad sex classes. FF: female-female dyads; FM: female-male dyads; MM: male-male dyads.



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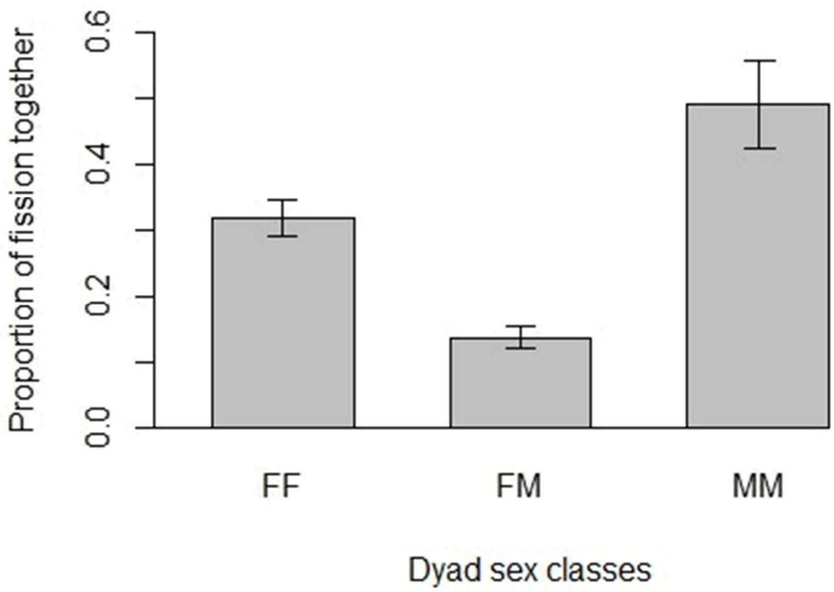

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