International Journal of Primatology doi: 10.1007/s10764-017-9982-9

http://rdcu.be/uGZN

You are not welcome:
social exchanges between female spider monkeys (*Ateles geoffroyi*)

Juan Carlos Riveros[1], Colleen M. Schaffner[1] and Filippo Aureli[1,2]

[1]Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, México
Av. Dr. Luis Castelazo, Industrial de las animas, 91190
e-mail: jcriverosr@gmail.com
Tel.: +52-228-841-8900

[2]Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, United Kingdom

Abstract

Group-living leads to competition for food between group members. Two types of within-group food competition may occur: scramble competition, when all group members use the same resource, such that feeding opportunities are equal for everyone; and contest competition, when some group members monopolize resources through aggression and dominance. In species in which females disperse from the natal group and immigrate into other groups, immigrant females increase group size and thus possibly food competition. Under these circumstances, other females may use aggression to discourage new females from joining the group. We assessed the distribution of aggression, embraces and kisses among female spider monkeys (*Ateles geoffroyi*) in relation to group tenure. We recorded social interactions during 1688 10-minute focal animal samples on 11 females in Santa Rosa, Costa Rica. We found that aggression was rare between long-term resident females and aggression rates were not higher during feeding than in other contexts, suggesting there was little contest competition. Long-term residents and less recently immigrant females showed higher aggression rates towards the most recent immigrants than toward other females, especially during the first months after a female immigrated, which coincided with the dry season. We did not find similar patterns for embrace and kiss. These results suggest that other females target aggression towards the most recent immigrants to reduce scramble competition. This finding suggests that group tenure should be included in socioecological models for species with female dispersal.

Keywords: aggression, food competition, fission-fusion, female dispersal, tenure

Introduction

Competition for food is one of the most important costs of group living and one of the main factors affecting social relationships in primates (Wrangham 1980). Socioecological theory has been proposed as conceptual framework to account for variation in female-female social relationships (Wrangham 1980; van Schaik 1989; Isbell 1991; Sterck et al. 1997). Since food intake affects female reproductive success, the presence of group members leads to increased competition for food (Isbell 1991). Two types of food competition are recognized depending on the distribution and abundance of food resources: scramble and contest (Nicholson 1954; van Schaik 1989). Contest competition occurs when some group members can monopolize resources and exclude others through aggression and dominance. Scramble competition occurs when resources are unmonopolizable and feeding opportunities decrease when group size is larger. According to socioecological theory, female primates that feed on clumped and monopolizable resources, such as ripe fruits, are expected to have differentiated relationships with one another in terms of antagonistic and dominance interactions as well as grooming and coalitions; female philopatry and kin-bias interactions should be the rule under these conditions and thus the relationships among females are characterized as Resident-Nepotistic (Sterck et al. 1997). When resources are evenly distributed and are unmonopolizable, females are not expected to form dominance relationships or kin-bias alliances; therefore, female philopatry would not be beneficial and the relationships among females are characterized as Dispersal-Egalitarian (Sterck et al. 1997).

Several studies have supported the relationship predicted by socioecological theory between the distribution and monopolizability of food resources on one hand

and the type of social relationships among females on the other hand (e.g., Mitchell et al. 1991; Barton et al. 1996; Utami et al. 1997; Pruetz & Isbell 2000; Stahl & Kaumanns 2003). For example, in wild bearded capuchin monkeys (*Sapajus libidinosus*), which feed mainly on high-quality clumped resources, females experience contest competition, have clear dominance relationships and are philopatric (Verderane et al. 2013). In Bwindi gorillas (*Gorilla beringei*) contest competition occurs when group members feed on clumped resources, such as fruit trees (Robbins 2008), and older females tend to be dominant over newly immigrant females (Scott & Lockard 1999; Robbins et al. 2005).

In some primate species, group members form temporary subgroups of variable size and composition according to food availability and/or intensity of predation risk (Wrangham 1979; Sterck et al. 1997). Fissioning into smaller subgroups when food availability is low may serve to reduce food competition (Kummer 1971); when this is frequent the social organization is characterized by a high degree of fission-fusion dynamics (Aureli et al. 2008). In primate species with a high degree of fission-fusion dynamics, such as chimpanzees, bonobos (*Pan paniscus*) and spider monkeys (*Ateles* spp.), fission events mitigate the impact of within-group food competition by reducing the number of individuals feeding in a given food patch (Stevenson et al. 1998; Potts et al. 2011). For example, in Geoffroy’s spider monkeys (*A. geoffroyi*) the formation of smaller subgroups during the dry season resulted in no increase in aggression rates, although food resources were scarcer than in the wet season (Asensio et al. 2008). Likewise, in extreme situations of drastic changes in food availability, such as after hurricanes, spider monkeys cope with decreased fruit availability and reduce within-group competition by forming smaller subgroups after than before the hurricanes (Schaffner et al. 2012).

In species with female dispersal from the natal group the amount of time females have been in the group (i.e., group tenure) can affect their social interactions (Furuichi et al. 2015). In particular, group tenure can influence the pattern of aggression and food competition among females, with long-term resident females being aggressive to and using better-quality areas than newly immigrant females (*Gorilla gorilla gorilla*: Scott & Lockard 1999; *G. beringei beringei*: Robbins et al. 2005; *Ateles geoffroyi*: Asensio et al. 2008, 2015; *Pan troglodyes*: Kahlenberg et al. 2008a; Pusey & Schroepfer-Walker 2013). Thus, female reproductive success may be affected by social factors that are not considered in the socioecological model, such as group tenure in species with female dispersal.

Spider monkey females tend to disperse from their natal group once they reach sexual maturity (Symington 1990; Vick 2008). When recent immigrant females join a group, food competition is likely to intensify because of the increased number of group members. To reduce competition for food and aggression risk in a given food patch, individuals can fission into smaller subgroups. Nevertheless, the total number of individuals in the group is not reduced, which influences the use of available resources in the group home range. Thus, fission events are ineffective in coping with scramble food competition at the group level (Asensio et al. 2008, 2009). Although aggressive behaviors between group members are often taken as indicators of dominance relationships and contest competition, this pattern can also be viewed as the result of scramble competition (Asensio et al. 2008). Aggression by adult females against subadult females can be interpreted as a tactic to stop newly immigrated females settling into spider monkey groups (Asensio et al. 2008). Under this scenario, aggression may serve to manage the number of individuals using the resources in the group home range.

In contrast to fissions, fusions may create risky situations. Spider monkeys manage potential conflict and reduce uncertainty as well as the risk of aggression by using embraces often with pectoral sniffing after fusion events in the wild (Aureli & Schaffner 2007) and during reunions in captivity (Schaffner & Aureli 2005). Embraces with kisses have also been reported in post-fusion events in chimpanzees as an attempt to prevent aggression (Nishida et al. 1999). In spider monkeys kisses are considered a greeting variant of embraces (Santorelli et al. 2011) and may mitigate the risk of aggression in a similar way to embraces (Aureli & Schaffner 2007). Due to the risk associated with handling other females' infants, spider monkey females often give embraces when approaching mothers (Schaffner & Aureli 2005; Slater et al. 2007). In addition, a principal component analysis found that embraces and aggressive interactions had a high loading in the same component, whereas affiliative interactions, such as grooming, loaded highly on a different component (Rebecchini et al. 2011). The function of embraces, pectoral sniffing and kisses may be similar to the tension regulation of socio-sexual contacts reported for bonobos (Hohmann & Fruth 2000). However, there is no established measure of tension in spider monkeys. Given the evidence that links embraces, pectoral sniffing and kisses to risk in spider monkeys, we refer to them collectively as risk-reducing interactions.

Frugivorous primates, such as spider monkeys, are expected to exhibit female philopatry, kin-biased interactions among females and contest competition (Sterck et al. 1997) but instead spider monkeys are characterized by female dispersal and unclear dominance relationships among adult females (Aureli & Schaffner 2008). Therefore, spider monkeys provide good models to assess the predictive power of socioecological theory under challenging circumstances and to better understand the relationship between food distribution, the arrival of immigrant females and the patterns of social interactions over time (Aureli & Schaffner 2002). In addition, there is a growing understanding about the relationships among a variety of socioecological variables in spider monkeys. For example, fruit availability influences subgroup size, with larger subgroups when more food is available than when less food is available (Symington 1990; Chapman et al. 1995; Asensio et al. 2009); and group tenure affects individual core-area quality, with females with longer tenure having better core areas than females with shorter tenure (Asensio et al. 2015).

Spider monkey females have higher aggression rates in feeding than in non-feeding contexts but there is no difference in aggression rates between seasons, although seasons vary greatly in food availability (Asensio et al. 2008). Aggression is also strongly affected by the relative age and group tenure of the interacting individuals (Asensio et al. 2008). We built on these findings, by investigating whether patterns of female-female interactions in spider monkeys were influenced by factors typical of the socioecological model, such as food-related factors, and the novel factor of group tenure. If spider monkeys experience contest competition as expected based on their highly frugivorous diet, we predicted higher aggression rates in the dry season, where less food is usually available, than in the wet season, and in feeding contexts than in non-feeding contexts. Alternatively, if the high degree of fission-fusion dynamics reduces contest competition, we predicted no difference in aggression rates between seasons or contexts. If females attempt to reduce food scramble competition, we predicted higher aggression rates from long-term resident females against recent immigrant females than the reverse. Similarly we predicted higher aggression rates by long-term resident females against recent immigrant females than against other long-term resident females. We also explored whether the most recent immigrant females received the majority of aggression from less recent immigrant females. We extended Asensio et al.'s (2008) approach, which focused on aggressive interactions, by including predictions about risk-reducing interactions. We predicted higher rates of risk-reducing interactions when aggression rates were higher (e.g., in the dry season and in feeding contexts) than when aggression rates were lower (in the wet season and in non-feeding contexts). We also predicted higher rates of risk-reducing interactions in female-female dyads with higher aggression rates than in dyads with lower aggression rates.

Methods

Subjects and study site

We carried out the study in the Santa Rosa sector, located in the Guanacaste Conservation Area, Northwestern Costa Rica (10°50'N, 85°38'W). Santa Rosa comprises 108 km^2 of tropical dry forest, which is characterized by a severe dry season between December and May and a wet season during the rest of the year (Janzen 1986). Food availability for spider monkeys at the site is lower during the dry season than during the wet season (Chapman 1988; Asensio et al. 2009).

We studied one group of spider monkeys, previously studied by Chapman (1988, 1990a,b) and Asensio et al. (2008, 2009), which was well habituated to being followed by researchers and ranged in size from 19 to 25 individuals during the study period, due to births, immigration and disappearances. We studied all 11 adult and subadult females in the group. We considered a female as subadult from when she was sexually mature until she gave birth for the first time (Vick 2008). We classified females according to their group tenure as long-term resident (hereafter resident) or recent immigrant (hereafter immigrant). We considered females as immigrant from the first time we saw them in a subgroup with resident females until they gave birth to their first infant as females are more integrated in the group after this (Shimooka 2015). At the onset of the study there were 7 resident females and 2 immigrant females. During the study period these 2 immigrant females gave birth and 2 immigrant females joined the study group. Thus, at the end of the study there were 9 resident and 2 immigrant females (Table 1). Immigrant females were all subadult. All resident females were adult and there were no natal subadult females. For one analysis we divided immigrant females into two additional categories: the last female who immigrated into the group and the other immigrant females. The most recent immigrant changed during the study period depending on immigration time of new females into the group.

[Table 1]

Data collection

We conducted the study during 15 months between February 2014 and June 2015, including eight months in the dry season and seven months in the wet season. We collected data for 8 hours on each study day (mean±SE: 8.5±1.0 days per month). We collected social interactions using 10-minute focal-animal sampling of each female with continuous recording (Altmann 1974). We selected focal subjects from the females in the subgroup we were following, giving preference to the individual with the fewest observations. We sampled the same female again at least one hour after her last focal observation. We recorded the following social interactions based on Slater et al. (2007, 2009), Asensio et al. (2008) and Santorelli et al.'s (2011) definitions: aggressive interactions (including spatial displacements, threats, chases, strikes and bites) and risk-reducing interactions, including embraces (face-to-face interactions in which an individual wraps one or two arms around the shoulder or back of another individual), pectoral sniff (an individual places its nose at the chest or arm pit region of another individual) and kisses (face-to-face interactions in which an individual gets its face close to the one of another individual cheek-to-cheek, usually with no physical contact). For each social interaction, we recorded the identity of the individuals involved along with the season in which the interaction took place and the context (feeding, non-feeding, or mixed). We defined the context according to the subgroup activity. We scored feeding context when more than 50% of the subgroup members actively ingested or searched for food, and non-feeding context when this was not the case (Asensio et al. 2008); when an equal number of subgroup members engaged in feeding and non-feeding activities, we scored mixed context. We recorded subgroup activity continuously.

We also recorded all subgroup members, as well as changes in subgroup composition any time one or more individuals joined (fusion) or left (fission) the followed subgroup (Asensio et al. 2009). Two observers kept track of subgroup membership simultaneously. We defined subgroup membership using a criterion based on a chain rule (Ramos-Fernandez 2005; Croft et al. 2008), in which we considered individuals to be in the same subgroup if they were ≤50 m from at least one other subgroup member (Aureli et al. 2012). We scored a fission event when 1 or more individuals from the followed subgroup were more than 50 m from at least one current subgroup member for more than 30 min (Asensio et al. 2009). We scored fusion when one or more individuals not belonging to the followed subgroup came within ≤50 m of any member of the followed subgroup (Asensio et al. 2009). The critical distance of 50 m was empirically established for the study group (Aureli et al. 2012). For calculation of subgroup size we excluded juveniles and infants from the total count as they were always in the same subgroup as their mother. We used three categories of subgroup size based on the frequency distribution of all subgroup sizes observed during the study period as these three categories showed similar frequencies: small (2-4 individuals), medium (5-8) and large (9-13).

We carried out 1688 focal animal samples, for a total of 268 hours of observation with a mean (±SE) observation time per female of 26.8±2.1 h. This excludes the most recent immigrant female, whom we sampled for only 1.6 h because she immigrated into the study group about two months before the end of data collection. The potential interaction time for each of the 45 female-female dyads, (excluding dyads involving the most recent immigrant female, ranged 15.3-48.1 h, with a mean (±SE) time per dyad of 31.1±1.4 h.

Statistical analysis

We calculated the rate of aggressive and risk-reducing interactions for a given female-female dyad per context and season by dividing the frequency of interactions between the two females of the dyad by the total time they were observed in the same subgroup during their focal samples. For example, we calculated the interaction rate for each dyad in the feeding context during the wet season, in the feeding context during the dry season, as well as in the non-feeding context during the wet season and in the non-feeding context during the dry season.

We built two linear mixed models (LMM), with aggression rate as the response variable in one LMM and the rate of risk-reducing interactions as the response variable in the other. Both models included the season (wet or dry) in which the female-female interactions took place, context (feeding, non-feeding or mixed), and dyad type as explanatory variables. Given that subgroup size has no effect on female-female interaction rates (Riveros et al. unpub. data), we did not include subgroup size as an additional explanatory variable, but we included it as a control variable. We classified female-female dyads into four types depending on the group tenure of the actor (first term) and recipient (second term) of the social interaction: resident-immigrant, immigrant-resident, immigrant-immigrant and resident-resident. We further examined aggression against immigrant females by running another LMM with the same variables and dividing immigrant females into the most recent immigrant and the less recent immigrant females. We included the identities of the actor and recipient as random effects to account for the presence of the same individuals in multiple dyads (Zuur et al. 2009). We ran the LMMs using the lme4 package (version 1.1-9, Bates et al. 2015) in R (Core Team 2015). We checked for model assumptions and log-transformed the response variable when appropriate. We present results for the explanatory variables only when the full model was significantly different from the null model.

Ethical note

Our research conforms to the American Society of Primatologists principles for the ethical treatment of primates and adheres to the legal requirements of Costa Rica. We received permission to conduct research from the Ministry of Environment and Energy of Costa Rica. To the best of our knowledge, no conflict of interest, financial or other, exists.

Data availability

The datasets analyzed in this study are available from the corresponding author on reasonable request.

Results

The mean (± SE) hourly rate of aggressive interactions between females was 0.039 ± 0.014 and that for risk-reducing interactions was 0.014 ± 0.005. 95% of aggressive interactions did not involve physical contact, and they consisted of chases (71%) and spatial displacements (24%). Only one event involved strike, and we observed no bites. Risk-reducing interactions consisted of embraces (60%) and kisses (40%). All pectoral sniffs occurred during embraces.

The full model, testing the effects of season, context and dyad type on aggression rates between females, while controlling for subgroup size, was significantly different from the null model (χ^2=29.6, df=4, P=0.006). Females directed aggression toward other females more often in the dry than in the wet season ($F_{1,1077}$=5.33, P=0.02; Figure 1), but there was no effect of context ($F_{2,1051}$=1.39, P=0.25). There was also a significant effect of dyad type on the rate of aggression ($F_{3,173}$=8.35, P<0.001; Figure 2). As predicted, aggression rates by residents against immigrant females were higher than aggression rates by immigrants against resident females (β=0.18; SE=0.06; t_{122}=3.02; P=0.003) and by residents against other resident females (β=0.16; SE=0.05; t_{129}=3.5; P<0.001). The highest aggression rates were between immigrant females (higher than resident-immigrant dyads: β=0.35, SE=0.14, t_{517}=2.42, P=0.02; higher than resident-resident dyads: β=0.51; SE=0.14; t_{512}=3.6; P<0.001; and higher than immigrant-resident dyads: β=0.53; SE=0.15; t_{515}=3.6; P<0.001; Figure 2).

[Figure 1]

[Figure 2]

When we divided immigrant females into two categories, we found that resident females attacked the most recent immigrant females at higher rates than less recent immigrant females (β =0.32; SE=0.08; t_{113}=4; P<0.001, Figure 3). Furthermore, aggression rates by less recent immigrant females against the most recent immigrant females were higher than those by the most recent immigrant against less recent immigrant females (β =0.92; SE=0.26; t_{605}=3.5; P<0.001) and those by resident females against the most recent immigrant females (β =0.61; SE=0.18; t_{648}=3.4; P<0.001; Figure 3).

[Figure 3]

Given that the most recent immigrant females received most of the aggression and all four immigrant females spent their first months in the group during the dry season (Table 1), we carried out an additional LMM to test whether the higher aggression rates during the dry season were related to the timing of their immigration into the group, rather than to higher contest competition due to lower availability of food in the dry season. The full model, including aggression rates against immigrant females as the response variable and season and group tenure (i.e., the number of months each immigrant female was in the study group) as explanatory variables, was significantly different from the null model (χ^2=12.03, df=2, P=0.002). The results revealed a significant negative relationship between aggression rates and group tenure ($F_{1,17}$ =8.2, P=0.01; Figure 4), with higher aggression rates against immigrant females in the dry than in the wet season ($F_{1,62}$=6.9, P=0.01).

[Figure 4]

The full model, testing the effects of season, context and dyad type on risk-reducing interactions among females, while controlling for subgroup size, was not significantly different from the null model (χ^2=3.63, df=4, P=0.5).

Discussion

Our results support two of our three predictions about aggression patterns. We found seasonal variation in female-female aggression rates, with higher rates in the dry season, when less food is available, than in the wet season, when more food is available. However, we did not find support for the related prediction that rates of aggression would be higher during feeding than during other contexts. These two results provide mixed support for the hypothesis that spider monkeys experience contest competition, as expected from the socioecological model and their highly frugivorous diet (Sterck et al. 1997). Our results also support the prediction that aggression rates are higher from resident to immigrant females than from immigrant to resident females and than between resident females. Contrary to our predictions, season, context and group tenure did not affect the rates of risk-reducing interactions.

Aggression rates between resident females were extremely low, supporting the hypothesis that there is little or no contest competition among long-term resident spider monkey females. Since reproductive females depend mainly on access to food resources, the pattern of aggression against recent immigrant females, especially in the first months after their immigration, can be interpreted as a strategy to cope with an increase in the number of individuals in the group and to reduce scramble competition (Asensio et al. 2008; Pusey & Schroepfer-Walker 2013; Miller et al. 2014). However, given the small sample size of resident and immigrant females, we need to be cautious in drawing the conclusions from our findings. Nevertheless, chimpanzees also show overall low aggression rates among long-term resident females, and most aggressive interactions targeting recent immigrant females (Kahlenberg et al. 2008a,b). Among chimpanzees, severe aggression by long-term resident females against recently immigrated females' infants was interpreted in a similar vein (Townsend et al. 2007). We did not observe aggression against infants of recently immigrant females in our study. The low aggression rates between long-term resident chimpanzee females have been interpreted as a consequence of the stability in social relationships rather than as evidence of little or no contest competition (Emery Thompson et al. 2007; Wakefield 2008). This could be an alternative explanation of our findings, but stability in social relationships does not necessarily imply the existence of dominance relationships between long-term resident females, as there is very little evidence for such relationships in spider monkeys (Aureli & Schaffner 2008). Our results, together with the finding that immigrant females are more likely to be found in mixed-sex subgroups than in iso-sexual subgroups (Riveros et al. in prep.), also suggests another explanation. Females may compete to associate with potential male protectors (Palombit 2000; Palombit et al. 2001) and vulnerable immigrant females may select mixed-sex subgroups to receive male protection against aggression by other females.

Our findings are similar to those of a study conducted 10 years earlier on the same population (Asensio et al. 2008), in which recent immigrant females were also the main targets of aggression, even though there were differences in group size and composition and in the data collection methods (focal sampling in the present study; all occurrences in Asensio et al. 2008) and statistical analysis between the two studies. Our results reveal that the less time a female was in the group the more likely she was to be the target of aggression by females who have been in the group for longer. In addition to confirming Asensio et al.'s (2008) main finding, we found evidence for a pattern of interactions not previously identified in spider monkeys: the main perpetrators of aggression against most recent immigrant females were less recent immigrant females rather than long-term resident females. This suggests that less recent immigrant females may be perceived as valuable by resident females, who may become more tolerant of less recent immigrant females as the behavior of the latter could help reduce food scramble competition by targeting the most recent immigrant females.

In contrast to earlier findings (Asensio et al. 2008), we found that aggressive interactions occurred more often in the dry season, when there was lower food availability, compared to the wet season. This pattern could provide evidence for contest competition. However, our follow-up analysis revealed that this pattern seems to be related to the timing of female immigration in our study, which was the dry season. Given that females were target of aggression especially at the beginning of their group tenure and that the first phase of immigration for the four study immigrant females was during the dry season, the higher aggression rates were likely due to the presence of more recent immigrant females during the dry season. Therefore, the higher aggression rate in the dry season was unlikely the outcome of contest competition due to seasonal differences in resources availability, but it was due to demographic factors related to female group tenure. This interpretation, together with the failure to find higher aggression rates during feeding than other contexts, supports the prediction that a high degree of fission-fusion dynamics reduces contest competition. Similar findings suggesting a lack of contest competition were found in brown spider monkeys (*Ateles hybridus*) inhabiting a small forest fragment, which exhibited higher aggression rates in periods of higher fruit availability than in periods of lower fruit availability (Rimbach et al. 2014). The authors explained this pattern by relating it to overall lower fruit availability in these forest fragments compared to continuous forest and potential higher conflict when valuable food patches are present (Rimbach et al. 2014).

High female-female aggression rates have been reported in other primate species characterized by female dispersal from the natal group. For example, in Bwindi gorillas higher aggression levels occurred when there were more than when there were fewer adult individuals in a given food tree, independent of patch size. In addition, aggression levels were higher when group members fed in patchily distributed resources, such as fruit trees, than when they fed on evenly distributed herbaceous vegetation, although fruit was not the major dietary component for this gorilla population (Robbins 2008). Furthermore, in Virunga gorillas females with longer group tenure were dominant over younger females and immigrant females had a lower dominance rank than resident females with longer time in the group (Robbins et al. 2005), especially in groups where some of the resident females were closely related (Robbins & Robbins 2015). Similarly, aggression rates between female chimpanzees increase as subgroup size increases (Wittig & Boesch 2003), especially during periods after the arrival of new immigrant females (Kahlenberg et al. 2008a), with older females apparently having more opportunities to win the confrontations, suggesting that the time a female has been in the group affects aggressive interactions among females. Since higher-ranking female chimpanzees have better core areas (i.e., small areas of intense use within the home range) and higher reproductive success than lower-ranking females (Pusey et al. 1997; Kahlenberg et al. 2008a; Pusey & Schroepfer-Walker 2013), core area quality is important for survival and reproduction (Emery Thompson et al. 2007). This predicts an increase in aggression among females during periods when access to the core area is at stake (Kahlenberg et al. 2008a). In spider monkeys group tenure also affects food competition as the longer a female has been in the group the better quality her core area is (Asensio et al. 2015). In addition, we found a similar pattern to that observed in chimpanzees (Kahlenberg et al. 2008a) with a peak in aggressive interactions among females when new females immigrated. Collectively, these findings support the hypothesis that the relationships among female-female aggression rates, food availability and dispersal patterns are more complex than socioecological models suggest and contribute to the growing awareness of the need to include additional factors in the models (Snaith & Chapman 2007; Thierry 2008; Clutton-Brock & Janson 2012; Koenig et al. 2013).

Given the mismatch between expected and observed patterns for spider monkeys and other species, socioecological theory should incorporate additional factors such as group tenure and possibly interspecific variation in cognitive abilities (Thierry 2008), since such factors may affect food competition (Asensio et al. 2015) as well as improve foraging decisions (Amici et al. 2009). Differences in some cognitive skills, such as inhibitory control, are associated with a high degree of fission-fusion dynamics by enhancing behavioral flexibility that may promote effective as well as more subtle social interactions than those observed in species living in more cohesive groups (Amici et al. 2008; Aureli et al. 2008). Thus, females could exhibit alternative tactics and different spatial patterns to cope with food competition and reduce the risk of aggression. Long-term resident females are likely to know the group home range and the location of the tree food patches better than newly immigrated females. In fact, we observed resident females reaching food patches before other subgroup members did (Juan Carlos Riveros, personal observation). Conversely, newly immigrated females avoided the food patch used by the rest of subgroup members and fed at a nearby food patch (Juan Carlos Riveros, personal observation). In species in which there is no clear dominance and food competition appears to occur in more subtle ways, these two alternative tactics may serve in reducing overt food competition and coping with potentially increased aggression risk.

The use of these two alternative tactics combined with the high degree of fission-fusion dynamics would explain the overall low aggression rates observed in this study, in which females do not exhibit risk-reducing interactions as strategy to deal with potential aggression related to food contest competition. Additionally, as aggression was directed mostly against recent immigrant females with the probable function of discouraging their immigration, it is unlikely that long-term resident females were inclined to engage in risk-reducing interactions with unwanted females. Thus, the patterns of aggressive interactions we found explain the relatively low rates of risk-reducing interactions as the dyads expected to engage in these interactions (i.e., the dyads composed by long-term resident females) had little reason to do so because there was basically no risk of aggression between them.

In conclusion, our study confirms earlier findings (Asensio et al 2008) and provides further insights into the factors affecting social interactions among spider monkey females. First, the mixed model approach allowed us to evaluate the effect of three explanatory variables on aggressive and risk-reducing interactions simultaneously, while controlling for the relative effect of the other two variables and accounting for the same individuals being in multiple dyads, and allowed us to confirm the main conclusions of an earlier study of food competition and group tenure (Asensio et al 2008). Second, we identified a pattern of interactions among females that was not previously described for spider monkeys: earlier immigrant females attack more recent immigrant females. These findings emphasize the importance of including additional factors, such as group tenure, in socioecological models for species with female dispersal and the need for comparative data to fully evaluate how demographic changes relate to variation in social interactions. Third, our findings provide indirect evidence that a high degree of fission-fusion dynamics is effective in coping with food contest competition and reducing aggression, but careful attention should be given to the potential additional role of more subtle tactics, such as arriving earlier to food patches and feeding in nearby food patches. Finally, given that female immigration rate in the study group was relatively high compared to that of other populations (Shimooka et al. 2008) and that most of the study resident females were relatively recent immigrants (fewer than 7 years in the group), our study should be replicated in populations where resident females have been in the group for longer.

Acknowledgments

We would like to thank the Guanacaste Conservation Area, Santa Rosa sector, for facilitating our research at the site. Thanks to Elvin Murillo Chacon for the support in the field. We are grateful to two anonymous reviewers and the editor for their comments on an early version of the paper. This study was supported by a scholarship obtained by the first author from the Consejo Nacional de Ciencia y Tecnología, México (CONACYT). The long-term project has been supported by

Chester Zoo, the National Geographic Society, the Leakey Foundation and CONACYT.

References

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, 49, 227-267.

Amici, F., Aureli, F. & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. *Current Biology*, 18, 1415-1419.

Amici, F., Call, J. & Aureli, F. (2009). Variation in withholding of information in three monkey species. *Proceedings of the Royal Society B*, 276, 3311-3318.

Asensio, N., Korstjens, A. H., Schaffner, C. M. & Aureli, F. (2008). Intragroup aggression, fission–fusion dynamics and feeding competition in spider monkeys. *Behaviour*, 145, 983-1001.

Asensio, N., Korstjens, A. H. & Aureli, F. (2009). Fissioning minimizes ranging costs in spider monkeys: A multiple-level approach. *Behavioral Ecology and Sociobiology*, 63, 649-659.

Asensio, N., Schaffner, C. & Aureli, F. (2015). Quality and overlap of individual core areas are related to group tenure in female spider monkeys. *American Journal of Primatology,* 77, 777-785.

Aureli, F. & Schaffner, C. M. (2002). Relationship assessment through emotional mediation. *Behaviour*, 139, 393-420.

Aureli, F. & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters,* 3, 147-149.

Aureli, F. & Schaffner, C. M. (2008). Spider monkeys: social structure, social relationships and social interactions. In C. Campbell (Ed.), *Spider monkeys:*

Behavior ecology & evolution of the genus Ateles (pp. 236-265). Cambridge: Cambridge University Press.

Aureli, F., Schaffner, C. M., Boesch, C., et al. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology*, 49, 627-654.

Aureli, F., Schaffner, C. M., Asensio, N. & Lusseau, D. (2012). What is a subgroup? How socioecological factors influence interindividual distance. *Behavioral Ecology*, 23, 1308-1315. doi:10.1093/beheco/ars122

Barton, R., Byrne, R. & Whiten, A. (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology*, 38, 321-329.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, doi:10.18637/jss.v067.i01

Chapman, C. A. (1988). Patterns of foraging and range use by three species of neotropical primates. *Primates*, 29, 177-194.

Chapman, C. A. (1990a). Ecological constraints on group size in three species of neotropical primates. *Folia Primatologica*, 55, 1-9.

Chapman, C. A. (1990b). Association patterns of male and female spider monkeys: the influence of ecology and sex on social organization. *Behavioral Ecology and Sociobiology*, 26, 409-414.

Chapman, C. A., Wrangham, R. W. & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, 36, 59-70.

Clutton-Brock, T. H. & Janson, Ch. (2012). Primate Socioecology at the Crossroads: Past, Present, and Future. *Evolutionary Anthropology*, 21, 136-150.

Croft, D.P., James, R. & Krause, J. (2008). *Exploring animal social networks*. Princeton: Princeton University Press.

Emery Thompson, M., Kahlenberg; S. M., Gilby, I. C. & Wrangham, R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73, 501-512.

Furuichi, T., Yamagiwa, J. & Aureli, F. (Eds.). (2015). *Dispersing primate females: life history and social strategies in male-philopatric species*. Berlin: Springer.

Hohmann, G. & Fruth, B. (2000). Use and function of genital contacts among female bonobos. *Animal Behaviour*, 60, 107-120.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology*, 2, 143-155.

Janzen, D. H. (1986). *Guanacaste national park: ecological and cultural restoration*. San Jose: UNED.

Kahlenberg, S. M., Thompson, M. E. & Wrangham, R. W. (2008a). Female competition over core areas in *Pan troglodytes schweinfurthii*, Kibale National Park, Uganda. *International Journal of Primatology*, 29, 931-947.

Kahlenberg, S. M., Thompson, M. E., Muller, M. N. & Wrangham, R. W. (2008b). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. *Animal Behaviour*, 76, 1497-1509.

Koenig, A., Scarry, C. J., Wheeler, B. C. & Borries, C. (2013). Variation in grouping patterns, mating systems and social structure: what socio-ecological models attempt to explain. *Philosophical Transactions of the Royal Society B*, 368, 20120348.

Kummer, H. (1971). *Primate societies: group techniques of ecological adaptation.* Arlington Heights, IL: AHM Publishing Corporation.

Miller, J. A., Pusey, A. E., Gilby, I. C., Schroepfer-Walker, K., Markham, A. C. & Murray, C. M. (2014). Competing for space: female chimpanzees are more aggressive inside than outside their core areas. *Animal Behaviour*, 87, 147-152.

Mitchell, CL., Boinski, S. & van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedi* and *S. sciureus*). *Behavioral Ecology and Sociobiology*, 28, 5-60.

Nicholson, A. J. (1954). An outline of the dynamics of animal populations. *Australian Journal of Zoology*, 2, 9-65.

Nishida, T., Kano, T., Goodall, J., McGrew, W.C. & Nakumura, M. (1999). Ethogram and ethnography of Mahale chimpanzees. *Anthropological Science*, 107, 141-188.

Palombit, R. A. (2000). Male-female social relationships and infanticide in animals. In C. P. van Schaik & C. H. Janson (Eds.), *Male infanticide and its implications*. Cambridge: Cambridge University Press, pp 240-268.

Palombit, R. A., Cheney, D. L. & Seyfarth, R. M (2001). Female-female competition for male “friends” in wild chacma baboons, *Papio cynecephalus ursinus*. *Animal Behaviour*, 61, 1159-1171.

Potts, K. B., Watts, D. P. & Wrangham, R. W. (2011). Comparative feeding ecology of two chimpanzee communities in Kibale National Park (Uganda). *International Journal of Primatology*, 32, 669-690.

Pruetz, J. D. & Isbell, L. A. (2000). Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. *Behavioral Ecology and Sociobiology*, 49, 38-47.

Pusey, A, Williams, J. & Goodall, J. (1997). The influence of dominance rank on the reproductive success of female chimpanzees. *Science*, doi:10.1126/science.277.5327.828

Pusey, A. E. & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society B*, doi:10.1098/rstb.2013.0077

Ramos-Fernandez, G. (2005). Vocal communication in a fission-fusion society: do spider monkeys stay in touch with close associates? *International Journal of Primatology*, 26, 1077-1092.

Rebecchini, L., Schaffner, C. M. & Aureli, F. (2011). Risk is a component of social relationships in spider monkeys. *Ethology*, 117, 691-699.

Rimbach, R., Link, A., Montes-Rojas, A., Di Fiore, A., Heistermann, M. & Heymann, E. W. (2014). Behavioral and physiological responses to fruit availability of spider monkeys ranging in a small forest fragment. *American Journal of Primatology*, 76, 1049-1061.

Robbins, M. M., Robbins, A. M., Gerald-Steklis, N. & Steklis, H. D. (2005). Long-term dominance relationships in female mountain gorillas: strength, stability and determinants of rank. *Behaviour*, 142, 779-809.

Robbins, M. M. (2008). Feeding competition and agonistic relationships among Bwindi *Gorilla beringei*. *International Journal of Primatology*, 29, 999-1018.

Robbins, A. M. & Robbins, M. M. (2015). Dispersal patterns of females in the genus Gorilla. In T. Furuichi, J. Yamagiwa & F. Aureli (Eds.), *Dispersing primate females*. *Life history and social strategies in male-philopatric species* (pp 75-104). Tokyo: Springer.

Santorelli, C.J., Schaffner, C.M., Campbell, C.J., Notman, H., Pavelka, M.S., Weghorst, J.A. & Aureli, F. (2011). Traditions in spider monkeys are biased towards the social domain. *PLoS ONE*, doi:10.1371/journal.pone.0016863

Schaffner, C. M. & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology,* 26, 1093-1106.

Schaffner, C. M., Rebecchini, L., Ramos-Fernandez, G., Vick, L. G. & Aureli, F. (2012). Spider Monkeys (*Ateles geoffroyi yucatanensis*) Cope with the negative consequences of hurricanes through changes in diet, activity budget, and fission-fusion dynamics. *International Journal of Primatology*, 33, 922-936.

van Schaik, C. P. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. A. Foley (Eds.), *Comparative socioecology: the behavioural ecology of humans and other mammals* (pp. 195-218). Boston: Blackwell Scientific Publications.

Scott, J & Lockard, J. S. (1999). Female dominance relationships among captive western Lowland gorillas: comparisons with the wild. *Behaviour*, 136, 1283-1310.

Shimooka, Y, Campbell, C.J., Di Fiore, A., Felton, A.M., Izawa, K., Link, A., Nishimura, A., Ramos-Fernández, G. & Wallace, R.B. (2008). Demography and group composition of *Ateles*. In Campbell, C.J. (Ed.), *Spider monkeys: behavior, ecology and evolution of the genus* Ateles (pp. 329-348). Cambridge: Cambridge University Press.

Shimooka, Y. (2015). Association networks and life history of female spider Monkeys. In T. Furuichi, J. Yamagiwa & F. Aureli (Eds.), *Dispersing primate females*. *Life history and social strategies in male-philopatric species* (pp. 23-43). Tokyo: Springer.

Slater, K., Schaffner, C. & Aureli, F. (2007). Embraces for infant handling in spider monkeys: evidence for a biological market? *Animal Behaviour*, 74, 455-461.

Slater, K., Schaffner, C. M. & Aureli, F. (2009). Sex differences in the social behavior of wild spider monkeys (*Ateles geoffroyi yucatanensis*). *American Journal of*

Primatology, 71, 21-29.

Snaith, T. V. & Chapman C. A. (2007). Primate group size and interpreting socioecological models: do folivores really play by different rules? *Evolutionary Anthropology*, 16, 94-106.

Stahl, D. & Kaumanns, W. (2003). Food competition in captive female sooty mangabeys (*Cercocebus torquatus atys*). *Primates*, 44, 203-216.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, 41, 291-309.

Stevenson, P. R., Quiñones, M. J. & Ahumada, J. A. (1998). Effects of fruit patch availability on feeding subgroup size and spacing patterns in four primate species at Tinigua National Park, Colombia. *International Journal of Primatology*, 19, 313-324.

Symington, M. M. (1990). Fission–fusion social organization in *Ateles* and *Pan. International Journal of Primatology,* 11, 47-61.

Thierry, B. (2008). Primate Socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology*, 17, 93-96.

Townsend, S. W., Slocombe, K. E., Emery Thompson, M. & Zuberbuhler, K. (2007). Female-led infanticide in wild chimpanzees. *Current Biology*, doi:10.1016/j.cub.2007.03.020

Utami, S. S., Wich, S. A., Sterck, E. H. M. & van Hooff, J. A. R. A. M. (1997). Food competition between wild orangutans in large fig trees. *International Journal of Primatology*, 18, 909-927.

Verderane, M. P.; Izar, P.; Visalberghi, E. & Fragaszy, D. M. (2013). Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): an analysis of social relationships among female primates that use tools in feeding. *Behaviour*, 150, 659-689.

Vick, L. G. (2008). Immaturity in spider monkeys: a risky business. In C. Campbell (Ed.), *Spider monkeys: behavior ecology & evolution of the genus* Ateles (pp. 288-328). Cambridge: Cambridge University Press.

Wakefield, M. L. (2008). Grouping patterns and competition among female *Pan troglodytes schweinfurthii* at Ngogo, Kibale National Park, Uganda. *International Journal of Primatology*, 29, 907-929.

Wittig, R. M. & Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International Journal of Primatology*, 24, 847-867.

Wrangham R. W. (1979). On the evolution of ape social systems. *Social Science Information*, 18, 335-368.

Wrangham R. W. (1980). An ecological model of female-bonded primate groups. *Behaviour*, 75, 262-300.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.

Figure legends

Fig. 1 Mean (±SE) aggression rates between spider monkeys (*Ateles geoffroyi*) females according to season at Santa Rosa, Costa Rica, between February 2014 and June 2015.

Fig. 2 Mean (±SE) aggression rates between spider monkeys (*Ateles geoffroyi*) females according to dyad type (the first term of the dyad is the aggressor) at Santa Rosa, Costa Rica, between February 2014 and June 2015.

Fig. 3 Mean (±SE) aggression rates between spider monkeys (*Ateles geoffroyi*) females according to group tenure (the first term of the dyad is the aggressor) at Santa Rosa, Costa Rica, between February 2014 and June 2015.

Fig. 4 The relationship between aggression rates toward immigrant spider monkeys (*Ateles geoffroyi*) females and tenure measured as the number of months immigrant females had spent in the study group at Santa Rosa, Costa Rica, between February 2014 and June 2015.