

# You are Not Welcome: Social Exchanges between Female Spider Monkeys (*Ateles geoffroyi*)



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**Abstract** Group living leads to competition for food between group members. Two types of intragroup food competition may occur: scramble competition, in which all group members use the same resource, such that feeding opportunities are equal for everyone; and contest competition, in which 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-min 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 toward 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 toward 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 · Female dispersal · Fission–fusion · Food competition · Tenure

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## 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 a conceptual framework to account for variation in female–female social relationships (Isbell 1991; Sterck *et al.* 1997; van Schaik 1989; Wrangham 1980). 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 (Barton *et al.* 1996; Mitchell *et al.* 1991; Pruettz and Isbell 2000; Stahl and Kaumanns 2003; Utami *et al.* 1997). 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 and 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 (Sterck *et al.* 1997; Wrangham 1979). 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 intragroup food competition by reducing the number of individuals feeding in a given food patch (Potts *et al.* 2011; Stevenson *et al.* 1998). 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 intragroup 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 and Lockard 1999; *G. beringei beringei*: Robbins *et al.* 2005; *Ateles geoffroyi*: Asensio *et al.* 2008, 2015; *Pan troglodyes*: Kahlenberg *et al.* 2008a; Pusey and 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's 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 and Schaffner 2007) and during reunions in captivity (Schaffner and 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 and Schaffner 2007). Owing to the risk associated with handling other females' infants, spider monkey females often give embraces when approaching mothers (Schaffner and 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 sociosexual contacts reported for bonobos (Hohmann and 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 and 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 among food distribution, the arrival of immigrant females, and the patterns of social interactions over time (Aureli and 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 (Asensio *et al.* 2009; Chapman *et al.* 1995; Symington 1990); 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 nonfeeding 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 nonfeeding 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 the approach of Asensio *et al.* (2008), 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 nonfeeding 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 conducted 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<sup>2</sup> 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 (Asensio *et al.* 2009; Chapman 1988).

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, owing 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 a 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 seven resident females and two immigrant females. During the study period these two immigrant females gave birth and two immigrant females joined the study group. Thus, at the end of the study there were nine resident and two immigrant females (Table I). 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 that 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.

## Data Collection

We conducted the study during 15 mo between February 2014 and June 2015, including 8 mo in the dry season and 7 mo in the wet season. We collected data for 8 h on each study day (mean  $\pm$  SE:  $8.5 \pm 1.0$  days/mo). We collected social interactions using

**Table I** Adult and subadult females belonging to the study group of spider monkeys (*Ateles geoffroyi*) at Santa Rosa between February 2014 and June 2015

ID	Age class	Resident status	Immigration month	Number of hours of focal observation
AL	Subadult/adult	Immigrant	November 2012	37.3
EC	Adult	Resident	August 2009	26.3
ES	Adult	Resident	— <sup>a</sup>	30.2
GA	Adult	Resident	January 2009	28.4
HU	Adult	Resident	December 2004	26.7
IR	Subadult	Immigrant	April 2015	1.6
MX	Subadult/adult	Immigrant	May 2013	25.6
NE	Adult	Resident	August 2007	17.9
NO	Adult	Resident	January 2009	21.2
TI	Adult	Resident	January 2010	35.2
UC	Subadult	Immigrant	April 2014	17.2

<sup>a</sup> Already in the study group in 2003

10-min 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  $\geq 1$  h after her last focal observation. We recorded the following social interactions based on the definitions of Asensio *et al.* (2008), Santorelli *et al.* (2011), and Slater *et al.* (2007, 2009): 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 that 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, nonfeeding, or mixed). We defined the context according to the subgroup activity. We scored feeding context when  $>50\%$  of the subgroup members actively ingested or searched for food, and nonfeeding context when this was not the case (Asensio *et al.* 2008); when an equal number of subgroup members engaged in feeding and nonfeeding 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 (Croft *et al.* 2008; Ramos-Fernandez 2005), in which we considered individuals to be in the same subgroup if they were  $\leq 50$  m from at least one other subgroup member (Aureli *et al.* 2012). We scored a fission event when one or more individuals from the followed subgroup were  $>50$  m from at least one current subgroup member for  $>30$  min (Asensio *et al.* 2009). We scored fusion when one or more individuals not belonging to the followed subgroup came within  $\leq 50$  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 h of observation with a mean ( $\pm$ SE) observation time per female of  $26.8 \pm 2.1$  h. This excludes the most recent immigrant female, which we sampled for only 1.6 h because she immigrated into the study group ca. 2 mo 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 from 15.3 to 48.1 h, with a mean ( $\pm$ SE) time per dyad of  $31.1 \pm 1.4$  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 nonfeeding context during the wet season and in the nonfeeding context during the dry season.

We built two linear mixed models (LMMs), 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, nonfeeding, 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.

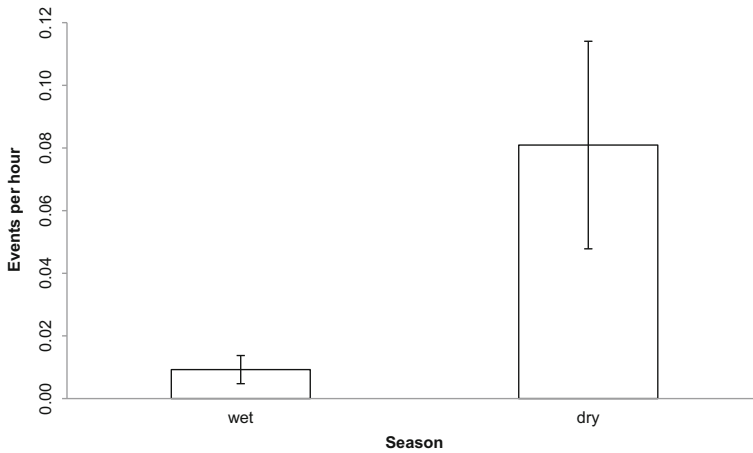
## Ethical Note

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.

## Results

The mean ( $\pm$  SE) hourly rate of aggressive interactions between females was  $0.039 \pm 0.014$  and that for risk-reducing interactions was  $0.014 \pm 0.005$ . Ninety-five percent 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.

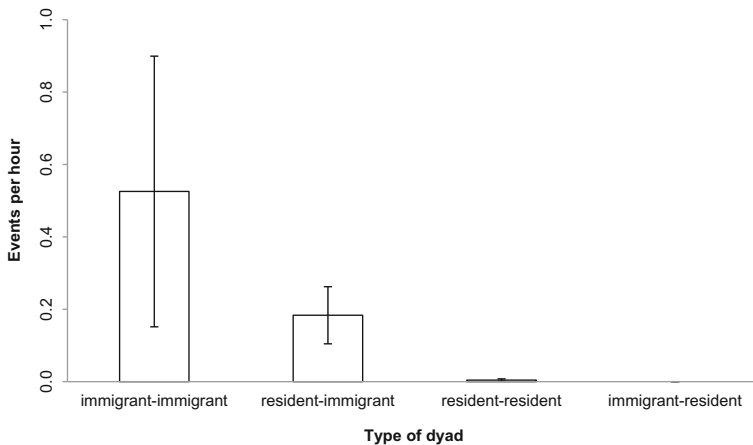
The full model, testing the effects of season, context, and dyad type on aggression rates between females, while controlling for subgroup size, was significantly different from the null model ( $\chi^2 = 29.6$ ,  $df = 4$ ,  $P = 0.006$ ). Females directed aggression toward other females more often in the dry than in the wet season ( $F_{1,1077} = 5.33$ ,  $P = 0.02$ ; Fig. 1), but there was no effect of context ( $F_{2,1051} = 1.39$ ,  $P = 0.25$ ). There was also a significant effect of dyad



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

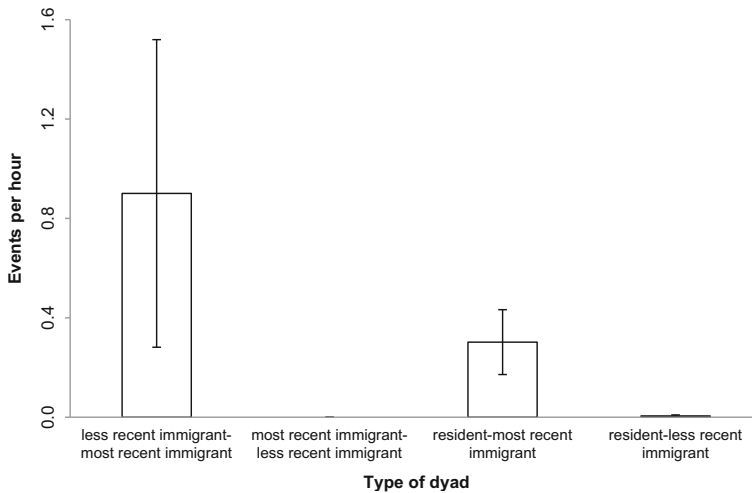
type on the rate of aggression ( $F_{3,173} = 8.35, P < 0.001$ ; Fig. 2). As predicted, aggression rates by residents against immigrant females were higher than aggression rates by immigrants against resident females ( $\beta = 0.18$ ; SE = 0.06;  $t_{122} = 3.02$ ;  $P = 0.003$ ) and by residents against other resident females ( $\beta = 0.16$ ; SE = 0.05;  $t_{129} = 3.5$ ;  $P < 0.001$ ). The highest aggression rates were between immigrant females (higher than resident-immigrant dyads:  $\beta = 0.35$ , SE = 0.14,  $t_{517} = 2.42$ ,  $P = 0.02$ ; higher than resident-resident dyads:  $\beta = 0.51$ ; SE = 0.14;  $t_{512} = 3.6$ ;  $P < 0.001$ ; and higher than immigrant-resident dyads:  $\beta = 0.53$ ; SE = 0.15;  $t_{515} = 3.6$ ;  $P < 0.001$ ; Fig. 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 ( $\beta = 0.32$ ; SE = 0.08;  $t_{113} = 4$ ;  $P < 0.001$ ; Fig. 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



**Fig. 2** Mean ( $\pm$ SE) aggression rates between female spider monkeys (*Ateles geoffroyi*) 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 ( $\pm$ SE) aggression rates between female spider monkeys (*Ateles geoffroyi*) according to group tenure (the first term of the dyad is the aggressor) at Santa Rosa, Costa Rica, between February 2014 and June 2015.

immigrant females ( $\beta = 0.92$ ;  $SE = 0.26$ ;  $t_{605} = 3.5$ ;  $P < 0.001$ ) and those by resident females against the most recent immigrant females ( $\beta = 0.61$ ;  $SE = 0.18$ ;  $t_{648} = 3.4$ ;  $P < 0.001$ ; Fig. 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 I), 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 owing 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 ( $\chi^2 = 12.03$ ,  $df = 2$ ,  $P = 0.002$ ). The results revealed a significant negative relationship between aggression rates and group tenure ( $F_{1,17} = 8.2$ ,  $P = 0.01$ ; Fig. 4), with higher aggression rates against immigrant females in the dry than in the wet season ( $F_{1,62} = 6.9$ ,  $P = 0.01$ ).

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 ( $\chi^2 = 3.63$ ,  $df = 4$ ,  $P = 0.5$ ).

## 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



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 longer. In addition to confirming the main finding of Asensio *et al.* (2008), 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 the 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 and Robbins 2015). Similarly, aggression rates between female chimpanzees increase as subgroup size increases (Wittig and 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 (Kahlenberg *et al.* 2008a; Pusey *et al.* 1997; Pusey and 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 pattern similar 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 (Clutton-Brock and Janson 2012; Koenig *et al.* 2013; Snaith and Chapman 2007; Thierry 2008).

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 (J. C. Riveros, *pers. obs.*). Conversely, newly immigrated females avoided the food patch used by the rest of subgroup members and fed at a nearby food patch (J. C. Riveros, *pers. obs.*). 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 a strategy to deal with potential aggression related to food contest competition. In addition, 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 longer.

## Data Availability

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

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## 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: Biological Sciences*, 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., Bearder, S. K., Call, J., 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.
- 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, C. H. (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 José: La Universidad Estatal a Distancia.
- 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: Biological Sciences*, *368*, 20120348.
- Kummer, H. (1971). *Primate societies: Group techniques of ecological adaptation*. Arlington Heights: AHM Publishing.
- 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, C. L., Boinski, S., & van Schaik, C. P. (1991). Competitive regimes and female bonding in two species of squirrel monkeys (*Saimiri oerstedii* 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., & Nakamura, 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* (pp. 240–268). Cambridge: Cambridge University Press.

- 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. E., & Schroepfer-Walker, K. (2013). Female competition in chimpanzees. *Philosophical Transactions of the Royal Society, B: Biological Sciences*. doi:10.1098/rstb.2013.0077.
- 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.
- 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.
- R Core Team (2015). R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria.
- 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. (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.
- 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.
- Santorelli, C. J., Schaffner, C. M., Campbell, C. J., Notman, H., Pavelka, M. S., et al (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.
- Scott, J., & Lockard, J. S. (1999). Female dominance relationships among captive western lowland gorillas: Comparisons with the wild. *Behaviour*, *136*, 1283–1310.
- 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.
- Shimooka, Y., Campbell, C. J., Di Fiore, A., Felton, A. M., Izawa, K., et al (2008). Demography and group composition of *Ateles*. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology and evolution of the genus Ateles* (pp. 329–348). Cambridge: Cambridge University Press.
- 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., & Frigaszy, 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 Science+Business Media.