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You are not welcome:

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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 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

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Introduction

45 Competition for food is one of the most important costs of group living and one of
46 the main factors affecting social relationships in primates (Wrangham 1980).

47 Socioecological theory has been proposed as conceptual framework to account for
48 variation in female-female social relationships (Wrangham 1980; van Schaik 1989;
49 Isbell 1991; Sterck et al. 1997). Since food intake affects female reproductive
50 success, the presence of group members leads to increased competition for food
51 (Isbell 1991). Two types of food competition are recognized depending on the
52 distribution and abundance of food resources: scramble and contest (Nicholson
53 1954; van Schaik 1989). Contest competition occurs when some group members can
54 monopolize resources and exclude others through aggression and dominance.

55 Scramble competition occurs when resources are unmonopolizable and feeding
56 opportunities decrease when group size is larger. According to socioecological
57 theory, female primates that feed on clumped and monopolizable resources, such as
58 ripe fruits, are expected to have differentiated relationships with one another in terms
59 of antagonistic and dominance interactions as well as grooming and coalitions;
60 female philopatry and kin-bias interactions should be the rule under these conditions
61 and thus the relationships among females are characterized as Resident-Nepotistic
62 (Sterck et al. 1997). When resources are evenly distributed and are
63 unmonopolizable, females are not expected to form dominance relationships or kin-
64 bias alliances; therefore, female philopatry would not be beneficial and the
65 relationships among females are characterized as Dispersal-Egalitarian (Sterck et al.
66 1997).

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

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

78 In some primate species, group members form temporary subgroups of variable
79 size and composition according to food availability and/or intensity of predation risk
80 (Wrangham 1979; Sterck et al. 1997). Fissioning into smaller subgroups when food
81 availability is low may serve to reduce food competition (Kummer 1971); when this is
82 frequent the social organization is characterized by a high degree of fission-fusion
83 dynamics (Aureli et al. 2008). In primate species with a high degree of fission-fusion
84 dynamics, such as chimpanzees, bonobos (*Pan paniscus*) and spider monkeys
85 (*Ateles* spp.), fission events mitigate the impact of within-group food competition by
86 reducing the number of individuals feeding in a given food patch (Stevenson et al.
87 1998; Potts et al. 2011). For example, in Geoffroy's spider monkeys (*A. geoffroyi*) the
88 formation of smaller subgroups during the dry season resulted in no increase in
89 aggression rates, although food resources were scarcer than in the wet season
90 (Asensio et al. 2008). Likewise, in extreme situations of drastic changes in food
91 availability, such as after hurricanes, spider monkeys cope with decreased fruit
92 availability and reduce within-group competition by forming smaller subgroups after
93 than before the hurricanes (Schaffner et al. 2012).

94 In species with female dispersal from the natal group the amount of time females
95 have been in the group (i.e., group tenure) can affect their social interactions
96 (Furuichi et al. 2015). In particular, group tenure can influence the pattern of
97 aggression and food competition among females, with long-term resident females
98 being aggressive to and using better-quality areas than newly immigrant females
99 (*Gorilla gorilla gorilla*: Scott & Lockard 1999; *G. beringei beringei*: Robbins et al.
100 2005; *Ateles geoffroyi*: Asensio et al. 2008, 2015; *Pan troglodytes*: Kahlenberg et al.
101 2008a; Pusey & Schroepfer-Walker 2013). Thus, female reproductive success may
102 be affected by social factors that are not considered in the socioecological model,
103 such as group tenure in species with female dispersal.

104 Spider monkey females tend to disperse from their natal group once they reach
105 sexual maturity (Symington 1990; Vick 2008). When recent immigrant females join a
106 group, food competition is likely to intensify because of the increased number of
107 group members. To reduce competition for food and aggression risk in a given food
108 patch, individuals can fission into smaller subgroups. Nevertheless, the total number
109 of individuals in the group is not reduced, which influences the use of available
110 resources in the group home range. Thus, fission events are ineffective in coping
111 with scramble food competition at the group level (Asensio et al. 2008, 2009).

112 Although aggressive behaviors between group members are often taken as
113 indicators of dominance relationships and contest competition, this pattern can also
114 be viewed as the result of scramble competition (Asensio et al. 2008). Aggression by
115 adult females against subadult females can be interpreted as a tactic to stop newly
116 immigrated females settling into spider monkey groups (Asensio et al. 2008). Under
117 this scenario, aggression may serve to manage the number of individuals using the
118 resources in the group home range.

119 In contrast to fissions, fusions may create risky situations. Spider monkeys
120 manage potential conflict and reduce uncertainty as well as the risk of aggression by
121 using embraces often with pectoral sniffing after fusion events in the wild (Aureli &
122 Schaffner 2007) and during reunions in captivity (Schaffner & Aureli 2005). Embraces
123 with kisses have also been reported in post-fusion events in chimpanzees as an
124 attempt to prevent aggression (Nishida et al. 1999). In spider monkeys kisses are
125 considered a greeting variant of embraces (Santorelli et al. 2011) and may mitigate
126 the risk of aggression in a similar way to embraces (Aureli & Schaffner 2007). Due to
127 the risk associated with handling other females' infants, spider monkey females often
128 give embraces when approaching mothers (Schaffner & Aureli 2005; Slater et al.
129 2007). In addition, a principal component analysis found that embraces and
130 aggressive interactions had a high loading in the same component, whereas
131 affiliative interactions, such as grooming, loaded highly on a different component
132 (Rebecchini et al. 2011). The function of embraces, pectoral sniffing and kisses may
133 be similar to the tension regulation of socio-sexual contacts reported for bonobos
134 (Hohmann & Fruth 2000). However, there is no established measure of tension in
135 spider monkeys. Given the evidence that links embraces, pectoral sniffing and kisses
136 to risk in spider monkeys, we refer to them collectively as risk-reducing interactions.

137 Frugivorous primates, such as spider monkeys, are expected to exhibit female
138 philopatry, kin-biased interactions among females and contest competition (Sterck et
139 al. 1997) but instead spider monkeys are characterized by female dispersal and
140 unclear dominance relationships among adult females (Aureli & Schaffner 2008).
141 Therefore, spider monkeys provide good models to assess the predictive power of
142 socioecological theory under challenging circumstances and to better understand the
143 relationship between food distribution, the arrival of immigrant females and the

144 patterns of social interactions over time (Aureli & Schaffner 2002). In addition, there
145 is a growing understanding about the relationships among a variety of
146 socioecological variables in spider monkeys. For example, fruit availability influences
147 subgroup size, with larger subgroups when more food is available than when less
148 food is available (Symington 1990; Chapman et al. 1995; Asensio et al. 2009); and
149 group tenure affects individual core-area quality, with females with longer tenure
150 having better core areas than females with shorter tenure (Asensio et al. 2015).

151 Spider monkey females have higher aggression rates in feeding than in non-
152 feeding contexts but there is no difference in aggression rates between seasons,
153 although seasons vary greatly in food availability (Asensio et al. 2008). Aggression is
154 also strongly affected by the relative age and group tenure of the interacting
155 individuals (Asensio et al. 2008). We built on these findings, by investigating whether
156 patterns of female-female interactions in spider monkeys were influenced by factors
157 typical of the socioecological model, such as food-related factors, and the novel
158 factor of group tenure. If spider monkeys experience contest competition as expected
159 based on their highly frugivorous diet, we predicted higher aggression rates in the dry
160 season, where less food is usually available, than in the wet season, and in feeding
161 contexts than in non-feeding contexts. Alternatively, if the high degree of fission-
162 fusion dynamics reduces contest competition, we predicted no difference in
163 aggression rates between seasons or contexts. If females attempt to reduce food
164 scramble competition, we predicted higher aggression rates from long-term resident
165 females against recent immigrant females than the reverse. Similarly we predicted
166 higher aggression rates by long-term resident females against recent immigrant
167 females than against other long-term resident females. We also explored whether the
168 most recent immigrant females received the majority of aggression from less recent

169 immigrant females. We extended Asensio et al.'s (2008) approach, which focused on
170 aggressive interactions, by including predictions about risk-reducing interactions. We
171 predicted higher rates of risk-reducing interactions when aggression rates were
172 higher (e.g., in the dry season and in feeding contexts) than when aggression rates
173 were lower (in the wet season and in non-feeding contexts). We also predicted higher
174 rates of risk-reducing interactions in female-female dyads with higher aggression
175 rates than in dyads with lower aggression rates.

176

177 **Methods**

178 *Subjects and study site*

179 We carried out the study in the Santa Rosa sector, located in the Guanacaste
180 Conservation Area, Northwestern Costa Rica (10°50'N, 85°38'W). Santa Rosa
181 comprises 108 km² of tropical dry forest, which is characterized by a severe dry
182 season between December and May and a wet season during the rest of the year
183 (Janzen 1986). Food availability for spider monkeys at the site is lower during the dry
184 season than during the wet season (Chapman 1988; Asensio et al. 2009).

185 We studied one group of spider monkeys, previously studied by Chapman
186 (1988, 1990a,b) and Asensio et al. (2008, 2009), which was well habituated to being
187 followed by researchers and ranged in size from 19 to 25 individuals during the study
188 period, due to births, immigration and disappearances. We studied all 11 adult and
189 subadult females in the group. We considered a female as subadult from when she
190 was sexually mature until she gave birth for the first time (Vick 2008). We classified
191 females according to their group tenure as long-term resident (hereafter resident) or
192 recent immigrant (hereafter immigrant). We considered females as immigrant from
193 the first time we saw them in a subgroup with resident females until they gave birth to

194 their first infant as females are more integrated in the group after this (Shimooka
195 2015). At the onset of the study there were 7 resident females and 2 immigrant
196 females. During the study period these 2 immigrant females gave birth and 2
197 immigrant females joined the study group. Thus, at the end of the study there were 9
198 resident and 2 immigrant females (Table 1). Immigrant females were all subadult. All
199 resident females were adult and there were no natal subadult females. For one
200 analysis we divided immigrant females into two additional categories: the last female
201 who immigrated into the group and the other immigrant females. The most recent
202 immigrant changed during the study period depending on immigration time of new
203 females into the group.

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[Table 1]

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Data collection

208 We conducted the study during 15 months between February 2014 and June
209 2015, including eight months in the dry season and seven months in the wet season.
210 We collected data for 8 hours on each study day (mean \pm SE: 8.5 \pm 1.0 days per
211 month). We collected social interactions using 10-minute focal-animal sampling of
212 each female with continuous recording (Altmann 1974). We selected focal subjects
213 from the females in the subgroup we were following, giving preference to the
214 individual with the fewest observations. We sampled the same female again at least
215 one hour after her last focal observation. We recorded the following social
216 interactions based on Slater et al. (2007, 2009), Asensio et al. (2008) and Santorelli
217 et al.'s (2011) definitions: aggressive interactions (including spatial displacements,
218 threats, chases, strikes and bites) and risk-reducing interactions, including embraces

219 (face-to-face interactions in which an individual wraps one or two arms around the
220 shoulder or back of another individual), pectoral sniff (an individual places its nose at
221 the chest or arm pit region of another individual) and kisses (face-to-face interactions
222 in which an individual gets its face close to the one of another individual cheek-to-
223 cheek, usually with no physical contact). For each social interaction, we recorded the
224 identity of the individuals involved along with the season in which the interaction took
225 place and the context (feeding, non-feeding, or mixed). We defined the context
226 according to the subgroup activity. We scored feeding context when more than 50%
227 of the subgroup members actively ingested or searched for food, and non-feeding
228 context when this was not the case (Asensio et al. 2008); when an equal number of
229 subgroup members engaged in feeding and non-feeding activities, we scored mixed
230 context. We recorded subgroup activity continuously.

231 We also recorded all subgroup members, as well as changes in subgroup
232 composition any time one or more individuals joined (fusion) or left (fission) the
233 followed subgroup (Asensio et al. 2009). Two observers kept track of subgroup
234 membership simultaneously. We defined subgroup membership using a criterion
235 based on a chain rule (Ramos-Fernandez 2005; Croft et al. 2008), in which we
236 considered individuals to be in the same subgroup if they were ≤ 50 m from at least
237 one other subgroup member (Aureli et al. 2012). We scored a fission event when 1 or
238 more individuals from the followed subgroup were more than 50 m from at least one
239 current subgroup member for more than 30 min (Asensio et al. 2009). We scored
240 fusion when one or more individuals not belonging to the followed subgroup came
241 within ≤ 50 m of any member of the followed subgroup (Asensio et al. 2009). The
242 critical distance of 50 m was empirically established for the study group (Aureli et al.
243 2012). For calculation of subgroup size we excluded juveniles and infants from the

244 total count as they were always in the same subgroup as their mother. We used
245 three categories of subgroup size based on the frequency distribution of all subgroup
246 sizes observed during the study period as these three categories showed similar
247 frequencies: small (2-4 individuals), medium (5-8) and large (9-13).

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

255

256 *Statistical analysis*

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

264 We built two linear mixed models (LMM), with aggression rate as the response
265 variable in one LMM and the rate of risk-reducing interactions as the response
266 variable in the other. Both models included the season (wet or dry) in which the
267 female-female interactions took place, context (feeding, non-feeding or mixed), and
268 dyad type as explanatory variables. Given that subgroup size has no effect on

269 female-female interaction rates (Riveros et al. unpub. data), we did not include
270 subgroup size as an additional explanatory variable, but we included it as a control
271 variable. We classified female-female dyads into four types depending on the group
272 tenure of the actor (first term) and recipient (second term) of the social interaction:
273 resident-immigrant, immigrant-resident, immigrant-immigrant and resident-resident.
274 We further examined aggression against immigrant females by running another LMM
275 with the same variables and dividing immigrant females into the most recent
276 immigrant and the less recent immigrant females. We included the identities of the
277 actor and recipient as random effects to account for the presence of the same
278 individuals in multiple dyads (Zuur et al. 2009). We ran the LMMs using the lme4
279 package (version 1.1-9, Bates et al. 2015) in R (Core Team 2015). We checked for
280 model assumptions and log-transformed the response variable when appropriate. We
281 present results for the explanatory variables only when the full model was
282 significantly different from the null model.

283

284 *Ethical note*

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

290

291 *Data availability*

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

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Results

The mean (\pm 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 ($\chi^2=29.6$, $df=4$, $P=0.006$). Females directed aggression toward other females more often in the dry than in the wet season ($F_{1,1077}=5.33$, $P=0.02$; 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 ($\beta =0.18$; $SE=0.06$; $t_{122}=3.02$; $P=0.003$) 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: $\beta =0.53$; $SE=0.15$; $t_{515}=3.6$; $P<0.001$; Figure 2).

[Figure 1]

319 **[Figure 2]**

320

321 When we divided immigrant females into two categories, we found that resident
322 females attacked the most recent immigrant females at higher rates than less recent
323 immigrant females ($\beta = 0.32$; $SE = 0.08$; $t_{113} = 4$; $P < 0.001$, Figure 3). Furthermore,
324 aggression rates by less recent immigrant females against the most recent immigrant
325 females were higher than those by the most recent immigrant against less recent
326 immigrant females ($\beta = 0.92$; $SE = 0.26$; $t_{605} = 3.5$; $P < 0.001$) and those by resident
327 females against the most recent immigrant females ($\beta = 0.61$; $SE = 0.18$; $t_{648} = 3.4$;
328 $P < 0.001$; Figure 3).

329

330 **[Figure 3]**

331

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

344

345

[Figure 4]

346

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

350

351

Discussion

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

364 Aggression rates between resident females were extremely low, supporting the
365 hypothesis that there is little or no contest competition among long-term resident
366 spider monkey females. Since reproductive females depend mainly on access to
367 food resources, the pattern of aggression against recent immigrant females,
368 especially in the first months after their immigration, can be interpreted as a strategy

369 to cope with an increase in the number of individuals in the group and to reduce
370 scramble competition (Asensio et al. 2008; Pusey & Schroepfer-Walker 2013; Miller
371 et al. 2014). However, given the small sample size of resident and immigrant
372 females, we need to be cautious in drawing the conclusions from our findings.
373 Nevertheless, chimpanzees also show overall low aggression rates among long-term
374 resident females, and most aggressive interactions targeting recent immigrant
375 females (Kahlenberg et al. 2008a,b). Among chimpanzees, severe aggression by
376 long-term resident females against recently immigrated females' infants was
377 interpreted in a similar vein (Townsend et al. 2007). We did not observe aggression
378 against infants of recently immigrant females in our study. The low aggression rates
379 between long-term resident chimpanzee females have been interpreted as a
380 consequence of the stability in social relationships rather than as evidence of little or
381 no contest competition (Emery Thompson et al. 2007; Wakefield 2008). This could be
382 an alternative explanation of our findings, but stability in social relationships does not
383 necessarily imply the existence of dominance relationships between long-term
384 resident females, as there is very little evidence for such relationships in spider
385 monkeys (Aureli & Schaffner 2008). Our results, together with the finding that
386 immigrant females are more likely to be found in mixed-sex subgroups than in iso-
387 sexual subgroups (Riveros et al. in prep.), also suggests another explanation.
388 Females may compete to associate with potential male protectors (Palombit 2000;
389 Palombit et al. 2001) and vulnerable immigrant females may select mixed-sex
390 subgroups to receive male protection against aggression by other females.

391 Our findings are similar to those of a study conducted 10 years earlier on the
392 same population (Asensio et al. 2008), in which recent immigrant females were also
393 the main targets of aggression, even though there were differences in group size and

394 composition and in the data collection methods (focal sampling in the present study;
395 all occurrences in Asensio et al. 2008) and statistical analysis between the two
396 studies. Our results reveal that the less time a female was in the group the more
397 likely she was to be the target of aggression by females who have been in the group
398 for longer. In addition to confirming Asensio et al.'s (2008) main finding, we found
399 evidence for a pattern of interactions not previously identified in spider monkeys: the
400 main perpetrators of aggression against most recent immigrant females were less
401 recent immigrant females rather than long-term resident females. This suggests that
402 less recent immigrant females may be perceived as valuable by resident females,
403 who may become more tolerant of less recent immigrant females as the behavior of
404 the latter could help reduce food scramble competition by targeting the most recent
405 immigrant females.

406 In contrast to earlier findings (Asensio et al. 2008), we found that aggressive
407 interactions occurred more often in the dry season, when there was lower food
408 availability, compared to the wet season. This pattern could provide evidence for
409 contest competition. However, our follow-up analysis revealed that this pattern
410 seems to be related to the timing of female immigration in our study, which was the
411 dry season. Given that females were target of aggression especially at the beginning
412 of their group tenure and that the first phase of immigration for the four study
413 immigrant females was during the dry season, the higher aggression rates were likely
414 due to the presence of more recent immigrant females during the dry season.
415 Therefore, the higher aggression rate in the dry season was unlikely the outcome of
416 contest competition due to seasonal differences in resources availability, but it was
417 due to demographic factors related to female group tenure. This interpretation,
418 together with the failure to find higher aggression rates during feeding than other

419 contexts, supports the prediction that a high degree of fission-fusion dynamics
420 reduces contest competition. Similar findings suggesting a lack of contest
421 competition were found in brown spider monkeys (*Ateles hybridus*) inhabiting a small
422 forest fragment, which exhibited higher aggression rates in periods of higher fruit
423 availability than in periods of lower fruit availability (Rimbach et al. 2014). The
424 authors explained this pattern by relating it to overall lower fruit availability in these
425 forest fragments compared to continuous forest and potential higher conflict when
426 valuable food patches are present (Rimbach et al. 2014).

427 High female-female aggression rates have been reported in other primate
428 species characterized by female dispersal from the natal group. For example, in
429 Bwindi gorillas higher aggression levels occurred when there were more than when
430 there were fewer adult individuals in a given food tree, independent of patch size. In
431 addition, aggression levels were higher when group members fed in patchily
432 distributed resources, such as fruit trees, than when they fed on evenly distributed
433 herbaceous vegetation, although fruit was not the major dietary component for this
434 gorilla population (Robbins 2008). Furthermore, in Virunga gorillas females with
435 longer group tenure were dominant over younger females and immigrant females
436 had a lower dominance rank than resident females with longer time in the group
437 (Robbins et al. 2005), especially in groups where some of the resident females were
438 closely related (Robbins & Robbins 2015). Similarly, aggression rates between
439 female chimpanzees increase as subgroup size increases (Wittig & Boesch 2003),
440 especially during periods after the arrival of new immigrant females (Kahlenberg et
441 al. 2008a), with older females apparently having more opportunities to win the
442 confrontations, suggesting that the time a female has been in the group affects
443 aggressive interactions among females. Since higher-ranking female chimpanzees

444 have better core areas (i.e., small areas of intense use within the home range) and
445 higher reproductive success than lower-ranking females (Pusey et al. 1997;
446 Kahlenberg et al. 2008a; Pusey & Schroepfer-Walker 2013), core area quality is
447 important for survival and reproduction (Emery Thompson et al. 2007). This predicts
448 an increase in aggression among females during periods when access to the core
449 area is at stake (Kahlenberg et al. 2008a). In spider monkeys group tenure also
450 affects food competition as the longer a female has been in the group the better
451 quality her core area is (Asensio et al. 2015). In addition, we found a similar pattern
452 to that observed in chimpanzees (Kahlenberg et al. 2008a) with a peak in aggressive
453 interactions among females when new females immigrated. Collectively, these
454 findings support the hypothesis that the relationships among female-female
455 aggression rates, food availability and dispersal patterns are more complex than
456 socioecological models suggest and contribute to the growing awareness of the need
457 to include additional factors in the models (Snaith & Chapman 2007; Thierry 2008;
458 Clutton-Brock & Janson 2012; Koenig et al. 2013).

459 Given the mismatch between expected and observed patterns for spider
460 monkeys and other species, socioecological theory should incorporate additional
461 factors such as group tenure and possibly interspecific variation in cognitive abilities
462 (Thierry 2008), since such factors may affect food competition (Asensio et al. 2015)
463 as well as improve foraging decisions (Amici et al. 2009). Differences in some
464 cognitive skills, such as inhibitory control, are associated with a high degree of
465 fission-fusion dynamics by enhancing behavioral flexibility that may promote effective
466 as well as more subtle social interactions than those observed in species living in
467 more cohesive groups (Amici et al. 2008; Aureli et al. 2008). Thus, females could
468 exhibit alternative tactics and different spatial patterns to cope with food competition

469 and reduce the risk of aggression. Long-term resident females are likely to know the
470 group home range and the location of the tree food patches better than newly
471 immigrated females. In fact, we observed resident females reaching food patches
472 before other subgroup members did (Juan Carlos Riveros, personal observation).
473 Conversely, newly immigrated females avoided the food patch used by the rest of
474 subgroup members and fed at a nearby food patch (Juan Carlos Riveros, personal
475 observation). In species in which there is no clear dominance and food competition
476 appears to occur in more subtle ways, these two alternative tactics may serve in
477 reducing overt food competition and coping with potentially increased aggression
478 risk.

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

490 In conclusion, our study confirms earlier findings (Asensio et al 2008) and
491 provides further insights into the factors affecting social interactions among spider
492 monkey females. First, the mixed model approach allowed us to evaluate the effect
493 of three explanatory variables on aggressive and risk-reducing interactions

494 simultaneously, while controlling for the relative effect of the other two variables and
495 accounting for the same individuals being in multiple dyads, and allowed us to
496 confirm the main conclusions of an earlier study of food competition and group tenure
497 (Asensio et al 2008). Second, we identified a pattern of interactions among females
498 that was not previously described for spider monkeys: earlier immigrant females
499 attack more recent immigrant females. These findings emphasize the importance of
500 including additional factors, such as group tenure, in socioecological models for
501 species with female dispersal and the need for comparative data to fully evaluate
502 how demographic changes relate to variation in social interactions. Third, our findings
503 provide indirect evidence that a high degree of fission-fusion dynamics is effective in
504 coping with food contest competition and reducing aggression, but careful attention
505 should be given to the potential additional role of more subtle tactics, such as arriving
506 earlier to food patches and feeding in nearby food patches. Finally, given that female
507 immigration rate in the study group was relatively high compared to that of other
508 populations (Shimooka et al. 2008) and that most of the study resident females were
509 relatively recent immigrants (fewer than 7 years in the group), our study should be
510 replicated in populations where resident females have been in the group for longer.

511

512

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713

714 **Figure legends**

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

718

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

722

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

726

727 **Fig. 4** The relationship between aggression rates toward immigrant spider monkeys
728 (*Ateles geoffroyi*) females and tenure measured as the number of months immigrant
729 females had spent in the study group at Santa Rosa, Costa Rica, between February
730 2014 and June 2015.