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Fruit availability has a complex relationship with fission–fusion dynamics in spider monkeys

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Abstract
Understanding the ecological and social factors that influence group size is a major focus of primate behavioural ecology. Studies of species with fission–fusion social organizations have offered an insightful tool for understanding ecological drivers of group size as associations change over short temporal and spatial scales. Here we investigated how the fission–fusion dynamics of spider monkeys (*Ateles geoffroyi*) at Runaway Creek, Belize were affected by fruit availability. When males and females were analyzed together, we found no association between fruit availability and subgroup size. However, when females were analyzed separately, we found that when fruit availability increased, so did subgroup size. In all analyses, higher fruit availability did not influence subgroup spatial cohesion. Our results point to the complexity of understanding grouping patterns, in that while ecological factors make groups of specific sizes advantageous, social factors also play an important determining role.

Keywords Subgroup · Group size · Food resources · *Ateles geoffroyi*

Introduction

Animal social groups vary along a continuum from highly cohesive (low fission–fusion dynamics) to highly fluid (high fission–fusion dynamics; Aureli et al. 2008; Strier 1989). Group-living animals tend toward cohesiveness, forming social groups in which members synchronize their movements and activity, but species with a high degree of fission–fusion dynamics do not. Species in this latter type of grouping pattern include *Tursiops* spp. (Dolphins, Connor and Wells 2000), several species of bats (Altringham and Senior 2006; Bradbury and Vehrencamp 1976), chimpanzees (*Pan troglodytes*), and *Ateles* (spider monkeys, Chapman et al. 1995; Symington 1990). Group members often leave (fission) and join (fusion) others, and thus subgroups are frequently changing their size, composition, and spatial cohesion.

Theory predicts that high fission–fusion dynamics mitigates the costs of group living by adjusting subgroup size to changes in the spatial and temporal availability of food resources (Chapman 1990a; Chapman and Chapman 2000; Klein and Klein 1977; Wrangham and Smuts 1980). Researchers argue that by foraging in smaller subgroups, individuals can reduce feeding competition and time spent travelling between food resources (Chapman and Chapman 2000; Korstjens et al. 2006; Lehmann et al. 2007). Consequently, larger food patches or high food density should be able to support larger subgroups, and vice versa. While current theory focuses on the spatial and temporal variation in food supply as the primary factor influencing variation in grouping patterns, other parameters, such as group demographic structure (Altmann and Altmann

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1979), neighboring group number and composition (Aureli et al. 2006; Chapman et al. 1989), and climatic conditions (Schaffner et al. 2012), likely play a role, but here we focus on food availability.

The actual relationship between food availability and subgroup size, however, is not clear, and research in this area has yielded conflicting results (Aguilar-Melo et al. 2018; Asensio et al. 2009; Pinacho-Guendulain and Ramos-Fernández 2017). In chimpanzees and spider monkeys, for example, some studies have found a positive correlation between temporal variation in habitat-wide fruit availability and the size of subgroups (Chapman et al. 1995; Mitani et al. 2002; Shimooka 2003; Symington 1990), while others have found little or no correlation (Hashimoto et al. 2003; Hohmann and Fruth 2002; Newton-Fisher et al. 2000; Wakefield 2008). A study on spider monkeys (*A. hybridus*) living in a small fragment in Colombia revealed that subgroups were smaller when fruit availability was high compared to when it was low; the opposite to what would be expected (Rimbach et al. 2014). While the authors of this study concede that the fragmented habitat may have affected subgrouping patterns in this population, the conflicting results between this research and other studies indicate that factors other than fruit availability affect subgroup size, or that there are other aspects to fruit availability affecting subgroup size to be understood. The conflicting results of studies on both primate genera may also be due to different methodology and/or the difficulty of quantifying fruit availability.

Spider monkeys are ripe fruit specialists, and ripe fruit typically constitutes > 75% of their diet, supplemented with young leaves, flowers, seeds, and sometimes decayed wood, insects, and other small prey items during periods of fruit scarcity (reviewed in Di Fiore et al. 2008; González-Zamora et al. 2009). Those populations living in highly seasonal forests (Stevenson et al. 2000; Wallace 2005), small forest fragments (Chaves et al. 2012; Rimbach et al. 2014), or areas damaged from hurricanes or fires (Champion 2013; Schaffner et al. 2012) cope with periods of fruit scarcity by increasing their consumption of leaves and including a greater variety of food items in their diet (Chapman 1987; González-Zamora et al. 2009).

Here we quantify the feeding ecology of spider monkeys (*Ateles geoffroyi yucatanensis*) at Runaway Creek, Belize to examine the relationship between fruit availability and subgrouping dynamics using behavioural and ecological data collected over five and a half consecutive years. Our objectives are, first, to quantify the diet of this spider monkey population; second, to evaluate the effect of fruit availability on diet; and third, to build on these data to examine the theory that proposes a relationship between fruit availability and two important aspects of fission–fusion dynamics: subgroup size and subgroup spatial cohesion. In the middle of our study, a Category 2 hurricane passed over the area, causing substantial habitat damage, providing a unique opportunity to examine grouping dynamics under extreme conditions.

Socio-ecological theory predicts that greater fruit availability will lead to larger group size; thus we expect that spider monkeys will follow this general theoretical pattern (Asensio et al. 2009; Chapman 1990a, b; Shimooka 2003; Wrangham et al. 1993). In addition, we anticipate that periods of high fruit availability will lead to more cohesive subgroups, as individual monkeys tolerate closer inter-individual proximity as contest competition is reduced (Asensio et al. 2009; Chapman 1988; Symington 1988a, 1988b). Since the reproductive strategies of males and females differ, with females trying to maximize access to food while males first try to increase mating opportunities (Wrangham 1980), we considered how subgroup size and subgroup spatial cohesion varied as a function of fruit availability for females separately.

Methods

Study site and study group

Runaway Creek Nature Reserve is a 2469-ha private reserve in central Belize, located 11 km inland from the Caribbean coast. The reserve has two main vegetation zones: pine savannah and low broadleaf, semi-deciduous tropical forest. The forest comprises steep karst hills with caves, low valleys, and seasonal swamps and is connected to approximately 58 km^2 of similar habitat to the west but is otherwise surrounded by pine savannah and citrus plantations. This area has a dry season from December to May and a wet season from June to November and receives 2000–2200 mm of rain annually (Meerman 1999).

Between 2008 and 2014, we studied the behaviour and ecology of spider monkeys at Runaway Creek. All individuals in the community were habituated to researchers' presence and individually recognizable. Over this time, the community ranged in size from 31 to 37 individuals (5–7 adult males, 12–14 adult females, and 12–18 immatures) due to births, immigrations, disappearances, and immatures maturing to adulthood.

Behavioural data collection

Behavioural data were collected in full- or part-day follows by KH with the help of trained graduate students and field assistants. Individual identification of spider monkeys is a difficult task and typically must be made by subtle differences in coat colour, freckling patterning around the eyes, and characteristic of the genitalia unless there are obvious scars or injuries; thus KH was responsible for individual identification, which removed inter-observer error. We

defined a subgroup using a "chain-rule" (Ramos-Fernández 2005; we followed the same procedure, but obtained a slightly larger cut-off point) and considered any individual seen within 50 m of another individual as part of the same subgroup. "Fissions" occurred when an individual or group of individuals moved more than 50 m from any other subgroup member, and "fusions" occurred when an individual moved within 50 m of another subgroup member. When subgroups are more than 50 m apart, it is unlikely that they can efficiently visually track each other, and it is not possible for an observer following one subgroup to also monitor the second subgroup.

During a subgroup follow, we conducted an instantaneous scan sample every 30 min to record the subgroup size and composition, the subgroup spread (defined below), and the identity and behaviour of each monkey. The 30-min interval was used to ensure that the observer could be with the subgroup in the difficult terrain and adequately evaluate composition, and to partially ensure the independence of the observations. When a monkey was feeding, we recorded the plant part [ripe and unripe fruit, young and mature leaves, flowers, other (insect, limestone, and soil)]. Our identification was aided by considerable efforts made by previous researchers who have worked in the area and who had sought the help of botanists and local plant experts (Behie and Pavelka 2005; Behie and Pavelka 2013; Griffin 2013; Hartwell 2016; Hartwell et al. 2014), but if the taxonomic identity of a tree was unknown, it was flagged for later identification with the assistance of a botanist, including Drs. Steven Brewer and Colin Young. This was an ongoing process throughout the five and a half years of study and was aided by a local vegetation expert and the assigning of common names to start the identification process. Vines are particularly difficult to identify because voucher specimens are hard to obtain, but we were able to identify all the major vines used by the spider monkeys to species ($n=7$) or genus level ($n=3$). We monitored a phenology trail twice a month, but for the analysis of fruit availability, we included one phenology sample per month to calculate a monthly fruit availability score ($n=52$), as this is how data of this nature are typically reported. This score was analysed in relation to size and spread of subgroups drawn from 1 week before and 1 week after the date of the phenology sample used to determine the fruit availability score.

Our data comprise 4770 subgroup scans collected over 67 months on 1033 days from January 2008 to September 2013. A total of 6428 h were spent in the forest searching, while 2686 h were spent in visual contact with monkeys; this difference is due to the difficulty in following fast-travelling spider monkeys over the steep karst hills and cliffs that characterize the terrain, and the density of the animals. On 25th October 2010, in the middle of the study, a Category 2 hurricane (Hurricane Richard) passed over the area, causing extensive habitat damage, which was exacerbated 6 months later by forest fires (Champion 2013). The tree falls after the hurricane made it even more difficult to follow these fast-moving animals.

Measures of fission–fusion dynamics

For the following measures of fission–fusion dynamics (described below), we used data on independently travelling individuals; thus, we treated adults and subadults (approximately ≥ 5 years of age—the age was estimated based on observing animals in this population grow, maturity was based on when individuals started to reproduce and on body size) as independent individuals and excluded immatures (< 5 years of age). Subgroup spatial cohesion is sometimes measured directly using subgroup spread; however, spread is likely not independent of subgroup size, as larger subgroups are likely to occupy more area. To account for different subgroup sizes, we therefore built models with the spread of the subgroup, measured in meters between the two individuals furthest apart, as the outcome variable, and included the number of individuals in addition to fruit availability as predictor variable (see below). Thus, this model tests whether fruit availability affects the spread of a subgroup after accounting for the effect of subgroup size. This approach estimates how fruit availability is associated with the space available to each individual (i.e., subgroup spatial cohesion), assuming they are spaced evenly within a subgroup. In contrast to the investigation of subgroup sizes, we here included only subgroups containing at least two individuals.

Vegetation data

We sampled twenty-one 40×40 m (total 3.36 ha) vegetation plots in the group's range and in all habitats used, which include swamp, low valley, karst hilltop, ridge side, and the vegetation that is transitional between forest and savanna. We identified and measured the diameter at breast height (DBH) of all trees over 10 cm DBH. If a tree species was unknown, we flagged the tree for later identification with the assistance of a botanist (see above). A tree's DBH is an indicator of the size of the tree and has been shown to reflect the tree's fruit production (Chapman et al. 1992). We then calculated species basal area (sum of the area for each tree of species A) and species dominance (total basal area of species A/total area sampled).

To track temporal variation in ripe fruit availability, we monitored a phenology trail monthly from January 2009 to July 2013. The trail included 225 trees from 15 food tree species, each represented by 15 individual trees. We chose species for the phenology trail based on the tree species that constituted greater than 2% of the population's diet

(Table 1). Each phenology tree was scored with an estimate of ripe fruit as 0, 25, 50, 75, or 100%. We then took the mean proportion ripe fruit coverage score for each tree species and multiplied it by the dominance value for that species. To provide a monthly ripe fruit availability score, we summed all scores across the 15 species for each month. Hereafter, fruit availability refers to ripe fruit availability score.

Data analysis

We quantified the diet composition as the proportion of feeding records devoted to the different plant parts (ripe fruit, unripe fruit, immature leaves, mature leaves, flowers, and "other"). We then describe the general changes in the diet of spider monkeys across years. To investigate how diet is affected by environmental factors, we first explore the relationship between fruit availability, season, and the occurrence of the hurricane. To do so, we calculated a Bayesian model with fruit availability as the outcome variable and either season or hurricane as the categorical predictor variable. For the effect of the hurricane, we calculated two separate models: First, we compared the availability of fruit between the entire period before versus the entire period after the hurricane (pre- vs. post-hurricane). Then, we compared the 12 months directly following the hurricane with all other months (post 12 months vs. other periods). Because each month should be similar to the same month in other years, we included month as a grouping variable (similar to a random effect in a model using a frequentist approach). However, because of the high variability in fruit availability within and across years (see "Results"), and because we assume that the availability of ripe fruit is more important

for the composition of the diet and behaviour of spider monkeys than season or the occurrence of the hurricane per se, we use fruit availability as predictor variable in all of the following models.

To investigate how fruit availability is linked to diet, we calculated a Bayesian multinomial (or categorical) model, with records of eaten plant parts (see above) as the outcome variable and the availability of ripe fruit as predictor variable. We used such a multinomial model to account for the dependence of the different proportions of eaten food parts (i.e., a larger proportion of one food part makes lower proportions of the other food parts more likely). To account for the dependence of records collected during the same month and linked to the same monthly fruit availability score, we also included the month in combination with the specific year (e.g., January 2010; hereafter year-month) as a grouping variable.

To investigate the fission–fusion dynamics in relation to fruit availability, we calculated a Bayesian model with the outcome variable subgroup size and the predictor variable fruit availability. Because subgroup size is a count variable, and first model attempts indicated that this model was overdispersed, we used a model with a negative binomial likelihood function. Furthermore, we specified that the value of the outcome variable group size was limited to values larger than 0 (because subgroups with a size of 0 do not exist). We included the date of data collection as grouping variable to account for the dependence of different group scans recorded on the same day. Furthermore, we included the date of phenology data collection linked to the 2-week period of behavioural data as grouping variable because all behavioural data within these 2 weeks were linked to the same fruit availability score.

Finally, to investigate how fruit availability affects the cohesion of subgroups, we calculated a model with subgroup spread (in meters) as the outcome variable, and the size of the subgroup and fruit availability as predictor variables. As outlined above, this model tests whether fruit availability affects the spread of a subgroup after accounting for the effects of subgroup size, which reflects the cohesion of a subgroup. We considered the spread in meters as a count variable and fitted a model with a Poisson distribution. As for the model for subgroup size, we included date of data collection and the associated phenology date as grouping variables.

As male and female reproductive strategies and competitive regimes differ (Chapman et al. 1995; Wrangham 1980), the two analyses for subgroup sizes and spread were conducted both for all adults and just for subgroups with female members only.

All models were fitted with the brms package v. 2.13.3v (Bürkner 2017, 2018) in R v. 4.0.2 (R-Core-Team 2020). We used the default priors, four chains and 2000 iterations,

Table 1 List of phenology tree species monitored in this study and their percentage in the spider monkey diet at Runaway Creek, Belize

Family	Genus	Species	% Diet
Moraceae	*Ficus*	*insipida*	14
Sapotaceae	*Manilkara*	*staminodella*	10
Moraceae	*Ficus*	*pertusa*	8
Arecaceae	*Attalea*	*cohune*	8
Burseraceae	*Protium*	*copal*	8
Anacardiaceae	*Metopium*	*brownei*	7
Anacardiaceae	*Spondias*	*radlkoferi*	6
Moraceae	*Pseudolmedia*	*spuria*	5
Arecaceae	*Sabal*	*yapa*	4
Moraceae	*Brosimum*	*alicastrum*	4
Ulmaceae	*Ampelocera*	*hottlei*	3
Caesalpiniaceae	*Dialium*	*guianense*	3
Fabaceae	*Caesalpinia*	*gaumeri*	3
Moraceae	*Trophis*	*racemosa*	2
Simaroubaceae	*Simarouba*	*glauca*	2

which resulted in stable models with relatively large effective sample sizes (Bulk_ESS and Tail_ESS all above 1000) and Rhat values equal to 1.
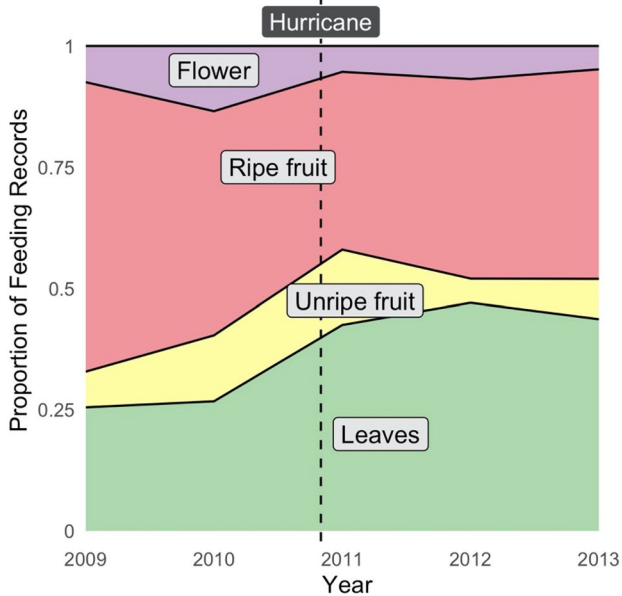
Fig. 1 Yearly variation in dietary composition of spider monkeys at Runaway Creek from 2009 to 2013. The dashed line indicates Hurricane Richard, which occurred on 25th October 2010

Results

Diet composition

The monkeys fed on 121 plant species from 83 genera and 47 families. Three families (Moraceae, Anacardiaceae, and Arecaceae) represented over half of their diet, and most notably, Moraceae constituted 39% of all plant items consumed. Their overall diet was composed of 60% fruit (48% ripe and 12% unripe fruit), 30% young leaves, 8% flowers, and 0.5% "other" items (limestone, soil, and insect eggs). The remaining 1.5% of their diet were items that were unknown and/or could not be identified. The diet composition varied over the five and a half years of study (Fig. 1).

Seasonal differences in diet

There were two fruiting peaks in an annual cycle: one smaller peak at the very end of the dry season (May) and a larger fruiting peak toward the end of the wet season (around October; Fig. 2a). However, there was considerable variation within and across years, and differences in fruit availability between the wet and dry season were not consistent (Table 2, model a). With regard to the occurrence of the hurricane, the model indicated that fruit availability tended to be lower during the months following the hurricane (Table 2, model b; Fig. 2b and c), and this difference was more pronounced when only considering the 12 months directly following
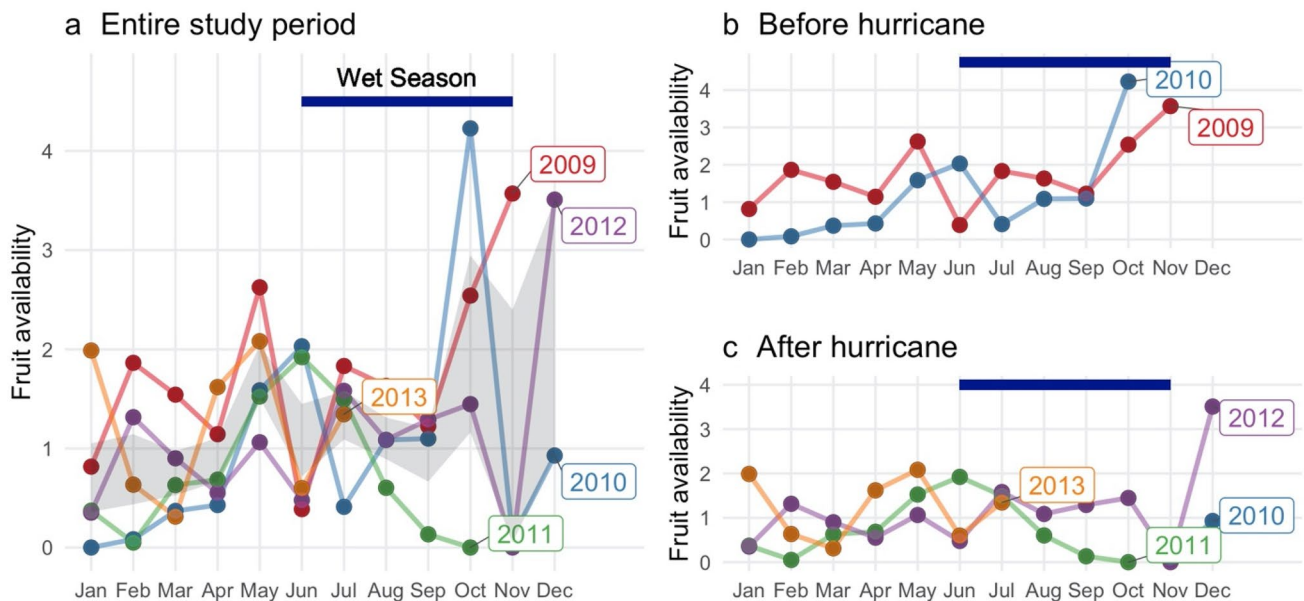
Fig. 2 Temporal changes in monthly fruit availability scores across 2009–2013. Changes are shown for the entire study duration (**a**), and the period before (**b**) and after (**c**) the hurricane. Each line represents a single year, and the grey shaded area in **a** denotes the monthly mean ± SE. The dark blue horizontal line in each of the plots indicates the wet season

Table 2 Results of the models testing for an effect of season and hurricane on monthly fruit availability

Model	Parameter	Estimate (median)	CI$_{95}$_low	CI$_{95}$_high
a. Season	Intercept	−0.09	−0.55	0.42
	Season (wet)	0.21	−0.51	0.96
b. Hurricane (pre vs. post)	Intercept	0.31	−0.14	0.79
	Hurricane (post)	−0.51	−1.06	0.02
c. Hurricane (within 12 months post vs. other periods)	Intercept	0.17	−0.19	0.55
	Hurricane— (12 months post)	−0.68	−1.28	−0.03

In addition to the median of the estimate, the boundaries of the 95% credibility interval of the posterior distribution are shown in the table (CI$_{95}$ low and high). Fruit availability was scaled to a mean of 0 and a SD of 1 before calculating the models

Table 3 Results of the multinomial model testing for an effect of fruit availability on the proportion of ripe fruit, unripe fruit, leaves, and flowers in the diet of spider monkeys

| Parameter	Estimate (median)	CI$_{95}$_low	CI$_{95}$_high
Ripe fruit—Intercept	2.17	1.76	2.6
Unripe fruit—Intercept	−0.07	−0.76	0.51
Leaves—Intercept	1.97	1.56	2.38
Ripe fruit—Fruit availability	1.07	0.63	1.55
Unripe fruit—Fruit availability	0.14	−0.56	0.84
Leaves—fruit availability	0.46	0.02	0.89

The parameter estimates for the intercepts and the effects of fruit availability for the different food items are in relation to the proportion of eaten flowers (the pivot in this model). Fruit availability was scaled to a mean of 0 and a SD of 1 before calculating the model

the hurricane in comparison to all other periods (Table 2, model c). However, as for season, there was considerable variation within and across years. Therefore, fruit availability scores seem to be a more meaningful predictor variable for behavioural variables than either season or hurricane, and we therefore use monthly fruit availability scores in the following models.

Diet and fruit availability

The multinomial model indicated that as fruit availability increased, the proportion of fruit in the diet increased, whereas the proportion of leaves, unripe fruit, and flowers decreased [Table 3; for an easier interpretation of these coefficients, which are on a logit-scale and in relation to the

Fig. 3 Proportion of ripe fruit, unripe fruit, leaves, and flowers in the diet of spider monkeys in relation to monthly ripe fruit availability. The circles show the observed proportion of different food items in the diet, combined for four different intervals of ripe fruit availability. The area of the circles is proportional to the number of feeding events included. The lines illustrate the model predictions of the multinomial model shown in Table 3, with the shaded areas showing the 95% credibility intervals
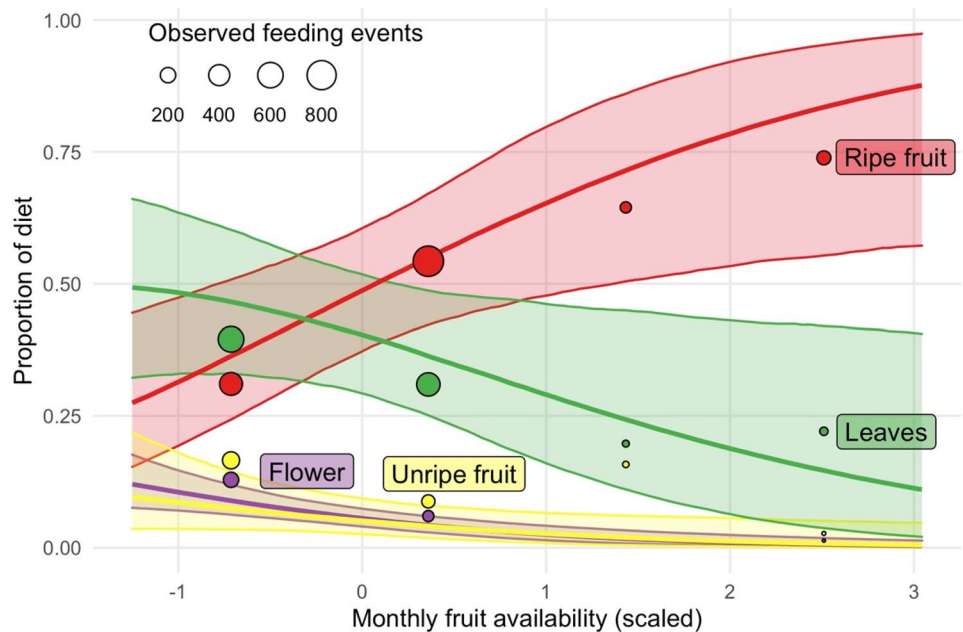
pivot, flowers in this case, the effects are illustrated in Fig. 3; see (McElreath 2020)].

When fruit availability was low, the spider monkeys increased their consumption of flowers (primarily from *Brosimum alicastrum*, *Pseudobombax ellipticum*, and the vine *Combretum fruticosum*) and preyed on the seeds of unripe fruit from *Brosimum alicastrum*, *Pseudolmedia spuria*, and *Caesalpinia gaumeri*.

Fruit availability and fission–fusion dynamics

The calculated model indicated no clear evidence for a relationship between the availability of ripe fruit and the size of the subgroups (Table 4, Fig. 4a) or fruit availability and subgroup cohesion (Table 5, Fig. 5a).

To assess how fruit availability might affect female subgrouping patterns when males were not present, we re-ran the analyses on all-female subgroups, omitting all-male and

Table 4 Results of the negative binomial models testing for the relationship between fruit availability and size of spider monkey subgroups

Included individuals	Parameter	Estimate (median)	CI$_{95}$_low	CI$_{95}$_high
All individuals	Intercept	0.99	0.91	1.08
	Fruit availability	0.05	−0.03	0.13
Females only	Intercept	0.76	0.66	0.86
	Fruit availability	0.10	0.00	0.19

Fruit availability was scaled to a mean of 0 and SD of 1 before calculating the models

Table 5 Results of the Poisson models testing for the effect of fruit availability and subgroup size on the spread of spider monkey subgroups

Included individuals	Parameter	Estimate (median)	CI$_{95}$_low	CI$_{95}$_high
All individuals	Intercept	26.03	24.08	27.95
	Fruit availability	1.37	−0.51	3.35
	Group size	6.57	5.65	7.45
Females only	Intercept	26.51	24.13	28.74
	Fruit availability	1.3	−1.02	3.63
	Group size	6.14	4.79	7.52

Fruit availability and subgroup size were scaled to a mean of 0 and SD of 1 before calculating the model

mixed-sex subgroups. Here, fruit availability was positively related to the size of subgroups consisting of only females (Table 4; Fig. 4b). However, there was no such relationship for fruit availability and the spread of female-only subgroups (Table 5; Fig. 5b).

Discussion

Our study of the spider monkeys at Runaway Creek revealed a complex set of relationships between food availability, diet, and subgroup dynamics. Diet was variable from year to year, but consistently contained a large proportion of fruit. Fruit availability positively predicted the amount of fruit in their diet. Spider monkeys are typically characterized as ripe fruit specialists, and between roughly
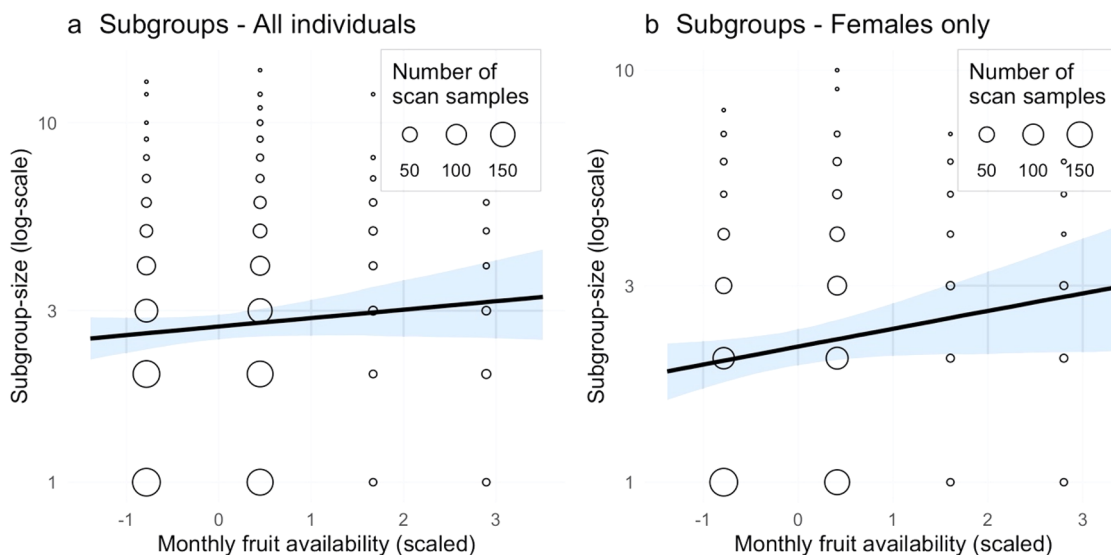
Fig. 4 Relationship between fruit availability and the size of spider monkey subgroups for all individuals (**a**) and for females only (**b**). The circles indicate the observed size of subgroups, and the line the predicted relationships from the models shown in Table 4, with 95% credibility intervals indicated by the shaded area
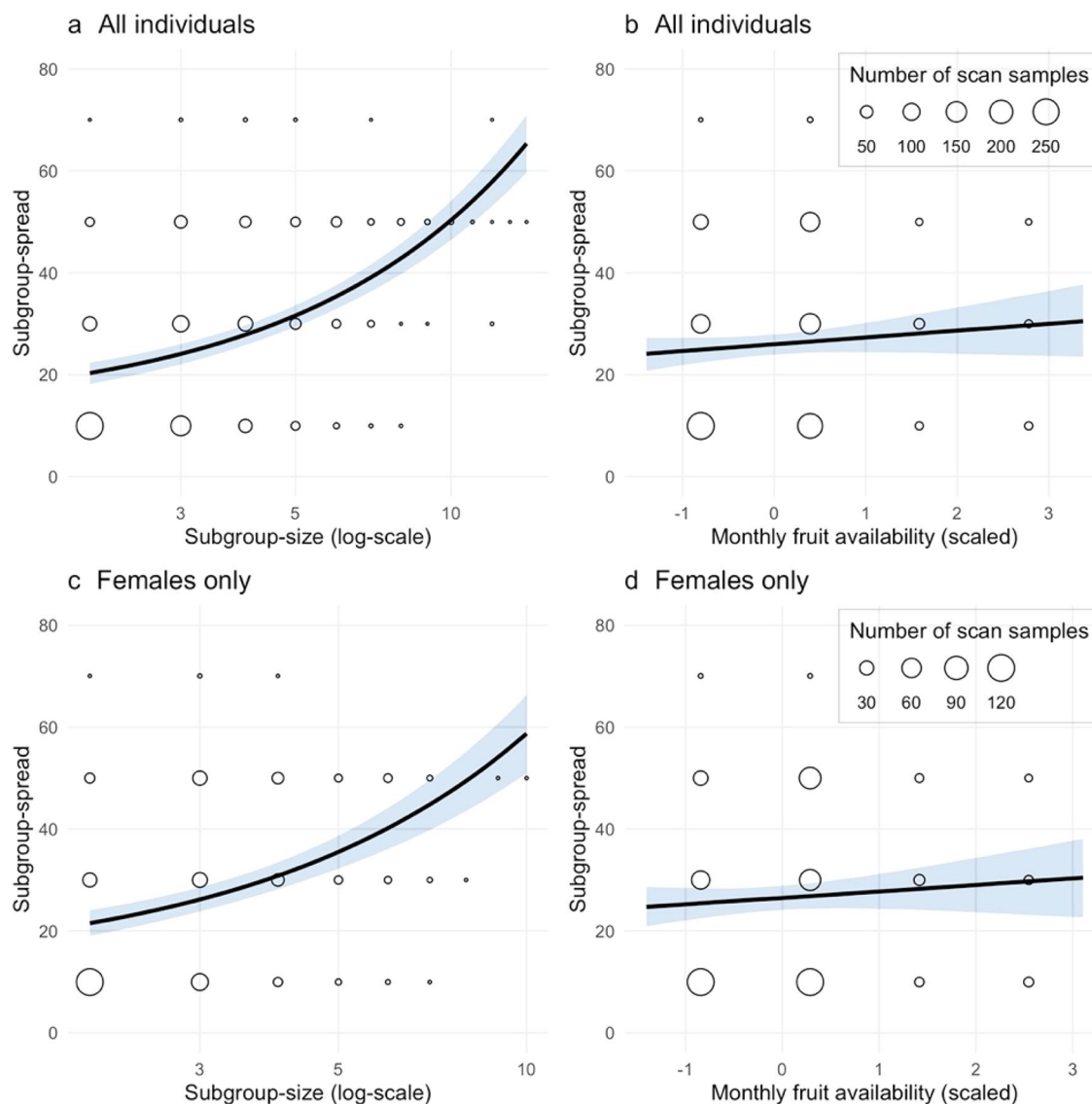
Fig. 5 Relationship between the spread of spider monkey subgroups and subgroup size for all individuals (**a**) and for female-only subgroups (**c**), and between subgroup spread and fruit availability for all individuals (**b**) and female-only subgroups (**d**). The circles indicate the observed spread of subgroups, combined into regular intervals for fruit availability and subgroup spread with the area proportional to the number of scans. The lines indicate the predicted relationship between the different variables from the models shown in Table 5, with 95% credibility intervals indicated by the shaded area. These effects are conditional on a mean effect of the omitted variables; thus **a**, **c** show the effects of subgroup size on subgroup spread conditional on a mean value for fruit availability, and vice versa for **b** and **d**

75% and 90% of their diet is fruit (Di Fiore et al. 2008; Wallace 2005). In our study, *ripe* fruit consumption never exceeded 75%, but when unripe fruit is included, the category of "fruit" accounts for 48–82% of their annual diet. Ripe fruit consumption was highest before the hurricane, as fruiting trees ceased fruit production in many parts of the forest that sustained the most severe wind damage (Champion 2013). Given this, our results are consistent with previous studies demonstrating that spider monkeys typically show a strong preference for fruit (Dew 2005; Stevenson et al. 2000). However, our results also show that

spider monkeys can substitute leaves and flowers for fruit when fruit availability is low (see also Chapman 1987). In fact, leaf consumption approached 50% in 2012 after the hurricane. In the post-hurricane years, both leaf and flower consumption increased. A study of *Ateles geoffroyi* in the Yucatan similarly found that the animals increased the time spent feeding on leaves after a hurricane, and in the dry seasons both pre- and post-hurricane, the monkeys spent more time eating leaves (Schaffner et al. 2012). Similarly, *Ateles belzebuth* in Bolivia is highly frugivorous, except for 1 or 2 months during the dry season when

leaves constitute up to 36% of their diet (Wallace 2005). Spider monkeys did consume more fruit when fruit was more abundant.

Our investigation of fission–fusion dynamics revealed theoretically interesting complexities. High fission–fusion dynamics is hypothesized to result from contest competition over patchily distributed and temporally unpredictable fruit resources (Aureli et al. 2008; Janson 1988; Schaffner et al. 2012). Accordingly, we predicted that larger subgroups would occur during periods of higher fruit availability, and we expected that subgroup spatial cohesion would increase during periods of fruit abundance. When males and females were analyzed together, we found no link between fruit availability and subgroup size. However, when females were analyzed separately, fruit availability did affect subgroup size in the predicted direction. There are several ways to interpret these results. One possibility is that males and females associate at random with respect to fruit availability, so male membership in subgroups was not affected by fruit availability, but rather by social factors (see also Aureli et al. 2006; Chapman et al. 1995). Interestingly, our prior research has shown that this population of spider monkeys are significantly sexually segregated for most months of the year, and that males and females are more often segregated during periods of higher fruit availability (Hartwell et al. 2014). This might explain why, when males were included in this analysis, subgroup size did not increase with fruit availability, because it was during periods of relatively lower fruit availability that larger, mixed-sex subgroups were formed, possibly because they were attracted to the same few fruiting trees. As female reproductive fitness is limited by access to food, females are predicted to distribute themselves to best take advantage of food resources and minimize contest competition, thus rendering their behavioural patterns more sensitive to ecological pressures, such as food availability (Snaith and Chapman 2007; Wrangham 1979). In other words, changes in fruit availability may be more accurately reflected by variation in female subgrouping patterns than by variation in all-male or mixed-sex subgroups, which could reflect other factors, such as the availability of reproductively available females, the need for territorial defense, or more consistent rates of association among males (Ramos-Fernandez et al. 2009).

Higher fruit availability did not influence subgroup spatial cohesion, and this result did not change when females were analyzed separately. We expected higher fruit availability to lead to higher spatial cohesion, as closer inter-individual proximity between subgroup members might be tolerated when contest competition is potentially reduced; however, we did not find this. It is possible that our measure of spatial cohesion was too crude to capture the effects of fruit availability. However, in a recent study by Aguilar-Melo et al. (2020), the authors used inter-individual distances as a measure of spatial cohesion and found a minimal effect of fruit availability on proximity patterns. These authors conclude that social factors are more important than fruit availability in determining spatial cohesion within subgroups. Similarly, for our study group, non-ecological factors such as social preferences likely have a larger effect on spatial cohesion, even for female subgroup members.

A growing body of evidence suggests that demographic and social factors interact with ecological drivers in determining the spatial arrangement of group members (Fury et al. 2013; Murray et al. 2007). Thus, examining such variables may help to refine our understanding of spider monkey subgrouping dynamics. Furthermore, future studies of subgrouping dynamics may benefit from incorporating other ecological measures of fruit availability that can influence travel costs and food competition, such as patch size and fruiting tree density and distribution throughout the home range, and by considering the temporal dependency of the variables [e.g., what is the temporal time scale over which food items of each species are available (see also suggestions in Asensio et al. 2009; Asensio et al. 2012a, b)]. In addition, a consideration of foods less frequently consumed, but which nonetheless are nutritionally important (e.g., sources of salt Fashing et al. 2007; Rode et al. 2003; Rothman et al. 2012, 2006), will help understand fission–fusion dynamics more thoroughly.

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