RESEARCH ARTICLE

Behavioral and Physiological Responses to Fruit Availability of Spider Monkeys Ranging in a Small Forest Fragment

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Numerous animal species currently experience habitat loss and fragmentation. This might result in behavioral and dietary adjustments, especially because fruit availability is frequently reduced in fragments. Food scarcity can result in elevated physiological stress levels, and chronic stress often has detrimental effects on individuals. Some animal species exhibit a high degree of fission–fusion dynamics, and theory predicts that these species reduce intragroup feeding competition by modifying their subgroup size according to resource availability. Until now, however, there have been few studies on how species with such fission–fission dynamics adjust their grouping patterns and social behavior in small fragments or on how food availability influences their stress levels. We collected data on fruit availability, feeding behavior, stress hormone levels (measured through fecal glucocorticoid metabolites (FGCM)), subgroup size, and aggression for two groups of brown spider monkeys (*Ateles hybridus*) in a small forest fragment in Colombia and examined whether fruit availability influences these variables. Contrary to our predictions, spider monkeys ranged in smaller subgroups, had higher FGCM levels and higher aggression rates when fruit availability was high compared to when it was low. The atypical grouping pattern of the study groups seems to be less effective at mitigating contest competition over food resources than more typical fission–fusion patterns. Overall, our findings illustrate that the relationship between resource availability, grouping patterns, aggression rates, and stress levels can be more complex than assumed thus far. Additional studies are needed to investigate the long-term consequences on the health and persistence of spider monkeys in fragmented habitats. Am. J. Primatol. 76:1049–1061, 2014. © 2014 The Authors. *American Journal of Primatology* Published by Wiley Periodicals, Inc.

INTRODUCTION

The spatio-temporal dynamics of animal societies vary from groups in which individual members live in almost constant cohesion and coordinate their travel to groups with highly flexible grouping patterns [Aureli et al., 2008]. Most group-living animals form more cohesive groups, whereas a few others exhibit flexible fission–fusion dynamics, like giant noctule bats (*Nyctalus lasiopterus* [Popa-Lisseanu et al., 2008]), giraffes (*Giraffa camelopardalis reticulata* [Shorrocks & Croft, 2009]), spotted hyenas (*Crocuta crocuta* [Holekamp et al., 1997]), dolphins (*Tursiops truncatus* [Würsig, 1978]), elephants (*Loxodonta africana* [Couzin, 2006]), spider monkeys (genus *Ateles* [Fedigan & Baxter, 1984; Klein, 1972]), chimpanzees and bonobos (genus *Pan* [Itani & Suzuki, 1967; Kano, 1982; Nishida &

Hiraiwa-Hasegawa, 1987]). In these species members of a stable group form smaller subgroups that vary in size and composition [Aureli et al., 2008; Klein, 1972; Kummer, 1971; Symington, 1987]. It has been proposed that these flexible grouping patterns constitute a strategy that aims to balance the costs and benefits of group-living and to cope with changes in the spatial and temporal availability of food resources [Chapman, 1990a,b; Dunbar, 1987; Klein & Klein, 1977; Kummer, 1971; Shimooka, 2003; Strier, 1992; Symington, 1988]. Several studies have shown a positive relationship between measurements of habitat-wide food availability and subgroup size in both spider monkeys and chimpanzees (*Ateles*: [Asensio et al., 2009; Chapman, 1990b; Shimooka, 2003; Symington, 1988]; *Pan*: [Basabose, 2004; Itoh & Nishida, 2007; Potts, 2011]). However, other studies on the genus *Pan* have found a negative or no relationship between measurements of food availability and subgroup size (chimpanzee: [Hashimoto et al., 2003; Moscovice et al., 2007; Newton-Fisher et al., 2000; Wakefield, 2008]; bonobo: [Hohmann & Fruth, 2002]). Comparable results have not yet been reported for spider monkeys.

Most studies that have examined changes in food availability and subgroup size in primates have been conducted in large and continuous forests. However, currently many animal species are confronted with and threatened by habitat loss and habitat fragmentation [Janson, 2000; Pimm & Raven, 2000; Turner, 1996]. To ensure their survival, animals often adjust aspects of their behavior and/or demographics (e.g., activity patterns, population density, social behavior, group size) in response to these anthropogenic disturbances [Boyle & Smith, 2010; Cristóbal-Azkarate et al., 2004; Hargis et al., 1999; Menon & Poirier, 1996; Umapathy et al., 2011; Wauters et al., 1994]. In addition, many species (particularly frugivorous ones) modify their diet when living in fragments because fragmentation often results in reduced availability of fruit for forest-dwelling animals [Arroyo-Rodríguez & Mandujano, 2006; Cordeiro & Howe, 2001; Dunn et al., 2010; Laurance et al., 1997; Putz et al., 1990]. Availability of leaves, by contrast, can increase in fragments due to changed microclimatic parameters [Ganzhorn, 1995; Johns, 1988]. Consequently, primates living in fragments are generally forced to rely more heavily on leaves than on fruit [Abondano & Link, 2012; Chaves et al., 2012; Dunn et al., 2010; González-Zamora et al., 2009; Irwin, 2007; Juan et al., 2000; Lopez et al., 2005; Tesfaye et al., 2013; Tutin, 1999]. Additionally, primates with flexible grouping patterns might modify subgroup sizes in order to adjust to reduced levels of fruit availability in fragments as occurred in habitats that became more fragmented after hurricanes [Champion, 2013; Schaffner et al., 2012]. However, the limitation of space in small fragments could potentially restrict the effectiveness of fission–fusion dynamics to reduce intragroup feeding competition.

Periods of food scarcity, during which animals cannot feed on their preferred food items and thus potentially experience a decreased caloric intake, result in many vertebrate taxa in an elevation of glucocorticoid levels to cope with these periods of nutritional stress (mammals: red colobus monkeys (*Procolobus rufomitratus*) [Chapman et al., 2007], yellow baboons (*Papio cynocephalus*) [Gesquiere et al., 2008], black howler monkeys (*Alouatta pigra*) [Behie et al., 2010], ringtailed lemurs (*Lemur catta*) [Cavigelli, 1999], African elephants (*Loxodonta africana*) [Foley et al., 2001]; birds: Black-legged Kittiwakes (*Rissa tridactyla*) [Kitaysky et al., 1999]; reptiles: Galápagos marine iguanas (*Amblyrhynchus cristatus*) [Romero & Wikelski, 2001]). Short-term elevations of glucocorticoids (GCs) are considered adaptive responses because they provide readily available energy which enables vertebrates to respond to stressors [Breazile, 1987; Selye, 1956; Stratakis & Chrousos, 1995]. Long-term GC elevations, however, can have deleterious effects on reproduction, growth and immune system activity [Charbonnel et al., 2008; Ellenberg et al., 2007; French et al., 2010; Martin, 2009; Pickering et al., 1991; Setchell et al., 2010].

The current rate of habitat loss and fragmentation worldwide [Ellis et al., 2010; Foley et al., 2005] makes it crucial to study the link between fruit availability and animal GC levels in forest fragments, especially with regard to the potentially deleterious effects of long-term elevations in GC output. Low availability of fruit can potentially increase intragroup feeding competition, and, thus, species with fission–fusion dynamics are an interesting study system as they might be able to reduce or avoid high levels of feeding competition by adjusting their grouping patterns [Asensio et al., 2009; Basabose, 2004; Chapman, 1990b; Itoh & Nishida, 2007; Shimooka, 2003; Symington, 1988]. However, so far we lack information on the functioning and effectiveness of fission–fusion dynamics of populations that live in small fragments.

In this study we investigated the relationship between fruit availability and subgroup size in brown spider monkeys (*Ateles hybridus*) ranging in a small forest fragment in Colombia. In addition, we investigated how fruit availability influenced physiological stress levels as indexed by GC levels, and we examined the relationship between aggression rates and GC levels and between fruit availability and aggression rate. We collected data on habitat-wide fruit availability, feeding behavior, fecal glucocorticoid metabolite (FGCM) levels, subgroup size, and agonistic behavior for two study groups. Due to the physiological function of GCs in the vertebrate stress response (i.e., energy release through gluconeogenesis), we predicted that FGCM levels of brown spider

monkeys would be lower during periods of high fruit availability compared to during periods of low fruit availability. We also predicted that spider monkeys would range in smaller subgroups during periods of low fruit availability to avoid intragroup feeding competition, and range in larger subgroups during periods of high fruit availability [Asensio et al., 2009; Chapman, 1990b; Shimooka, 2003]. Such grouping patterns seem to be effective in managing direct feeding competition as aggression rates of *Ateles geoffroyi* do not differ between periods of high and low food availability [Asensio et al., 2008]. Accordingly, we predicted that aggression rates would not differ between periods of low and high fruit availability. Moreover, high population densities can result in high levels of aggression [Cristóbal-Azkarate et al., 2004, 2006; Macdonald et al., 2004]. The study groups live at high population density [Link et al., 2010], and, thus, we predicted that aggression rates would be elevated compared to studies on *Ateles* ranging in continuous forests. Finally, many studies have found a positive relationship between aggression and GC levels in many vertebrate taxa [Creel, 2005; Creel et al., 1996; Crockford et al., 2008; Emery Thompson et al., 2010; Goymann et al., 2001; Hackländer et al., 2003; Pride, 2005; Wallner et al., 1999]. Thus, we also predicted that FGCM levels would be higher when aggression rates were higher.

METHODS

Study Site and Study Subjects

This study was conducted in a small forest fragment located within the private cattle ranch "Hacienda San Juan del Carare" (06°43′ N, 74°09′ W; 150–200 m a.s.l) in Colombia. At the site, spider monkeys have been habituated, identified and studied since 2007 [Link et al., 2010]. The study fragment comprises 65 ha of seasonally flooded tropical rainforest, located between the central and eastern cordilleras of the Andes in the Magdalena River Valley. The area has bimodal rainy seasons, with peak rains occurring from March to May and from October to November. During intense rainy seasons, the fragment regularly floods entirely for a period lasting from several weeks up to 3 months. The area receives an annual median rainfall of 3,496 mm, has a mean temperature of 27.9°C and a mean humidity of 80% [IDEAM, 2008].

Brown spider monkeys are endemic to Colombia and Venezuela. They are among the 25 most endangered primate species worldwide [Mittermeier et al., 2012] and are listed as critically endangered by the IUCN due to a dramatic population decline over the past 45 years. The most severe threats for the species' survival are habitat loss, fragmentation, and high hunting pressure [Link et al., 2013; Urbani et al., 2008]. For this study we collected data on two brown spider monkey groups (SJ-1 and SJ-2). During the study period SJ-1 consisted of three to four adult males, five adult females, one subadult female, one to three subadult males, zero to two juvenile males, three to four juvenile females, one infant male, and one infant female (total = 14–16). SJ-2 consisted of one adult male, five adult females, one subadult female, two subadult males, two to three juvenile females, two infant males, and zero to one infant female (total = 10–14). The feasibility of following SJ-2 was generally more restricted as some parts of its home range are flooded for 11 months a year. Thus, both fecal sample collection and behavioral data collection were less intensive than for SJ-1.

All research was non-invasive and complied with protocols approved by the German Primate Center and the Animal Welfare and Use and IACUC committees at New York University and the University of Texas at Austin. Further, the research adhered to the legal requirements of Colombia and to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Fecal Sample Collection

Between July 2010 and April 2012 we collected a total of 470 fecal samples from the two study groups (Table I). Due to severe floods associated with the "La

TABLE I. Group Composition and Number of Fecal Samples Collected Per Individual in Both Study Groups

Study group	Adult females	No. of fecal samples	Adult males	No. of fecal samples	Subadult males	No. of fecal samples
SJ-1	Ba	48	Nw	50	Vt	9
	Pe	43	Wa	39	Db	11
	Vi	34	Pk	31		
	Dl	49	Rk	56		
	Ku	39				
SJ-2	Cle	13	Ky	14	Het	1
	Gat	12				
	Man	11				
	Mel	7				
	Iwa	3				

Niña" phenomenon, fecal sample collection, as well as behavioral and phenological data collection, was interrupted from November to December 2010, from March to June 2011, and from November to December 2011. We collected fecal samples from identified adult and subadult individuals. For each sample, we recorded sex and age-class, reproductive state of females (when identifiable), collection time and the date. For the period in which females were nursing dependent offspring we categorized them as "lactating." Pregnancy cannot reliably be detected by observation in this species and therefore, we inferred "pregnancy" for females post hoc. To determine the approximate conception date and to assess which fecal samples had been collected during gestation we combined known parturition dates with average gestation length of spider monkeys (~7.5 months; [Di Fiore & Campbell, 2007]). We categorized all females that did not fall within either of these two classes ("pregnant" or "lactating") as "cycling" (even though their actual cycle status was unknown; [Slater et al., 2008; Rimbach et al., 2013]).

Before collecting a sample, we homogenized the fecal bolus and removed undigested matter such as large seeds. We then placed approximately 0.5 g of feces into a 15 ml polypropylene tube pre-filled with 5 ml of 96% ethanol and subsequently shook the tube until the feces were suspended in the solvent [Rimbach et al., 2013; Shutt et al., 2012]. We kept the samples at ambient temperatures until we extracted them in the evening (see below).

Behavioral Sampling

We conducted all-day focal animal sampling on all adult and subadult individuals of both study groups and collected a total of 1,503 hr of focal data on SJ-1 (2010: 392 hr; 2011: 783 hr; 2012: 328 hr) and a total of 186 hr of focal data on SJ-2 (2010: 36 hr; 2011: 122 hr; 2012: 28 hr) between July 2010 and April 2012. All individuals could reliably be identified, and we attempted to balance the sampling effort between individuals belonging to each study group. We recorded subgroup composition upon encountering a subgroup and thereafter every 15 min. for the entire length of the focal animal sample. Changes in subgroup composition were recorded whenever one or more individuals left ("fissioned") or joined ("fused") the subgroup containing the focal animal. We considered individuals as belonging to the same subgroup when they were at a distance of ≤50 m from at least one other subgroup member following a chain rule [Asensio et al., 2009, 2012; Ramos-Fernández, 2005].

Given the conspicuous nature of aggressive interactions (chasing, grabbing, vocalizing, and biting) in spider monkeys, we recorded all aggressive events during both continuous focal observations and ad libitum sampling and identified the actor and

recipient of each antagonistic encounter whenever possible.

Finally, during focal animal sampling we also collected data on the feeding behavior of the focal animal. We recorded the duration of all feeding bouts and noted the item (e.g., fruit, young leaves, flowers, decaying wood) consumed by the focal animal. We collected a total of 632 hr of feeding data for SJ-1 and 42 hr for SJ-2.

Fruit Availability

Every 2 weeks we monitored eight phenological transects (6.45 km) following the methods described in detail by Stevenson [2002]. Briefly, we registered all trees that bore fruit and/or flowers and, recorded the plant species or morphospecies. In order to estimate the sampling area we measured the perpendicular distance of each tree to the center of the transect. To calculate the sampling area we determined the average perpendicular distance to the transect (multiplied by two) and multiplied it by the total length of transects monitored. Finally, we measured each tree's diameter at breast height (DBH) at approximately 1.3 m high in order to derive estimates of fruit availability based on "basal area" estimation (see below).

Data Analysis

Steroid extraction and analysis

Prior to extraction we determined fecal wet weight by calculating the difference between the weight of the tube before and after addition of the sample. For steroid extraction, we manually shook the tubes rigorously for 5 min and, then centrifuged the fecal suspension using a manually operated centrifuge for 1 min [Rimbach et al., 2013; Shutt et al., 2012]. We decanted ~2 ml of each resultant fecal extract into 2 ml polypropylene tubes, covered them with parafilm and stored them at ambient temperatures (~25°C) in a dark place. In a previous study we showed that storing fecal extracts this way does not affect FGCM levels [Rimbach et al., 2013]. We transported the extracts to the Universidad de Los Andes, Bogotá every 8–10 weeks where we stored them at −20°C until shipment to the endocrinology laboratory at the German Primate Center for analysis.

We analyzed all fecal samples using a previously validated [Rimbach et al., 2013] group-specific 11β-hydroxyetiocholanolone enzyme-immunoassay (EIA), designed to measure 5β-reduced metabolites of glucocorticoids [Ganswindt et al., 2003] with a 3α,11β-dihydroxy structure. We performed the EIA as described in detail by Heistermann et al. [2004]. Depending on the original concentration of the sample, we diluted extracts 1:250–1:2,000 in assay buffer prior to steroid measurement and took

duplicate aliquots to assay. Intra- and inter-assay coefficients of variation were 7.4% and 13.0% for low-value and 6.1% and 7.8% for high-value quality controls. All hormone concentrations are expressed as ng/g fecal wet weight.

Behavioral data

We only included adult and subadult individuals in calculating subgroup size because infants and juveniles always ranged in the same subgroup as their mothers. To avoid pseudoreplication of subgroup sizes, we calculated the size of the first subgroup encountered each day [Asensio et al., 2009; Schaffner et al., 2012] and the daily modal subgroup size. Both measurements were highly correlated ($R = 0.78$, $P < 0.001$), therefore we constructed two LMMs in order to decide which measurement of subgroup size to include in the final model. Each model also included the random factors group ID and individual ID. We compared the Akaike information criterion (AIC) of both models and found that the scores were very similar (first subgroup: 949.1; modal subgroup size: 950.2). The lower AIC score indicates a better fit of the data to the model and thus we used first subgroup size in all further analyses.

To calculate aggression rates we used only agonistic interactions for which all participants, actor(s), and recipient(s), were identified ($N = 294$ aggressive interactions). We calculated aggression rates per dyad and counted coalitionary aggressions (e.g., when two individuals jointly aggressed one individual) as two aggressive interactions. For example when A + B aggressed C, we counted this as one aggression from A towards C and one from B towards C. To account for the fact that aggressive interactions can only occur between individuals that are present in the same subgroup, we corrected for the time actor and recipient were observed together in a subgroup by dividing the number of aggressive interactions between a dyad by the time both individuals were observed together in the same subgroup.

To investigate whether the study groups' diet differed between periods of high and low fruit availability we calculated the percentage of time (of the total time a focal animal was feeding) a focal animal spent feeding on different food items (e.g., fruit, young leaves, flowers, and decaying wood). To avoid a sampling bias due to short focal animal samplings we only included focal animal samplings with a duration of ≥ 5 hr.

Fruit availability index (FAI)

We calculated two different fruit availability indices (FAI): (1) number of fruiting trees/area (density) and (2) basal fruiting area of trees (m²/ha). To avoid overestimation of fruit production by trees that have long fruiting periods we assumed a triangular distribution of fruit production for the calculation of the basal fruiting area. Thus, we assumed that the fruit production for each individual tree increased up to the median fruit period and subsequently decreased [Stevenson et al., 1994]. Accordingly, for trees that bore fruit for more than one consecutive phenological sampling period (i.e., for longer than 2 weeks) we distributed their basal area over the sampling periods in a way that the proportion of the basal area in each period followed the coefficients of the Pascal's triangle [Stevenson, 2004; Stevenson et al., 1994]. Both indices of fruit availability were correlated (Spearman: $R = 0.61$, $T = 3.68$, $P = 0.001$, $N = 25$), and because several studies have found a positive relation between basal fruiting area of a tree and fruit crop size [Leighton & Leighton, 1982; Peters et al., 1988], we used only basal fruiting area of trees in further analysis.

Statistical Analyses

To assess whether fruit availability influenced FGCM levels (Model 1), we matched each fecal sample with the corresponding FAI on the date the fecal sample had been collected (FAI was kept constant in a way that the subsequent 2 weeks were presumed to be the same as the FAI at the start of the period). We used overall aggression rate in the groups (total of all aggressive events seen per day) to investigate whether aggression rate influenced FGCM levels (Model 2). For Model 2 we matched each fecal sample with the aggression rate observed on the day before sample collection. We thereby accounted for a ~24 hr time-lag of glucocorticoid metabolite excretion in feces of *A. hybridus* [Rimbach et al., 2013]. We used linear mixed models (LMM, [Baayen, 2010]) with a Gaussian error distribution for both models. As control variables we used sex, age, female reproductive state, fecal sample collection time (Model 1 + 2), and subgroup size (Model 1) as some of these variables have been shown to affect FGCM levels in *A. hybridus* [Rimbach et al., 2013]. We used group and individual ID (individual nested in group) as random factors in both models. In exploratory runs of Model 1, we tested for an interaction between fruit availability and subgroup size. The interaction was not significant ($P \geq 0.05$) and thus, not included into the final model. Because intergroup encounters, although rare, might potentially influence FGCM levels of the study groups we constructed an additional LMM including intergroup encounters as a variable. Adding this variable to the LMM did not change the results of the model and the variable intergroup encounters did not significantly influence FGCM levels. We also compared the AIC of both models and found that the score of the model without intergroup encounters was lower (775.0) than the score of the model including this factor (814.9). The lower AIC score indicates a better fit of the data to the model and thus we chose to report the results of the model excluding intergroup encounters.

Before running the models, we checked the distributions of the response and all predictor variables. To achieve a more symmetrical distribution, we log transformed the response variable (FGCM levels) and to obtain comparable estimates we z-transformed all predictor variables. By visually inspecting Q–Q plots and scatterplots of the residuals plotted against fitted values, we checked for the assumptions of homogeneous and normally distributed residuals. The plots did not reveal any obvious violations of these assumptions. To assess model stability, we ran diagnostics (dfbetas) that did not suggest the existence of influential cases, and variance inflation factors indicated that there was no collinearity between variables [Field, 2005; Zuur et al., 2009, 2010]. To derive variance inflation factors we used the function vif of the R package car [Fox & Weisberg, 2011]. We fit the models with the lmer function from the lme4 package [Bates & Maechler, 2010] in R 2.15.1 (R Development Core Team 2012). To determine the significance of the full models (all fixed and random effects) compared to the corresponding null models (only random effects) we used likelihood ratio tests (R function 'anova'). Finally, we used the function pvals.fnc of the package 'language R' [Baayen, 2010] to determine P values based on Markov Chain Monte Carlo (MCMC) sampling [Baayen, 2011].

We performed a Spearman rank correlation to test whether the two fruit availability indices (density and basal fruiting area of trees) were correlated (using Statistica 10). We used Mann–Whitney U tests to assess whether subgroup size changed between years and to test whether subgroup size differed between periods of high and low fruit availability (using Statistica 10). To evaluate whether aggression rates of different dyads (same-sex and opposite-sex dyads) differed between periods of high and low fruit availability we also used Mann–Whitney U tests. To avoid type I errors we adjusted the level of significance through a Bonferroni correction to a critical value of $P < 0.01$. We defined an index of fruit availability as "high" when it was higher than the median and as "low" when it was lower than that. To assess whether the percentage of time spent feeding on different food items differed between periods of high and low fruit availability we used Mann–Whitney U tests. We used a Bonferroni-adjusted significance level ($P < 0.008$) to account for the increased possibility of Type-I errors. Results from nonparametric tests are presented as the median and quartiles (and range when appropriate). All statistical tests were two-tailed, and the significance threshold was set at $P \leq 0.05$.

RESULTS

During the study period subgroup size of SJ-1 ranged from one to ten adult and subadult individuals (mean = 5; median = 6) and from one to seven adult and subadult individuals in SJ-2 (mean = 3.4; median = 3). Subgroup size of SJ-1 significantly increased from 2010 to 2011 (Mann–Whitney U-test: $Z = -3.31$, $P < 0.0001$) and from 2011 to 2012 (Mann–Whitney U-test: $Z = -3.88$, $P = 0.0001$; Fig. 1). Subgroup size of SJ-2 significantly decreased between 2010 and 2011 (Mann–Whitney U-test: $Z = 8.05$, $P < 0.0001$) and increased significantly from 2011 to 2012 (Mann–Whitney U-test: $Z = -15.92$, $P < 0.001$; Fig. 1).

Aggression rates ranged between 0.01 and 0.5/h (median = 0.027/h) and differed between different types of dyads (Table II). The aggression rate of female–female and male–female dyads was significantly higher when fruit availability was high compared to when it was low (Table II). Aggression rates of male–male and female–male dyads (the latter only includes subadult males) did not differ between periods of high and low fruit availability (Table II).

Both study groups spent half of their feeding time ingesting ripe fruit (SJ-1 = 58%, SJ-2 = 50%) and young leaves represent the other main food item of both groups (SJ-1 = 32%, SJ-2 = 39%). Both groups also included flowers (SJ-1 = 4%, SJ-2 = 8%) and decaying wood (SJ-1 = 5%, SJ-2 = 2%) in their diet. The percentage of time both study groups spent feeding on different food items did not differ between periods of high and low fruit availability (SJ-1: Mann–Whitney U-test: fruit: $Z = 1.35$, $P = 0.17$, leaves: $Z = -1.45$, $P = 0.14$, flowers: $Z = 1.04$, $P = 0.29$, decaying wood: $Z = -0.76$, $P = 0.44$; SJ-2: Mann–Whitney U-test: fruit: $Z = -1.17$, $P = 0.23$, leaves: $Z = -0.63$, $P = 0.52$, flowers: $Z = -2.26$, $P = 0.02$, decaying wood: $Z = -0.45$, $P = 0.65$, $P = 0.98$; Table III).
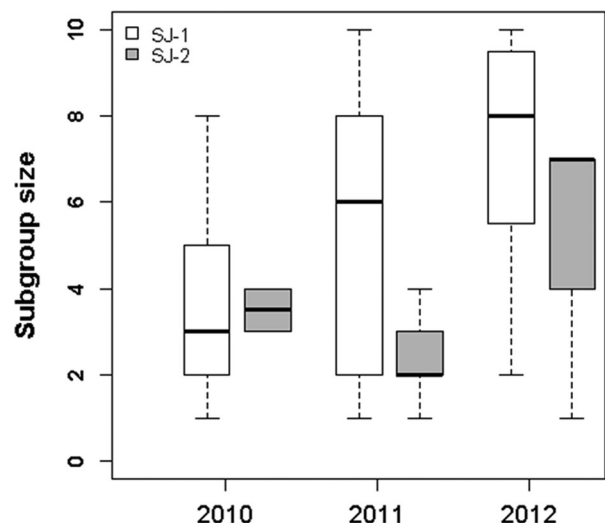

Fig. 1. Annual variation in median subgroup size of both study groups. The boxplots show the lower and upper quartile; and the minimum and maximum data values. The black lines indicate the median values.

TABLE II. Median Hourly Aggression Rates of Different Dyad Types (Only Including Adults and Subadults) in Periods of High and Low Fruit Availability (FAI) (Mann–Whitney U-Tests Adjusted With Bonferroni Correction, $P < 0.01$)

| Dyad (actor-recipient) | Median (range) aggression/h | | Mann–Whitney U | No. of aggressions (% of all observed) |
	Low FAI	High FAI		
Female–female	0.018 (0.012–0.3)	0.028 (0.012–0.5)	$Z = 4.09, P < 0.0001$	70 (23.8)
Female–male[a]	0.019 (0.012–0.16)	0.020 (0.012–0.028)	$Z = -0.50, P = 0.61$	15 (5.1)
Male–female	0.020 (0.015–0.11)	0.033 (0.013–0.25)	$Z = 4.04, P < 0.0001$	88 (29.3)
Male–male[b]	0.023 (0.015–0.13)	0.038 (0.02–0.11)	$Z = 1.53, P = 0.12$	54 (18.3)

[a]Only includes subadult males.
[b]In 62.9% of these aggressive events a subadult male was the recipient.

Estimated fruit availability in the forest fragment ranged from 1.7 to 60.5 m^2/ha (9.2–80.9 tress/ha) during the study period (median = 15.7 m^2/ha; median = 36.2 trees/ha). Subgroup size of SJ-1 was significantly larger in periods of low fruit availability than when fruit availability was high (Mann–Whitney U-test: $Z = 3.23, P = 0.001$; Fig. 2), whereas there was no significant difference in subgroup size of SJ-2 (Mann–Whitney U-test: $Z = 1.46, P = 0.14$; Fig. 2).

Overall, the full model (Model 1) estimating the influence of fruit availability on FGCM levels differed significantly from the null model ($X^2 = 141.07$, df = 7, $P < 0.0001$, $N = 366$ fecal samples). More specifically, fruit availability had a positive effect on FGCM levels (LMM: Estimate $\pm$ SE: 0.22 ± 0.03, $T = 5.82$, $P_{MCMC} = 0.0001$; Table IV, Fig. 3). The full model (Model 2) investigating the influence of aggression rate on FGCM levels did not differ from the null model ($X^2 = 3.34$, df = 3, $P = 0.34$, $N = 97$ fecal samples).

DISCUSSION

Overall, our analyses of the relationship between fruit availability and FGCM levels, subgroup size, and agonistic interactions of brown spider monkeys produced unexpected results. Against our prediction that FGCM levels would be higher when fruit availability was low, our results show the opposite pattern: spider monkeys showed elevated FGCM
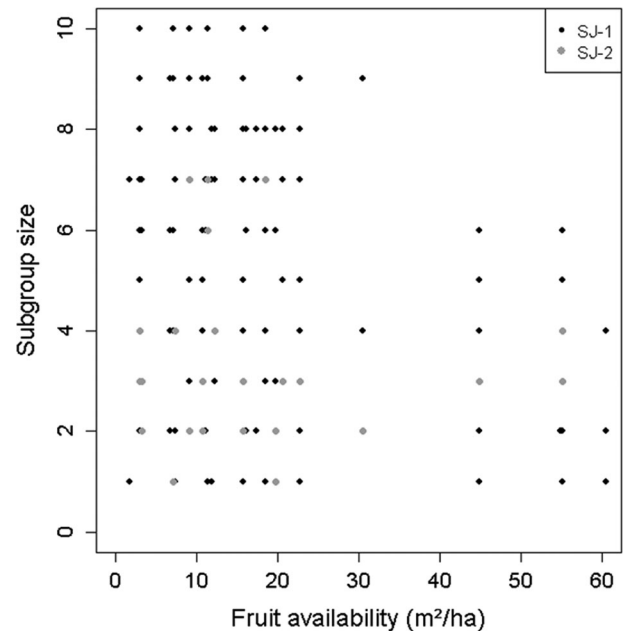

Fig. 2. Subgroup sizes of the study groups SJ-1 and SJ-2 during periods of varying fruit availability.

levels in periods of higher fruit availability. Also contrary to our predictions, the percentage of time the groups spent feeding on different food items did not differ between periods of high or low food availability, the animals ranged in smaller subgroups when fruit

TABLE III. Mean Percentage of Time Spent Feeding on Different Food Items in Periods of Low and High Fruit Availability (FAI)

| Item | SJ-1 | | SJ-2 | |
	Low FAI (%)	High FAI (%)	Low FAI (%)	High FAI (%)
Fruit	60	57	41	54
Leaves	32	33	43	41
Flowers	4	3	13	2
Decaying wood	4	6	3	3
Other	1	1	0	1
Unidentified	0	0	0	0

TABLE IV. Results of Model 1 Examining the Influence of Fruit Availability on Log Transformed FGCM Levels

Variable	Estimate $\pm$ SE	T	P_{MCMC}
Intercept	5.56 ± 0.12	43.89	**0.0190**
Fruit availability	0.22 ± 0.03	5.82	**0.0001**
Subgroup size	0.05 ± 0.03	1.45	0.1458
Time	-0.00 ± 0.00	-9.16	**0.0001**
Sex	0.37 ± 0.14	2.65	**0.0176**
Age	-0.43 ± 0.16	-2.67	**0.0118**
Lactating-cycling	0.06 ± 0.14	0.48	0.6180
Pregnant-cycling	0.70 ± 0.12	5.80	**0.0001**
Pregnant-lactating	-0.63 ± 0.14	-4.39	**0.0002**

Variables that significantly influenced FGCM levels appear in bold.
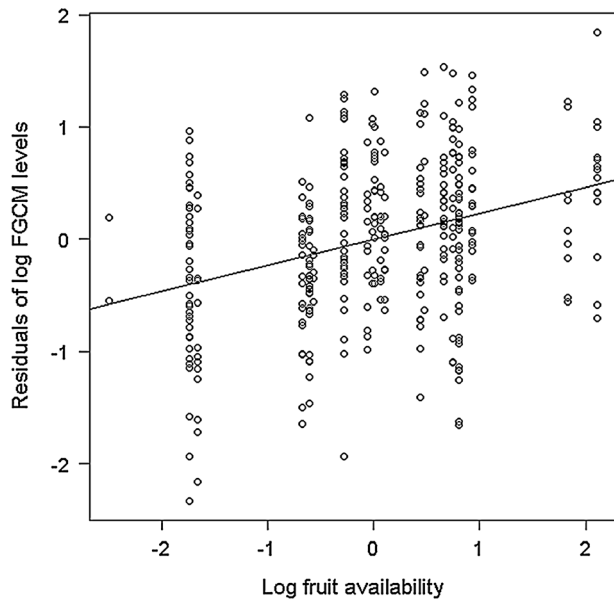
Fig. 3. Relationship between log transformed FGCM levels and fruit availability. The y-axis represents the residuals of FGCM levels obtained from a LMM including sex, age, female reproductive state, fecal sample collection time, and subgroup size as fixed factors, and individual ID and group as random factors.

availability was high compared to when it was low, and aggression rate did not influence FGCM levels. Aggression rates at San Juan were generally comparable to other studies conducted on *Ateles* (this study: 0.01–0.5/h; 0.03–0.49/h [Abondano & Link, 2012]; 0.05/h [Asensio et al., 2008]; males: 0.31/h and females: 0.07/h [Fedigan & Baxter, 1984]; 0.01–0.8/h [Slater et al., 2009]; 0.034/h [Symington, 1987]) and thus, it seems that aggression rates are not elevated in this small fragment compared to groups that range in more continuous forests.

Generally, primates that exhibit high fission–fusion dynamics increase subgroup size when fruit availability is high and feeding competition presumably is low and decrease subgroup size when fruit availability is low [e.g., Chapman et al., 1995; Itoh & Nishida, 2007; Symington, 1988]. However, the relationship between these two variables is not in all cases predictable, and several studies on the genus *Pan* report results deviating from this general pattern [Hashimoto et al., 2003; Hohmann & Fruth, 2002; Moscovice et al., 2007; Newton-Fisher et al., 2000; Wakefield, 2008]. In accordance with these latter studies, our results show a negative relationship between fruit availability and brown spider monkey subgroup size. Spider monkeys ranged in smaller subgroups in periods of high fruit availability, during which direct contest competition over fruit seems to occur as indicated by higher aggression rates compared to periods of low fruit availability. This atypical grouping pattern seems to be less effective at mitigating contest competition over food resources

than typical fission–fusion patterns. Spider monkeys that live in a more continuous forest and whose grouping patterns are more typical did not show seasonal differences in aggression rates [Asensio et al., 2008]. However, another study reports that after a hurricane occurred spider monkeys adopted a more folivorous diet and aggression rates were lower than before the storm, when patches of ripe fruit, which may be a defendable resource, were likely more common than after the hurricane [Champion, 2013]. Fruit availability in forest fragments is often reduced compared to continuous forests [e.g., Arroyo-Rodríguez & Mandujano, 2006; Putz et al., 1990]. Accordingly, fruit availability at San Juan was lower than fruit availability reported at less disturbed sites and was similar to the fruit availability reported at other fragments or logged forests (Table V). Thus, the presence of valuable fruit patches in fragments can create conflict over access to these. This might explain why aggression rates were higher in periods of high fruit availability than in periods of low availability. In contrast, in periods of low fruit availability, when the study groups ranged in larger subgroups, fissioning might not be as advantageous in this small fragment as it is in a continuous forest because there are no other areas (with additional fruit patches) that could be accessed to avoid contest competition. The few fruit patches available in these periods will be depleted quickly by the first individual(s) that arrive at the patch without the possibility of monopolization (scramble competition), which can explain why aggression rates were lower in periods of low fruit availability.

A high level of contest competition during periods of high fruit availability might also explain elevated FGCM levels during these periods, which might be the proximate factor that triggers a decrease in subgroup size. Still, FGCM levels could also have been influenced by other social factors (e.g., grooming) that we did not include in our analyses. Further, we did not find that aggression rate influenced FGCM levels. This was unexpected because many other studies on social mammals have reported a link between aggression, often aggression received, and GC levels [Creel, 2005; Creel et al., 1996; Crockford et al., 2008; Emery Thompson et al., 2010; Goymann et al., 2001; Hackländer et al., 2003; Pride, 2005; Wallner et al., 1999]. However, our result might be due to a small sample size and reflect the fact that we were not able to collect fecal samples of all individuals involved in aggressive interactions on the day after those incidents.

Primates, including spider monkeys, often shift their diet towards leaves when living in small fragments [Chaves et al., 2012; González-Zamora et al., 2009]. Consistent with this idea, both study groups had a much more leafy diet (40–50% of feeding time [this study; Abondano & Link, 2012; Montes-Rojas, 2012]) than is generally reported for spider monkeys (7–17% leaves and 54–91% fruit [reviewed

TABLE V. Fruit Availability Measured in Continuous and Disturbed Forests Inhabited by Spider Monkeys

Study site	Forest type	Forest size	Fruit availability	Refs.
San Juan, Colombia	Forest fragment	65 ha	1. Basal area: median: 15.7 m²/ha; range: 1.7–60.5 m²/ha 2. Density: median = 36.2 trees/ha; range: 9.2–80.9 tress/ha	This study
El Paujil Reserve, Colombia	Different forest types	—	1.1 m² (secondary forest); 21 and 19.7 m² (logged forest); 30.7 and 36.3 m² (undisturbed forest)	Aldana et al. [2008]
La Chonta, Bolivia	Continuous forest	100,000 ha	29.8 m²/ha (tall forest); 20.3 m²/ha (low forest); 20 m²/ha (Chaparral)	Felton et al. [2008]
Lacandona, Mexico	Different forest types	Continuous forest: 300,000 ha; fragments: 14, 31, 1,125 ha	Range: 0.4–28.9 m², (continuous forest); range: 0.6–16.5 m² (fragment)	Chaves et al. [2012][a]
Santa Rosa National Park, Costa Rica	Continuous forest	—	80.4 tress/ha (young successional forest); 154.8 trees/ha (older successional forest); 140.3 tress/ha (pristine semi-evergreen forest)	Chapman et al. [1995][b]

[a]Basal area was determined for the 10 most important plant species.
[b]All spider monkey food trees, any species that was fed upon, regardless of the importance of that food item in the diet, were included.

in: Di Fiore et al., 2010]), and both groups particularly included a high percentage of young leaves in their diet. Young leaves are often highly abundant in fragments, especially at edges with elevated light exposure [Ganzhorn, 1995, 1997; Irwin, 2008; Johns, 1988, 1991; Lynch & González, 1993]. Further, it is possible that spider monkeys are able to rely on leaves in this fragment because there are many fig trees (*Ficus* spp.) that permanently provide new leaves [Montes-Rojas, 2012]. In addition, leaves growing in this particular fragment might be highly nutritional because the soil is likely to be very rich in nutrients, given that during floods the entire forest fragment receives nutrients carried by the Magdalena River [Restrepo et al., 2006]. Young leaves are typically more digestible than mature leaves, have fewer chemical defenses (e.g., phenols and alkaloids) and a higher nutritional value compared to mature leaves [Bilgener, 1995; Coley & Barone, 1996; Waterman & Kool, 1994], and therefore can constitute an important food resource.

Intergroup competition might be an additional factor influencing the grouping patterns of the study groups. The fragment is very small (65 ha), and the home ranges of both groups only comprise roughly 30 ha each. Thus, the area shared by two groups is much smaller than the typical home-range size for a single group (average 278 ha, range: 80–963 ha) ranging in continuous forest [reviewed in: Di Fiore et al., 2010]. Moreover, spider monkey population density is very high in this fragment (42.8 ind./km²; [Link et al., 2010]). Together with small home-range sizes, this fact could intensify intergroup competition for space and potentially also resources. Over time both study groups increased their subgroup size, and ranging in larger subgroups can be advantageous during intergroup encounters and can increase the probability of success in competition for space and resources [McComb et al., 1994; Packer et al., 1990; Scarry, 2013]. Consistent with that idea, we have observed an increase over time in home-range overlap between the groups, and, although intergroup encounters were very rare, we observed an increase in both frequency and intensity of intergroup encounters (number of intergroup encounters: 2010 = 0; 2011 = 3: 2012 = 5; [Link & Di Fiore, unpublished data]). These observations support the idea that intergroup competition might be one factor shaping the subgrouping patterns of these particular groups.

Although we derived our predictions from current socio-ecological and behavioral theory, not all results of this study meet our predictions. Our study suggests that forest fragmentation can influence spider monkey diets and the effectiveness of fission–fusion dynamics to reduce contest competition. These results show that the relationship between resource availability, aggression rates, and stress levels is more complex than assumed thus far. To better understand how food availability in small fragments influences the grouping patterns of species that show a high degree of fission–fusion dynamics, it will be crucial to also investigate the nutritional values of resources and changes in the availability of food items other than fruit (e.g., young leaves and flowers). Additional studies are needed to clarify the relationship between "total" resource availability, subgroup size, and GC levels in spider monkeys, as well as the potential effects on individual health and population viability in fragments. Our results

suggest that the adoption of a more folivorous diet may permit spider monkeys to persist in small fragments. However, their long-term survival in such small fragments is less than certain, and fragments need to be included into management decisions to increase the probability of survival for these populations.

ACKNOWLEDGMENTS

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