RESEARCH ARTICLE

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Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest

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When making foraging decisions, female primates may follow specific behavioral strategies that reflect their reproductive state. Lactation is considered the most energetically costly phase for females, but we argue that gestation is also energetically expensive for squirrel monkeys. In this study, we examined whether female squirrel monkeys (a seasonally breeding primate) in different reproductive phases showed significant differences in their foraging ecology. We sampled two wild groups of squirrel monkeys (*Saimiri collinsi*) using the focal animal method, during 12 months (June 2014 to May 2015). During this time, we quantified the effect of reproductive state (mating, gestation, and lactation) and sex (females vs. males) on activity budgets, foraging efficiency, dietary composition, and nearest neighbors. We found significant effects of both sex and reproductive phase on the mean proportion of time spent foraging, resting, traveling, and being social. Females consumed more insects than did males at all times; among females, time spent eating prey and fruit varied according to reproductive state. These data suggest that, due to their life history and seasonal breeding, reproduction is a costly activity for female *Saimiri*, and not only during lactation. Therefore, adopting the appropriate behavioral strategies is essential to reduce energetic deficits in females.

KEYWORDS
foraging, life history, reproductive energetics, squirrel monkey

1 | INTRODUCTION

Life history theory predicts that females allocate their energy to optimize lifetime reproductive success, in the face of the social and energetic costs of reproduction. In order to mitigate such costs, female behavioral strategies (e.g., patterns of foraging, activity budgets, and social association patterns) may be altered according to their reproductive status (whether the female is lactating, pregnant, or non-reproductive). For example, in primates, female activity budgets are affected both by the temporal distribution of food resources and by their reproductive phases (Vasey, 2005). Most researchers consider lactation as the most expensive reproductive activity for female primates (Altmann, 1980; Pond, 1977), and lactation sometimes coincides with the period of highest fruit availability in the habitat (Boinski, 1988; Vasey, 2005). Accordingly, several studies on primates (e.g., Altmann, 1980; MacCabe & Fedigan, 2007) do not report an increase in female foraging time during gestation, but mainly during

lactation (but see Muruthi, Altmann, & Altmann, 1991; Sauther, 1994 for higher energy and protein intake during gestation in lemurs and baboons). However, as we argue here, gestation is also is an energetically costly phase for our seasonally breeding study species (Garber & Leigh, 1997), particularly given the ratio of neonatal body weight to maternal body weight (Dufour & Sauther, 2002), which can be used as a proxy for the burden of gestation (Gittleman & Thompson, 1989).

Lactating primates often spend more time foraging when compared to non-lactating females (Altmann, 1980; Koenig, Borries, Chalise, & Winkler, 1997; Sauther, 1994). In other cases, lactating females have a higher food intake (Tarnaud, 2006), forage more efficiently (MacCabe & Fedigan, 2007), or obtain more energy and protein (Herrera & Heymann, 2004; MacCabe & Fedigan, 2007; Muruthi et al., 1991; Serio-Silva, Hernandez-Salazar, & Rico-Gray, 1999). In some taxa such as baboons, female energetic costs increase as the infant grows, leading them to forage more during the second

half of lactation (Dunbar, Hannah-Stewart, & Dunbar, 2002). In other species, females may maximize their energy intake during early lactation (MacCabe & Fedigan, 2007; Tarnaud, 2006). Female activity budgets that reflect energy conservation strategies may also be present (Gittleman & Thompson, 1989). More time can be spent resting during lactation and gestation (Dufour & Sauther, 2002; Harrison, 1983; Sauther, 1994; Vasey, 2005), as one strategy to decrease energy metabolic expenditure during these periods. Finally, females caring for infants may spend more time near other females and juveniles in their group, in order to share the time and energy burdens of infant care (Mitchell, 1990).

Confirming the importance of reproductive costs, intersexual differences in foraging ecology are often seen in primates (Gautier-Hion, 1980; Hemingway, 1999; Vasey, 2005). When present, such differences may manifest themselves in diet, time dedicated to foraging, time dedicated to resting, and feeding efficiency (Fragaszy, 1986; Rose, 1994; Vasey, 2005). For example, adult male *Cebus olivaceus* spend less time foraging and more time resting, when compared to females (Fragaszy, 1990). Females may also spend more time feeding than do males (Boinski, 1988; Vasey, 2005), and eating more energetically-rich items (Sauther, 1998).

Squirrel monkeys (genus *Saimiri*) are highly seasonal breeders (Di Bitteti & Janson, 2000; Stone, 2006) and show an especially high level of maternal investment when compared to other small-bodied neotropical primates (Garber & Leigh, 1997; Tardif, 1994). For example, gestation length (5 months; Mitchell, 1990; Stone, 2006) is considered long when compared to similarly-sized platyrrhines (Hartwig, 1996). In addition, despite producing only one infant per reproductive event, pre-natal growth rates are high compared to the twin-producing callitrichines (Garber & Leigh, 1997; Hartwig, 1996; Ross, 1991). As a result, infant *Saimiri* are well-developed at birth (16–20% of the mother's body weight; Elias, 1977; Kaack, Walker, & Brizzee, 1979; Stone, unpublished trapping data) and infants have 60% of adult brain mass at birth (Elias, 1977). Therefore, gestation in squirrel monkeys appears to be particularly expensive for a small-bodied primate.

Rapid somatic and brain growth continues during the first 3 months of life (Kaplan, 1979; Manocha, 1979). Post-natal brain growth in infants also occurs extremely rapidly, with the brain reaching 96% of its size in the first 2 months (Garber & Leigh, 1997; Leigh, 2004; Manocha, 1979). Captive work also has shown that squirrel monkey milk is high in energy and fat, compared to milk produced by other platyrrhines such as marmosets (Milligan, Gibson, Willams, & Power, 2008). Although females do not share food with infants, infant protection/vigilance against aerial predators is an important part of maternal investment; infant mortality associated with predation may explain the high birth synchrony observed in *Saimiri* groups (Boinski, 1987; Stone, 2004). Furthermore, in some squirrel monkeys species, adult females share in infant carrying and engage in allonursing (Pinheiro, 2015; Williams et al., 1994), making female-female spatial proximity especially important, particularly among kin (Montague, Disotell, & Di Fiore, 2014).

Due to their omnivorous diet (fruits, flowers, and invertebrates; Janson & Boinski, 1992), activity budget (most of their time is spent on foraging; Stone, 2007a), seasonal breeding (Di Bitteti & Janson, 2000)

and high maternal costs compared to other small-bodied neotropical primates, squirrel monkeys are a good model to examine the effect of reproductive states on shifting female behavioral strategies. We know that in at least one *Saimiri* species (*S. oerstedii*) females foraged and fed more than did males, while males spent more time in vigilance against predators (Boinski, 1988). In addition, a recent study by Montague et al. (2014) found that female *S. macrodon* (Lynch et al., 2015) foraged more and rested less, compared to males. However, the specific effect of reproductive status on the behaviors of female squirrel monkeys has not been examined for any of the species. In the present study, we predict that female squirrel monkeys (*S. collinsi*) in different reproductive states will show significant differences in their activity patterns, foraging strategies, and spatial associations. Specifically, we predict that during the months of gestation and lactation, females will show behaviors that will help them cope with the high time and energy demands of these phase. We note that we did not directly measure the energetic states of our study animals (energy intake and expenditure), and instead use time spent in certain activities as a proxy for energy obtained/conserved and expended. The following variables are examined in females at three reproductive periods: (a) activity budgets (particularly time spent in foraging, travel, and rest); (b) foraging efficiency; (c) dietary composition; (d) social association patterns (age-sex class of nearest neighbors). We also examine these variables in males throughout the year, to control for the effect of changing seasons and corresponding fluctuating resource availability at our study site (Stone, 2007a). In this population of squirrel monkeys, mating occurs during July and August (8 weeks), and births occur in December and January of each year (8 weeks; Stone, 2006). Weaning is complete at 8 months of age.

2 | METHODS

Research was approved by the Animal Care and Use Committe of the Universidade Federal Rural da Amazônia. This study adhered to the American Society of Primatologists principles for the ethical treatment of primates.

2.1 | Study area

Field data on *S. collinsi* were collected in Eastern Amazonia, Brazil. The study site is located in the village of Ananim, 150 km east of Belém, Pará state (01° 11′ S, 47° 19′ W). The 800-ha site consists of primary forest and adjacent disturbed areas. Rainfall in the area is highly seasonal, with a wet season from January to June (corresponding to birth, lactation, and weaning) and a dry season from July to December (corresponding to mating and gestation; Stone, 2006). Fruit availability, including that of the most common fruit in the monkeys' diet (*Attalea maripa*, Araceae), is highest during the wet season (Stone, 2007a).

2.2 | Study population

We monitored this population of squirrel monkeys for 12 months (June 2014 to May 2015). Systematic data come from two habituated

groups of monkeys, group A (44 individuals) and group B (50 individuals). Group A lives in 120 ha and group B lives in 150, with some overlap in home range. Squirrel monkey groups are not territorial but generally avoid each other when they come into contact at a feeding tree, for example. The approximate group composition is: 10 adult males, 14–20 adult females, 20 juveniles, and infants. Their diet is insectivore-frugivore, with approximately 75% of foraging time being devoted to insects (Stone, 2007a). Fruits consumed by squirrel monkeys at this site range from berry-like fruits (e.g., *Lacistema pubescens*) to larger fruits (e.g., *Cecropia* sp). Adult males (>5 years) are easily distinguished from adult females by their larger body size, visible testicles, and flatter head shape. Adult females (>3 years) can be distinguished from juvenile females by having darker sideburns and visible nipples (in the case of non-nulliparous females). Very old females can be distinguished by their longer, ruffed coat.

2.3 | Behavioral data collection

Behavioral data were collected during 1,080 observation hours, equally distributed for groups A and B. Each group was followed and monitored for at least 5 days per month (0700–1500 hr), for 12 months. On the remaining days, the groups were followed by a field assistant, but only to collect data related to plant species consumed and birth dates for infants. In order to collect data throughout the year, the adult females were divided into three categories according to their reproductive state: not gestating nor lactating but likely cycling (mating period); gravid; lactating. Because of seasonal breeding, reproductive phases were synchronized among females, and most of the females in each group did become pregnant (at least 8 females in group A and at least 10 females in group B). We also were able to confirm gestation through visual observations. After approximately 6 weeks of gestation, female squirrel monkeys show a distended abdomen, and pregnancy is visible. In addition, trapping data from previous years has confirmed gestation based on initial visual observations in 100% of cases. Lactating females were identified by nursing behavior and/or by dark, distended nipples.

During daily follows of the groups, we collected systematic behavioral data via focal animal sampling (Altmann, 1974) on adult males (N = 245 focals) and females (N = 585 focals, non-reproductive N = 190; gestation N = 182; lactation = 207). The total number of focal samples collected was 830 (402 on group A and 428 on group B). Each individual was followed for a minimum of 4 and a maximum of 10 min. During the focals, we recorded the individual's activity (eat: consumption of plant or animal food material; forage: visual or manual searches for plant or animal material; rest: period of inactivity; travel: direct movement not associated with foraging; social: aggressive and affiliative behaviors between two or more animals such as mating, playing, and chasing). We also recorded their nearest neighbor category within 5 m (adult female; adult male; juvenile; alone), in 1 min intervals. This allowed us to obtain activity budgets, "nearest neighbor budgets," to calculate foraging efficiencies (proportion of eat observations divided by proportion of forage observations) and to identify specific dietary items (flowers, fruits,

arthropods). In addition, we collected *ad libitum* data on the consumption of fruits or flowers, and all plants in the monkeys' diet were collected and identified by specialists at the Museu Paraense Emílio Goeldi in Belém.

2.4 | Data analyses

Instantaneous observations within each focal animal sample are not statistically independent. To this end, we treated each focal sample, rather than each individual observation within a sample, as a data point. "Activity" was converted to a quantitative variable as the proportion of intervals an animal was engaged in a specific activity within the sample (Boinski, 1988; Fragaszy, 1990; Stone, 2007b). The same was done for the variable "nearest neighbor."

Regression model: effect of sex and reproductive phase on activity budgets

$$\text{Forage}_i = \beta_0 + \beta_1 \text{Ges}_i + \beta_2 \text{Lac}_i + \beta_3 \text{Male}_i + \beta_4 \text{Male}_i \cdot \text{Ges}_i \\ + \beta_5 \text{Male}_i \cdot \text{Lac}_i + U_i \tag{1}$$

where i denotes a single focal sample and $i = 1, 2, ..., 830 U_i$ is a mean zero error term.

We use least squares regression to estimate the coefficients in (1). We interpet β_0 as the mean proportion of time spent foraging by females during the mating phase of the reproductive cycle. β_1 is the change in the mean proportion of time spent foraging by females during the gestation phase—therefore, the mean proportion of time spent foraging by females during the gestation phase is $\beta_0 + \beta_1$. Similarly, β_2 is the change in foraging by females in the lactation phase. β_3 is the difference in mean proportion of time spent foraging by males in the mating cycle—therefore, the mean proportion of time spent foraging by males in the mating cycle is $\beta_0 + \beta_3$. β_4 and β_5 represent the differential effect of the gestation and lactation cycles, respectively, on male foraging.

Due to the large number of individual squirrel monkeys within the two social groups, it is not possible to identify a particular observation with an individual monkey. We realize the issue of pseudoreplication that arises. In particular, we acknowledge that sampling the same individual more than once does not provide as much additional information as sampling different individuals. As such, the random unit in this analysis is the group rather than the individual squirrel monkey. In order to account for this in the estimation of p-values, we defined four groups and clustered the standard errors by group. The four groups are: females in social group A, males in social group A, females in social group B, and males in social group B. Since the number of clusters is small, we make one other adjustment to mitigate the downward bias in our p-values created by the dependence of errors within groups. Rather than choose critical values from the standard normal distribution, following Cameron and Miller (2015). We chose critical values from the student-t distribution with G-1 degrees of freedom (where G is the number of groups). In the case of a two-tailed test with $\alpha = 0.05$, the critical value is 2.78 rather than 1.96 as implied by an assumption of normality. Five other versions of model (1) were

estimated in which we substituted different behaviors for the dependent variable. These additional behaviors are Eat, Rest, Travel, Social, and Foraging Efficiency. In each case, we estimated clustered standard errors based upon the four groups.

Regression model: effect of sex and reproductive phase on nearest neighbor budgets

$$AdultMale_i = \beta_0 + \beta_1 Ges_i + \beta_2 Lac_i + \beta_3 Male_i + \beta_4 Male_i \cdot Ges_i + \beta_5 Male_i \cdot Lac_i + U_i \qquad (2)$$

where i denotes a single focal sample and $i = 1, 2, ..., 830 U_i$ is a mean zero error term.

As before, we use least squares regression to estimate the coefficients in (2). We interpet β_0 as the mean proportion of time spent with an adult male as the nearest neighbor by females during the mating phase of the reproductive cycle. β_1 is the change in the mean proportion of time during the gestation phase—therefore, the mean proportion of time spent with an adult male as the nearest neighbor by females during the gestation phase is $\beta_0 + \beta_1$. Similarly, β_2 is the change in mean proportion of time during the lactation phase. β_3 is the difference in mean proportion of time for males—therefore, the mean proportion of time spent with an adult male as the nearest neighbor by males in the mating cycle is $\beta_0 + \beta_3$. β_4 and β_5 represent the differential effect of the gestation and lactation cycles, respectively. Three other versions of model (2) were estimated in which we substituted different nearest neighbors for the dependent variable. These additional nearest neighbors are Adult Female, Juvenile, and Alone. In all four versions of model (2), we estimated clustered standard errors based upon the four groups as defined earlier.

2.5 | Diet

Chi-squared analyses were used to test for possible differences in the diets of males and females, and of females in different reproductive states. All tests are two-tailed.

3 | RESULTS

3.1 | Activity budgets

We examined the effects of sex and reproductive phase on the frequency of each activity category. These results are summarized in Table 1 and Figure 1.

3.1.1 | Foraging

We find a significant effect of sex on the proportion of time spent foraging. In addition, we find a significant effect of the reproductive cycle on time spent foraging by females. Males averaged 23.7% of time spent foraging during the mating phase, while females averaged 27.7%. Our estimate of this difference is highly statistically significant. We do not find a statistically significant effect of the different phases of the reproductive cycle on male foraging. Females averaged more foraging during the lactation phase than during other phases in the reproductive cycle. This difference is large in magnitude and highly statistically significant (Table 1). Specifically, female squirrel monkeys increased the average proportion of time spent foraging by more than 70% (from an average of 28% of time to 48% of time). The effect of gestation on time spent foraging was not statistically significant at traditional levels.

TABLE 1 Regression analyses showing the effects of sex (male/female) and reproductive phase (mating/gestation/lactation) on the variables "activity," "foraging efficiency," and "nearest neighbor"

	Intercept	Gestation	Lactation	Males, mating period	Males, gestation period	Males, lactation period
Activity						
Forage	0.277	0.087	0.201	−0.040	0.008	−0.050
Eat	**0.198**	−0.009	0.024	0.053	−0.042	−0.057
Rest	**0.096**	**−0.067**	**−0.074**	**0.070**	−0.009	**−0.038**
Travel	**0.429**	−0.008	**−0.175**	**−0.124**	0.111	0.121
Social	**0.009**	**−0.009**	**0.015**	**0.048**	**−0.043**	**−0.063**
Efficiency						
Foraging efficiency	**0.592**	0.001	−0.026	0.187	−0.101	−0.178
Nearest neighbor						
Adult male	**0.261**	**−0.144**	**−0.183**	**−0.181**	**0.267**	**0.340**
Adult female	**0.214**	0.115	**0.192**	0.118	**−0.203**	**−0.314**
Juvenile	**0.108**	−0.059	**−0.028**	0.007	−0.027	**−0.032**
Alone	**0.401**	0.094	**−0.086**	0.059	−0.055	0.032

Statistically significant ($p < 0.05$) in bold.
Intercept column represents "females during mating season." The last three columns (males) represent the equivalent variables for males during the mating period, males during the female gestation period, and males during the female lactation period, respectively. Individual t statistics and p-values for each behavioral category are given in Appendix 1.
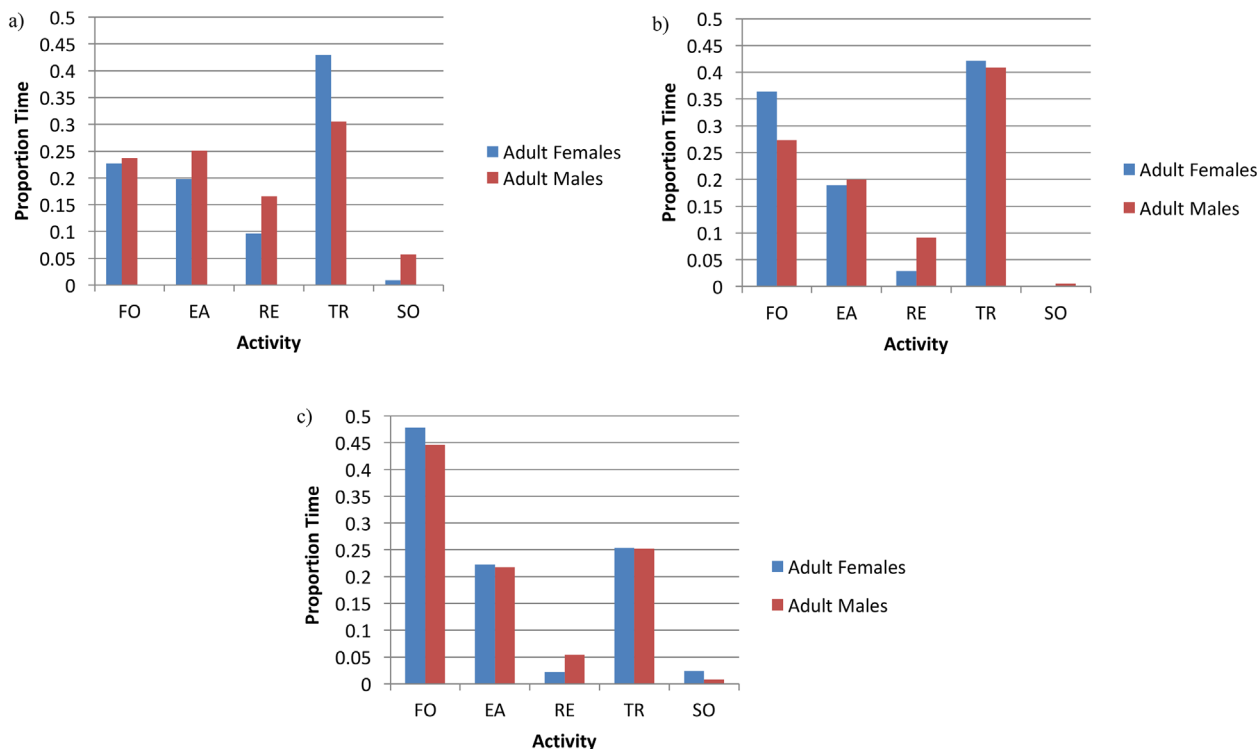
FIGURE 1 Activity budgets of male (AM) and female (AF) *Saimiri collinsi*, during 12 months. (a) Mating season; (b) Gestation season; (c) Birth and lactation season. FO, foraging; EA, eat; RE, rest; TR, travel; SO, social

3.1.2 | Eating

We did not find a statistically significant effect of either sex or reproductive phase on time spent eating by the squirrel monkeys.

3.1.3 | Resting

We find a significant effect of both sex and reproductive phase on the proportion of time spent resting. Males averaged 16.6% of time resting during the mating phase, compared to just 9.6 % of time for females. The effect of sex is highly statistically significant. Males spent significantly less time resting during the lactation phase, averaging just 5.4% of time. This difference is significant at the 5% level. For females, the average proportion of time spent resting declined during both gestation and lactation. Females averaged 9.6% of time spent resting during mating but only 3.0% of time during gestation and 2.2% of time during lactation. Both differences are highly statistically significant. We note that time spent resting decreases for both males and females during the lactation phase of the reproductive cycle, although the decrease in time spent resting is larger in percentage terms for females.

3.1.4 | Traveling

Again, we find a significant effect of sex on the proportion of time spent traveling. In addition, we find a significant effect of the reproductive cycle on time spent traveling by females. Males averaged 30.5% of time spent traveling during mating, while females averaged 42.9%. This difference is significant at the 5% level. Average proportion of time spent traveling decreased among females during

the lactation phase. Females averaged 25.4% of time spent traveling during lactation, compared to 42.9% of time during mating. This difference is significant at the 5% level.

3.1.5 | Socializing

We find a significant effect of both sex and reproductive phase on the proportion of time spent in social activities. Unlike the other behaviors, each phase of the reproductive cycle has a significant effect on time engaged in social behaviors for both males and females (Table 1). Females socialized the most during lactation (2.4% of their activity budget) and males socialized the most during mating season (5.7% of activity their budget).

3.1.6 | Foraging efficiency

We did not find a statistically significant effect of either sex or reproductive phase on foraging efficiency (ratio of time spent feeding to time spent foraging).

3.2 | Diet

Table 2 shows the proportional representation (foraging and eating samples) of prey, fruits, and flowers in the diet of males and females, according to reproductive phase of the year. Overall, females consumed more prey than did males ($\chi^2 = 17.9$, df = 1, $p < 0.0001$). We observed 29 instances of females consuming flowers, particularly *Passiflora glandulosa*, *Tapirira guianensis*, *Inga stipuloris*, and a non-identified vine flower. Males were observed consuming flowers six times in 12 months. We found a significant effect of reproductive

TABLE 2 Percentage of foraging and eating observations of male and female squirrel monkeys from two social groups, according to reproductive phase of the year

Food item	Females (N = 2,310 observations)			Males (N = 908 observations)		
	Mating season (%)	Gestation season (%)	Lactation season (%)	Mating season (%)	Gestation season (%)	Lactation season (%)
Prey	91.5	85	84.3	73	76	73
Fruits	8	10.2	15	27	24	26.2
Flowers	0.5	4.8	0.7	0	0	0.8

status on the amount of insects versus plants (fruits and flowers) consumed by females (χ^2 = 10.0, df = 1, p = 0.006). No seasonal effect was found for males (χ^2 = 5.8, df = 1, p = 0.06). Combining observations in both social groups, the monkeys consumed a total of 39 plant species. Females ate more species of plants than did males (females = 21, males = 10). During lactation, females consumed a greater variety of fruit and flower species.

3.3 | Nearest neighbors

We examined the effects of sex and reproductive phase on the frequency of association with each nearest neighbor age-sex class. These results are summarized in Table 1 and Figure 2.

3.3.1 | Adult males as nearest neighbors

We find a significant effect of sex on the proportion of time spent near adult males. In addition, we find a significant effect of the reproductive cycle on time that females spent near adult males. Males averaged 8%

of time near other males during mating season, while females averaged 26.1%. Our estimate of this difference is statistically significant. Futhermore, females significantly decreased the time spent with males during gestation (to 11.7%) and during lactation (to 7.8%).

3.3.2 | Adult females as nearest neighbors

There was a significant effect of the reproductive cycle on time that females and males spent near other adult females. During mating season, females spent 21.4% of their time near other females, but this number increased to 32.9% during gestation and to 40.6% during lactation. Conversely, during gestation and lactation, time spent near adult females decreased for adult males (24.5% gestation and 20.9% lactation), compared to mating season (33.2%).

3.3.3 | Juveniles as nearest neighbors

We find a significant effect of the reproductive cycle on time that both females and males females spent in proximity to juveniles, with time
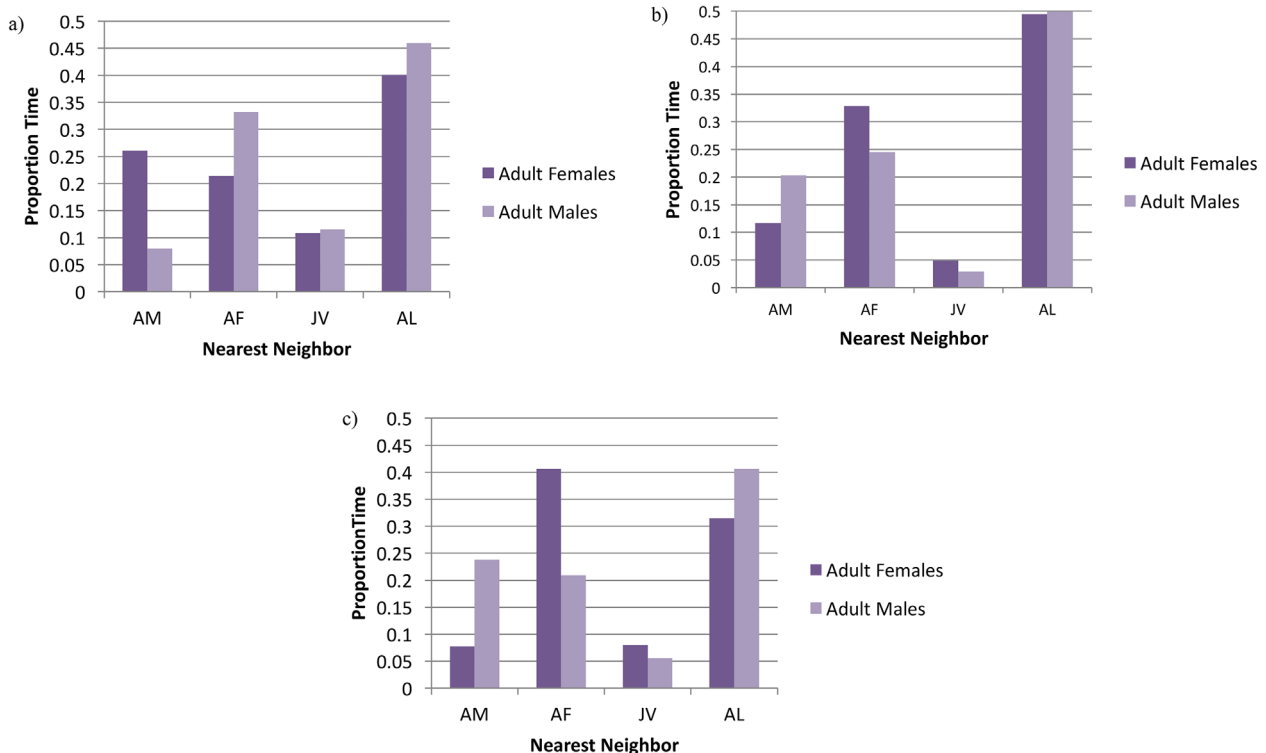
FIGURE 2 Nearest neighbor (within a 5 m radius) budgets of male (AM) and female (AF) *Saimiri collinsi*, during 12 months. (a) Mating season; (b) Gestation season; (c) Birth and lactation season. JV, juvenile; AL, alone

spent with juveniles decreasing during lactation lactation (8.0% females and 5.4% males).

3.3.4 | Alone (no neighbors within 5 m)

We find a significant effect of the reproductive cycle on the time that females spend alone. In the mating season, females spend an average of 40.1 of their time alone, with this number decreasing to 31.5% during the birth/lactation season. No significant effect was found for males.

4 | DISCUSSION

In this study, we examined several aspects of the feeding ecology and social association patterns of adult female squirrel monkeys over a 12 month period, according to their reproductive phase. Because squirrel monkeys are seasonal breeders, we also were able to simultaneously examine the same behavioral variables in adult males, providing us with a "control." As predicted, the reproductive phase of the females significantly influenced their activity budgets, diet, and nearest neighbors. Furthermore, the fact that female foraging efficiency did not vary across the year suggests that females are using effective strategies to cope with the energetic demands of each reproductive phase. Males and females differed in several aspects of their foraging ecology even when compared at the same time of the year, further supporting the notion that reproductive status influences female behavioral ecology in this species of primate.

4.1 | Gestation phase

Several studies have found variation in the activity budgets and feeding ecology of female primates when observed in different reproductive states, and propose that such variation correlates with changes in energy expenditure and intake by the females. In particular, the focus has been on lactation costs, since nursing is an energetically expensive activity (Altmann, 1980; Clutton-Brock, Albon, & Guinness, 1989). However, we found some shifts in the activity budget and diet of pregnant female squirrel monkeys; namely, they decreased their resting time and maintained a high proportion of time dedicated to travel. This result is not unexpected, given that gestation lengths in *Saimiri* are nearly a month longer than those of *Aotus* and are similar to those of the larger *Callicebus*, *Sapajus*, and *Cebus* (Hartwig, 1996). Furthermore, pregnancy in this population occurs during the driest part of the year, when fewer ripe fruits are available and troops spend more time is eating large arthropods and flowers (Stone, 2006, 2007a). The lack of easily accessible fruit resources in their environment would make it an especially challenging time for pregnant females. However, similarly to gestating ring-tailed lemurs (Sauther, 1994), they appear to shift their diet to include more flowers such that foraging time or foraging efficiency do not change when compared to the non-reproductive phase. It is interesting to note that a similar shift in time spent resting was not found for males in the groups (in fact, males rested twice as much as pregnant females), suggesting that gestation is likely the factor influencing changes in female activity budgets. We

also noted that both males and pregnant adult females continued to spend most of their time alone, rather than in association with other individuals, possibly because of an overall increase in insectivory occurs in the groups during the dry season (Stone, 2007a). This confirms the pattern observed by Stone (2007b)—during insect foraging, individuals are less likely to have a nearest neighbor within 5 m. In contrast, while fruit foraging, the group is more cohesive, with smaller interindividual distances (Stone, 2007b).

4.2 | Lactation phase

During lactation, females require energy for maintenance and to support offspring (not only via milk production but also for infant transport). We found that during lactation, females increased their foraging, decreased travel time, and increased time spent in social activities. The increase in foraging time is expected during lactation (Pond, 1977). But not all primate species follow this particular strategy. For example, Rose (1994) found that pregnant and lactating *Cebus capucinus* females foraged less than those who were cycling. In a later study, MacCabe and Fedigan (2007) demonstrated that while lactating *C. capucinus* did not increase overall time spent foraging, their ingestion rates for fruit and prey were higher during this phase. In contrast, female gelada baboons (*Theropitecus gelada*) did increase their foraging at the end of the lactation phase (when infants were beginning to wean), but not during the peak lactation period (Dunbar et al., 2002). In squirrel monkeys, lactating females decreased travel time, perhaps to avoid carrying infants over long distances. Infant squirrel monkeys are born relatively large (Elias, 1977) and grow quickly during the first three months (Garber & Leigh, 1997). An alternative explanation for why females traveled less in the birth/lactation season is that ripe fruits were abundant (wet season), leading to reduced travel time to fruiting trees. However, during the same period, adult males actually increased their travel time, leading us to believe that females travel less as an energy conservation strategy.

We were surprised to find that, while the females traveled less, they did not rest more (in fact, they decreased rest time). We suspect that any extra time that would be spent resting was channeled toward foraging activities and social interactions, particularly with other females (their most frequent nearest neighbor). In baboons, lactating females also trade resting time for increased foraging time (Dunbar & Dunbar, 1988). We may also hypothesize that females with infants spent part of their time engaged in antipredator vigilance. In one population of Costa Rican squirrel monkeys, predation by raptors caused an infant mortality rate of nearly 50% (Boinski, 1987). The threat of predators might pose an additional restriction to female activities during lactation, as found in other primates. Stone (2004) also found that female *S. collinsi* forage for insects in palm foliage more often than do males, possibly because palms offer greater conceal-ment from predators. Finally, we observed that lactating females participated in allocare, transferring their infants to other females and to older juveniles for short periods of time. On several occasions, we saw females that had not been pregnant that season later carrying the infant of another female, as has been observed for this species in captivity (Pinheiro, 2015).

Finally, our data show that females consumed a larger variety of fruits and flowers than they did during other phases, and also compared to males. The same pattern has been found in capuchins (MacCabe & Fedigan, 2007), vervet monkeys (Lee, 1987), and chimpanzees (Murray, Lonsdorf, Eberly, & Pusey, 2009). This further confirms that lactation is an energetically costly phase for females. On the other hand, lactating howler monkeys (Dias, Rangel-Negrin, & Canales-Espinosa, 2011; Serio-Silva et al., 1999), titi monkeys (Herrera & Heymann, 2004), and sakis (Deluycker, 2012) increased their consumption of protein during lactation. Interestingly, we found that female squirrel monkeys in all reproductive states consumed more invertebrate prey than did males. These results suggest that females may search for and consume higher-quality items year-round. We note, however, that we did not measure the nutritional value of the food items consumed by the primates in this study, which would confirm whether females indeed have a higher quality diet than do males.

4.3 | Male-female differences

Throughout the year, we observed significant differences in foraging strategies and association patterns between males and females in our study groups. In fact, between-sex variation in primate behavior often overrides age-class differences (Agostini & Visalberghi, 2005). While we argue that most of the intersexual differences we observed are due to differences in reproductive investment, it is possible that some may be related to sexual dimorphism. During the non-breeding season, adult males in our population are approximately 25–30% heavier than adult females (Stone, unpublished trapping data). In addition, female *Saimiri collinsi* are dominant over their male counterparts (Pinheiro, 2015; Stone, 2004); thus, males play very different social roles within their groups. In this study, we found that during the mating season males invested significantly more time in social behaviors than did females, as males actively pursue females and compete with other males for access to them (Stone, 2014). Time spent in social activities declines as soon as the mating season is over, and time spent in association with females decreases, while time in association with males increases. During the non-mating periods, but especially during lactation, when infants are present in the group, males spend most of their time at the periphery of their social group, interacting very little with females and juveniles (Stone, 2004; Zimbler-DeLorenzo & Stone, 2011).

Together, the data from our study suggest that female squirrel monkeys follow different feeding strategies when compared to males in their social group, particularly during the phases of gestation and lactation. Consistent with their life history and reproductive seasonality, it appears that female *Saimiri* behave as energy maximizers during most of the year, while males dedicate their time to other activities, such as pursuit of females during the short mating season (Schoener, 1971; Stone, 2014). Future studies focusing on the effect of reproductive status on female behavior in *Saimiri* species that show different socioecologies and variations in life history traits (e.g., length of lactation period; Mitchell, 1990) would be especially fruitful. Such field investigations would further illuminate how female *Saimiri* cope with the high costs of infant production and care.

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APPENDIX

APPENDIX 1. Individual Regression Tables For Variables Examined in This Study and Summarized in Table 1 (Results). T Statistics and *p*-Values are Given for Each Measured Variable

TABLE A1

Activity				
Variable	Coefficient	*p*-value	*t*-stat	Sig.
Forage				
Intercept	0.277	0	59.58	***
Ges	0.087	0.143	1.97	
Lac	0.201	0	33.97	***
Male	−0.040	0.004	−8.2	***
Male*Ges	0.008	0.412	−0.95	
Male*Lac	−0.050	0.574	0.63	
Eat				
Intercept	0.198	0.011	5.61	***
Ges	−0.009	0.781	−0.3	
Lac	0.024	0.68	0.45	
Male	0.053	0.231	1.5	
Male*Ges	−0.042	0.439	−0.89	
Male*Lac	−0.057	0.405	−0.97	
Rest				
Intercept	0.096	0	58.61	***
Ges	−0.067	0	−50.23	***
Lac	−0.074	0	−38	***
Male	0.070	0.01	5.83	***
Male*Ges	−0.009	0.867	−0.18	
Male*Lac	−0.038	0.029	−3.92	**
Travel				
Intercept	0.429	0.001	13.77	***
Ges	−0.008	0.924	−0.1	
Lac	−0.175	0.021	−4.46	**
Male	−0.124	0.033	−3.75	**
Male*Ges	0.111	0.338	1.14	
Male*Lac	0.121	0.057	3.01	*
Social				
Intercept	0.009	0.002	10.93	***
Ges	−0.009	0.002	−10.93	***
Lac	0.015	0.035	3.66	**
Male	0.048	0.004	7.95	***
Male*Ges	−0.043	0	−16.81	***
Male*Lac	−0.063	0.001	−12.24	***
Efficiency				
Foraging efficiency				
Intercept	0.592	0.007	6.57	***
Ges	0.001	0.992	0.01	
Lac	−0.026	0.887	−0.15	

(Continues)

TABLE A1 (Continued)

Activity				
Variable	**Coefficient**	**p-value**	**t-stat**	**Sig.**
Male	0.187	0.462	0.84	
Male*Ges	−0.101	0.834	−0.23	
Male*Lac	−0.178	0.61	−0.57	
Nearest neighbor				
Adult male				
Intercept	0.261	0.006	6.99	***
Ges	−0.144	0.035	−3.67	**
Lac	−0.183	0.009	−6.07	***
Male	−0.181	0.025	−4.2	**
Male*Ges	0.267	0.008	6.35	***
Male*Lac	0.340	0.006	9.4	***
Adult female				
Intercept	0.214	0.042	3.4	**
Ges	0.115	0.053	3.1	*
Lac	0.192	0.032	3.78	**
Male	0.118	0.157	1.88	
Male*Ges	−0.203	0.04	−3.49	**
Male*Lac	−0.314	0.018	−4.69	**
Juvenile				
Intercept	0.108	0.038	3.56	**
Ges	−0.059	0.243	−1.45	
Lac	−0.028	0.021	−4.42	**
Male	0.007	0.843	0.22	
Male*Ges	−0.027	0.612	−0.56	
Male*Lac	−0.032	0.015	−5.1	**
Alone				
Intercept	0.401	0	36.95	***
Ges	0.094	0.103	2.32	
Lac	−0.086	0.009	−6.15	***
Male	0.059	0.166	1.82	
Male*Ges	−0.055	0.549	−0.67	
Male*Lac	0.032	0.573	0.63	

Clustered Standard Errors (student-t, G-1 df).
***Highly significant (alpha <1%).
**Significant (alpha <5%).
*Marginally significant (alpha <10%).