

# The foraging ecology of male and female squirrel monkeys (*Saimiri collinsi*) in Eastern Amazonia, Brazil

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## Abstract

Sex differences in foraging behaviors of wild primates may be caused by sex differences in energetic requirements due to reproduction, body size or by differences in social behaviors. I investigated the feeding ecology of squirrel monkeys (*Saimiri collinsi*) in Eastern Amazonia during a 12 month period. Sex differences in behavior were investigated in relation to seasonal changes in food availability and reproductive events. The wet season corresponded to birth and lactation and the dry season corresponded to mating and gestation. Data were collected on adult males and females in two groups of squirrel monkeys using focal animal samples and intensive sampling of foraging bouts. Insects were the most common dietary item for both sexes (76% of feeding time), followed by the mesocarp of the palm *Attalea maripa* (28% of plant-feeding time). Sex differences in activity budgets and foraging success were significant throughout the year. Females ate more than males in the wet season. In the dry season, females foraged significantly more than adult males but did not eat more. Males were significantly more efficient at obtaining insects (0.72 captures/attempts *vs.* 0.35 for females). No differences existed in palm feeding rates. During fruit foraging, however, females stayed in closest proximity to other females and juveniles, whereas adult males foraged alone. These sex differences in foraging are best explained by differing reproductive investment of males and females, and by the female-dominant social structure of *Saimiri* troops.

## Resumo

### Ecologia alimentar de macacos-de-cheiro machos e fêmeas (*Saimiri collinsi*) na Amazonia Oriental, Brasil

Diferenças sexuais na ecologia alimentar de primatas podem ser causadas por diferenças em requerimentos energéticos referentes à reprodução, ao tamanho corporal ou a diferenças em comportamentos sociais de machos e fêmeas. Neste estudo, investiguei a ecologia alimentar de macacos-de-cheiro (*Saimiri collinsi*) na Amazônia Oriental durante um período de 12 meses. As diferenças comportamentais entre os sexos foram investigadas em relação a mudanças na disponibilidade de recursos alimentares e aos eventos reprodutivos. O comportamento de machos e fêmeas adultos de dois grupos sociais foi estudado pelo método animal-focal e em amostras intensivas de sessões de forrageio. O item mais comum na dieta de ambos os sexos foram insetos (76% do tempo

## Key words

Feeding, sex differences, reproduction, *Saimiri*.

## Palavras-chave

Alimentação, diferenças sexuais, reprodução, *Saimiri*.

de alimentação), seguido do mesocarpo da palmeira *Attalea maripa* (28% do tempo de alimentação em plantas). Diferenças sexuais no orçamento de atividades e no sucesso de forrageio foram evidentes ao longo do ano. No período chuvoso, as fêmeas passaram mais tempo se alimentando do que os machos. No período seco, as fêmeas forragearam mais que os machos, mas não passaram mais tempo comendo. Os machos foram mais eficientes na obtenção de insetos (0,72 capturas/tentativa *vs.* 0,35 para fêmeas). Não foram encontradas diferenças na taxa de ingestão de frutos de *A. maripa*. Porém, as fêmeas permaneceram predominantemente próximas de outras fêmeas e de juvenis durante o forrageio por frutos, enquanto os machos forragearam sozinhos por esse alimento. Tais diferenças na ecologia alimentar dos sexos podem ser atribuídas ao diferente investimento reprodutivo de machos e fêmeas e à estrutura social de *Saimiri collinsi*, onde as fêmeas são dominantes aos machos.

## INTRODUCTION

Sex differences in foraging ecology have been observed in primates and several other mammals. When present, these differences are apparent in dietary choices, time devoted to foraging, time spent resting, foraging efficiency and use of different foraging substrates and techniques (Fragaszy 1986; Rose 1994; Vasey 2005). For example, adult male capuchins (*Cebus olivaceus*) have been found to spend less time foraging and more time resting compared to females (Fragaszy 1990). In addition, *C. capucinus* males spend more time foraging near the ground (Rose 1994). Proposed explanations for these differences include factors such as sex differences in body mass/structure, female reproductive energetic demands, and avoidance of competition/dominance hierarchies between the sexes. In sexually dimorphic species, differences in body size between males and females could affect the amount of food consumed, as well as the type of food; e.g. those requiring more strength to process may be less available to females but those located on smaller substrates may be less available to males (Agostini & Visalberghi 2005). Unlike males, female primates must sustain the high energetic costs of gestation, lactation and infant care/transport. In particular, lactation is considered the most costly reproductive activity for female primates (Pond 1977; Altmann 1980; Weiner 1989), with lactation often coinciding with peak fruit availability in the habitat (Boinski 1988; Vasey 2005), and female food intake increasing during lactation (Tarnaud 2006). The intersexual differences in reproductive investment thus may account for sex differences in foraging ecology, such as time devoted to

foraging versus other activities (Gautier-Hion 1980; Hemingway 1999; Vasey, 2005). Competition over food is a third factor contributing to sex differences in foraging behavior. When males are dominant to females, the latter often spend more time procuring food and avoiding adult males while foraging. Conversely, in female-dominated primate species, females often have priority of access to food resources (Mitchell 1990).

Squirrel monkeys (genus *Saimiri*) are small (650-1000g; Smith & Jungers 1997), frugivorous-insectivorous neotropical primates (Janson & Boinski 1992) that spend up to 75% of their day foraging (Terborgh 1983; Stone 2007a) and live in large social groups (25-75 individuals; Boinski 1999). Sex differences in foraging have been reported in at least one species of squirrel monkey, where females foraged and fed more frequently than males, while males spent more time on anti-predator vigilance (*S. oerstedii*, Boinski 1988). During the non-breeding season, squirrel monkey males are approximately 25-30% heavier than adult females (Stone unpublished trapping data). Males also show weight gain (85 to 222 g; Dumond & Hutchison 1967) preceding and during the short mating season, which produces a “fattened” appearance in the upper arms, shoulders and torso. This occurs due to fat deposition and water retention, and is not related to increased food consumption by males (Mendoza *et al.* 1978; Stone 2004). In addition, squirrel monkeys are the most seasonal breeders of all neotropical primates (Di Bitteti & Janson 2000), with a well-defined birth season (sometimes as short as two weeks; Boinski 1986; Stone 2006). Due to their dietary diversity, almost continuous

foraging activity, seasonal breeding and high reproductive costs, squirrel monkeys are a good model to investigate the role of intrinsic and extrinsic factors on sex differences in foraging behaviors in primates.

I investigated the feeding ecology of squirrel monkeys (*S. collinsi*) in a forest in Eastern Amazonia during a 12 month period. Sex differences in behavior were investigated in relation to seasonal changes in food availability and in reproductive events. In this population of squirrel monkeys, mating occurs during July and August, and births occur in December and January of each year (Stone 2006). In addition, females are dominant to males; associations between males and females are weak because males remain at the periphery of troops during most of the year (Zimble-DeLorenzo & Stone 2011). Here I test the following (non-mutually exclusive) hypotheses: 1) due to differences in body size (sexual dimorphism hypothesis), males will spend more time feeding and foraging, will be more efficient foragers and have access to larger foraging substrates and, possibly, food items; 2) during periods of gestation and lactation (reproductive energetic hypothesis), females will employ foraging strategies that

Table 1. Predictions made in this study, associated with three hypotheses explaining sex-based differences in foraging ecology of squirrel monkeys (*Saimiri collinsi*).

Variable	H1: Sexual dimorphism	H2: Reproductive energetics	H3: Dominance and competition
Time feeding	Males higher	Females higher	Females higher
Time resting	No difference	Females lower	No difference
Foraging efficiency	Males higher	Females higher	Females higher
Foraging substrates	Males on larger	No difference	Spatial separation

counteract their reproductive investment, and thus intersexual foraging differences will be evident; 3) due to female-dominance (dominance and competition hypothesis), females will consume more energy-rich food items, compared to males. In testing these predictions, I compare the following variables for males and females: a) time spent foraging and resting, b) foraging efficiency and intake rates for selected food items, c) amount of time spent consuming different food types (e.g. plants *vs.* prey); d) use of foraging substrates and microhabitats. Table 1 illustrates the predictions made in this study, for each of the hypotheses.

## METHODS

### 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 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). Fruit availability, including that of the most common fruit in the monkeys' diet (*Attalea maripa*, Araceae), is highest during the wet season (Stone 2007a).

### Study population

I monitored this population of squirrel monkeys from 2000-2004. Systematic data come primarily from

two habituated groups of monkeys, group A (44 individuals) and group B (50 individuals). The approximate group composition is: 10 adult males, 16 adult females, 15-20 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. During the study, 13 adults were reliably recognized in group A (6 males and 7 females), either by physical characteristics or by having been marked with Nyanzol fur dye (Albanyl Dyestuffs International).

## Data collection

Behavioral data were collected during 1,102 observation hours. Most of the data presented here are from A troop (770 hours) and only behavioral samples from this troop are used for statistical analyses. Three methods were employed to sample behavior: focal animal samples (FAS); foraging focal samples (FFS); and *ad libitum* observations. I conducted 5 to 10-minute ( $7.9 \pm 1.9$ ) focal animal samples (Altmann 1974), with instantaneous observations taken at 1-minute intervals. Since only 13 of 44 troop members were recognized, behavioral samples were classed by sex class rather than by individual subjects. At each 1-min interval, the following variables were recorded: activity of the focal animal (eat, forage, travel, rest and social); party size: number of individuals within a 5 m radius (for adult females, this did not include their neonates).

In addition, 2 to 5-minute foraging focal samples (Mitchell 1990; Peres 1992; Wrangham *et al.* 1993) were used to quantify foraging success on insects and fruits. When a subject was foraging for insects, I continuously recorded all foraging attempts and captures that occurred within 1-minute periods, with note of prey size (small:  $\leq 1$  cm, medium: 1–4 cm; large:  $> 4$  cm) and taxon whenever possible. At the initiation of each minute, I noted the height above ground (visually estimated in meters) and party size. Similar data on fruit feeding rates were obtained through fruit focal samples. Variables noted in 1-minute feeding periods included: the number of fruits consumed, in the case of fruits consumed in natural units, or the approximate proportion of fruit consumed (e.g. one quarter, one eighth, five bites), and party size. Fruits most often consumed by the monkeys were those of the palm *Attalea maripa* (Stone 2007a) and constitute the majority of the fruit focal samples (63%). Observations of rare

feeding events, such as on vertebrates and eggs, as well as reactions to predators, were observed opportunistically. FFS were used to determine the foraging success (ratio of captures to attempts per minute) in the case of animal prey, and of fruit intake rates, in the case of fruit. Because food-specific time-budgets alone cannot reliably estimate amount consumed, FFS also were used to estimate the quantity of food consumed. Daily intake of fruit for each sex class was estimated from: the number or proportion of fruits consumed each minute, time spent foraging and the mean pulp weight of individual fruits (Altmann 1998). Aggressive behaviors and the context in which they occurred were noted *ad libitum*. I defined an agonistic interaction in a feeding context when I could see clearly that a food item was being contested, or if the interaction occurred in the crown of or under a fruiting tree. During each instance, I noted the age-sex class of the initiator, recipient and winner, when possible.

## Data analyses

Instantaneous observations within each focal animal sample are not statistically independent. To account for this, we treated each focal sample, and not each individual observation within a sample, as a data point. Categorical variables, such as activity, were converted to quantitative variables as the proportion of intervals an animal was engaged in that activity and numerical variables such as foraging success were averaged within a sample (Stone 2004). Samples were pooled by sex class. T-tests were performed to examine the effects of sex on behavioral variables within each season. Proportional data were arcsine-transformed. Chi-squared analyses were used to test for possible differences in the diets of males and females. All tests are two-tailed and data are reported as the mean  $\pm$  SE of untransformed data.

## RESULTS

### Activity budgets

Activity budgets for both seasons and sexes are shown in Figure 1. In the wet season (corresponding to birth and lactation), females spent more time eating and foraging than adult males, though this difference was

only significant for time spent eating ( $t_{67} = 2.82$ ;  $p = 0.03$ ). In the dry season (mating and gestation), females spent more time foraging than did adult males ( $t_{68} = 2.99$ ;  $p = 0.04$ ). No sex differences were found in time spent resting, in either season (wet:  $t_{67} = -1.78$ ;  $p = 0.07$ ; dry:  $t_{68} = -0.80$ ;  $p = 0.42$ ).

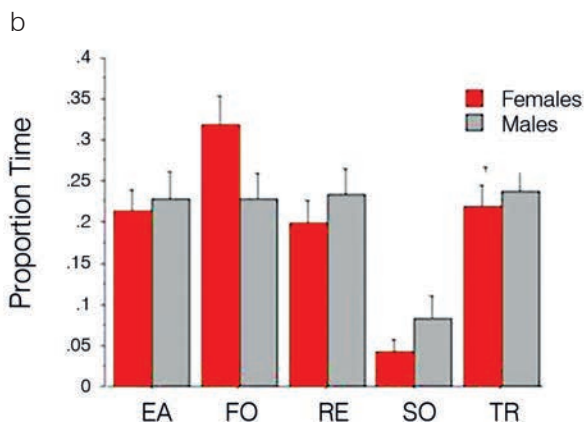
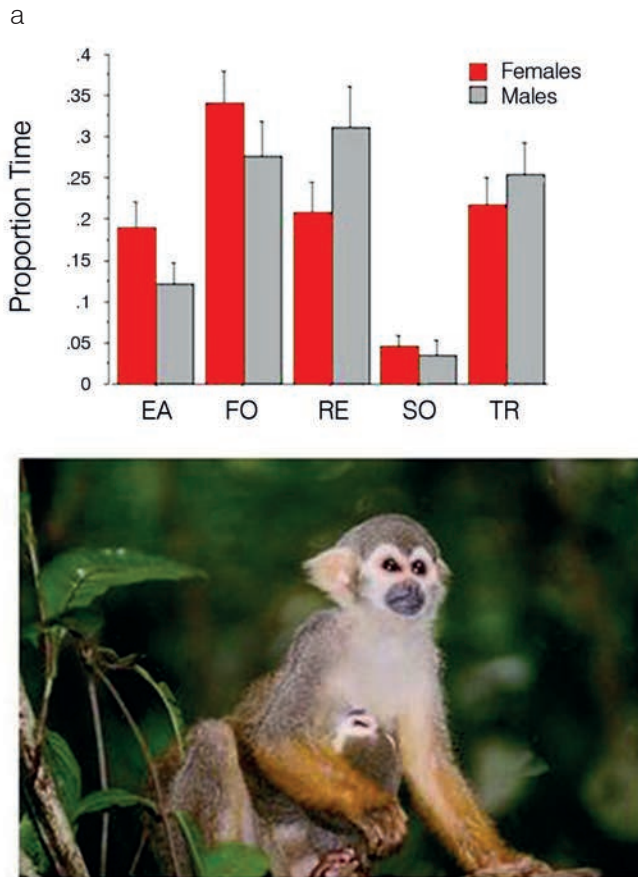


Figure 1. Activity budgets (mean  $\pm$  SE) for adult males and adult female *Saimiri collinsi*. a) Wet season; b) Dry season. EA=Eat, FO=Forage, TR=Travel, RE=Rest, SO=Social.

Table 2. Dietary composition for male and female *Saimiri collinsi* in this study (% feeding observations)

Food type	Wet season		Dry season	
	F	M	F	M
Fruits and flowers	53%	40%	21%	22%
Prey	46%	60%	79%	78%

## Diet

Fruits, flowers and insects were present in the squirrel monkey diet throughout the year, with insects accounting for 79% ( $n=983$  eat/forage observations) of annual feeding and foraging time. Squirrel monkeys in troop A consumed a total of 55 plant species. Adult males were observed feeding on 26 fruit species, while adult females ate 38 species. When available, *A. maripa* fruit comprised an average of 28% ( $n=1,062$  fruit feeding observations) of the monkeys' plant feeding time, and surpassed 50% in some months. These fruits were covered by a thin, fibrous husk that could be removed when ripe by *Saimiri*, and fruits were often consumed near the ground, especially by juveniles. Each fruit contained an average of  $11 \pm 5$  g of fleshy, yellow pulp, surrounding a hard woody endocarp. Monkeys were never observed to consume the seeds of these palm fruits. Orthopterans were the most frequent prey exploited by both sexes. No prey types were consumed exclusively by a particular sex. Most prey (65%) captured during insect FFS were small ( $< 1$  cm) and weighed under 1 g, and 95% were under 4 cm.

Both females and males consumed more arthropods in the dry season, with females consuming more plant-based items than did males during the wet season (Table 2).

## Foraging efficiency and intake rates

I determined the ratio of feeding to foraging observations from FAS for adult males and adult females, to derive a measure of foraging efficiency. In the wet season, no sex differences were found in foraging efficiency ( $t_{56} = 1.11$ ;  $p=0.27$ ). Similar results were found for the dry season ( $t_{57} = -0.91$ ;  $p=0.36$ ). Overall, the average foraging success for prey in the wet season was  $0.44 \pm 0.03$  (captures/attempts per minute). Mean foraging success did not vary significantly by sex class ( $t_{51} = -1.07$ ;  $p=0.28$ ). In the dry season, average foraging success increased to  $0.56 \pm 0.03$ , and adult males were more successful than adult females ( $0.72$  captures/attempts *vs.*  $0.35$  for females;  $t_{71} = -2.46$ ;  $p=0.01$ ). No sex differences existed in palm fruit (*Attalea maripa*) intake rates (g/min) ( $t_{73} = 0.22$ ;  $p=0.82$ ). Analyses were combined for wet and dry seasons, as most fruit intake occurred in the wet season.



Figure 2. Adult female *Saimiri collinsi* foraging on palm leaves.

### Use of foraging substrates

When foraging for prey, females foraged more frequently than males on palm fronds (Figure 2; Table 3). Males used lower substrates (including the ground) when prey foraging more than did adult females (males: 40 % of foraging observations; females: 22% of foraging observations).

### Association patterns and agonism

Foraging party size for both males and females are shown in Figure 3. Females had significantly more neighbors when foraging on fruits than did adult males ( $t_{284}=5.47$ ;  $p<0.001$ ). The rate of resource-based agonism was 0.004 events/hour/individual. Nine-two percent of resource-based agonism was over access to fruits ( $n=132$ ), and *A. maripa* accounted for 71% of fruit-related conflicts. Females won 74% of all conflicts against adult males ( $n= 33$  male-female conflicts). Parties of females

Table 3. Foraging substrates utilized by male and female *Saimiri collinsi*, while prey foraging (% feeding + foraging observations)

Foraging substrate	F	M
Live foliage	42%	50%
Dead foliage	20%	28%
Palm foliage	30%	9%
Other	8%	13%

and juveniles often chased adult males off a tree when resting or foraging ( $n= 34$  observations). The most pronounced example of direct resource-based aggression occurred in the dry season, when an adult male acquired a tinamou egg on the forest floor. A pregnant adult female soon discovered a second egg at the same location. The female moved off the floor and began to consume the egg, but was approached by a second adult male that attempted to steal it. This attracted several adults, and resulted in a chase involving at least six adults. The outcome of the interaction was unknown.

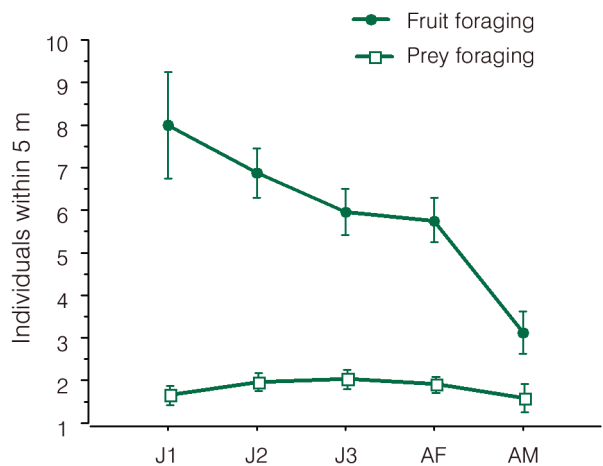


Figure 3. Average number of individuals within a 5-m radius of focal animal (mean  $\pm$  SE) for *Saimiri collinsi* age-sex classes when foraging on prey and fruit resources (Stone, 2007b).

## DISCUSSION

Two frequently cited evolutionary explanations for sex differences in foraging in primates are that these are consequences of sexual dimorphism in body size and structure, or of the costs of pregnancy and lactation (Clutton-Brock 1977). In fact, sex differences can often override age differences in foraging (Agostini & Visalberghi 2005). In this study, adult females for-

aged and ate more frequently than adult males, but only during the birth and lactation season. A different strategy was found by MacCabe & Fedigan (2007) for lactating *C. capucinus*: no additional time was spent on foraging activities, but ingestion rates of prey and fruit were faster. Contrary to predictions, males and females in this study did not vary in time resting, even when

infants were present in the group. In the dry season, adult males were more efficient in foraging for prey, possibly because females were pregnant and heavier at that time. However, the amount of *A. maripa* palm fruit (a resource rich in sugar and fat) consumed did not vary between the sexes. No sex difference existed in time spent feeding on fruit versus on prey in the dry season. These results suggest that females do not necessarily forage on higher-quality items compared to males throughout the year. However, they forage on more fruits and flowers during the birth and lactation months, as well as consume a greater variety of fruit types. Such dietary differences are also present in *C. nigrurus* (Agostini & Visalberghi 2005). On the other hand, Herrera & Heymann (2004) found that female titi monkeys (*Callicebus cupreus*) increase the proportion of insects in their diet during lactation. Taken together, the data from this study suggest that females follow different foraging strategies than males when reproductive costs are highest. Thus, females behave as feeding-time maximizers, while males may devote more time to other activities, which is especially important in the mating season (Schoener 1971). During mating season, males spend less time foraging and eating (Stone 2014).

In support of the sexual dimorphism hypothesis, adult males used the ground more frequently than did females, whereas females foraged on palm foliage more often than did males (Fragaszy 1986). This suggests that body size affects the use of foraging supports. However, this explanation is unlikely, since juveniles (which are lighter than adult females) use the ground even more frequently than do adult males (Stone 2007b). A more plausible explanation is that females forage on palms because they offer greater concealment from predators, which is especially important when carrying infants. Infant mortality due to predation by raptors can be as high as 50% in squirrel monkey species (Boinski 1987).

Finally, a third factor, female dominance, might lead to sex differences in foraging in *S. collinsi*. Because direct competition over food items was generally low, it was not apparent that females won most contests. However, the marked spatial separation in the sexes seen, particularly when foraging on *A. maripa* fruit, suggests that females may have priority of access to clumped resources. Each infructescence bore several hundred to over 1,000 fruits (Silvius, 2002;

Fragoso *et al.* 2003). Consequently, a large portion of the *Saimiri* troop (40-50% of individuals) could simultaneously forage on fruits from the same tree, particularly when ripe fruit had fallen to the ground. However, age-sex classes separated their foraging in time and space despite the large number of animals that fed in a tree. Adult females (particularly those carrying infants) and juveniles arrived first at a tree on 82% of visits (Stone 2004). Adult males rarely were seen to forage with the core of the group, usually appearing in a second “wave” after the females and juveniles had left. Particularly if juveniles returned, adult males would move temporarily off the infructescence into the foliage. Quantitative results support these observations. Adult males had four fewer neighbors, on average, than other age-sex classes while foraging on palm fruits (Stone 2004). We also know that adult males spend most of their time alone (Stone 2007b, 2014).

Reproductive energetics offer the best explanation for intersexual foraging differences observed in this population of squirrel monkeys, followed by spatial structure of the groups (females in the core, males on the periphery). An interesting follow-up to this study would be to compare the foraging ecology of female squirrel monkeys across different reproductive phases in order to test for differences. This study is currently underway (Ruivo and Stone, in review). Compared to costs for males, reproduction is expensive for all female mammals, but particularly expensive for female squirrel monkeys, as infants require a high allocation of maternal resources through lactation, transport and protection from predators. Squirrel monkeys females are subject to high maternal costs associated with relatively large neonates that have 60% of adult brain mass at birth (Elias 1977; Garber & Leigh 1997). Rapid somatic and brain growth continues during the first three months of life (Kaplan 1979; Manocha 1979). By six months, squirrel monkey infants weigh approximately 50%-69% of maternal body weight (Kaplan 1979; Scollay 1980). The brains of neonates are about 61% complete at birth (Elias 1977) and post-natal brain growth in *Saimiri* infants also occurs extremely rapidly (Manocha 1979; Hartwig 1995; Garber & Leigh 1997). Body growth rates are reduced around six months of age (Garber & Leigh 1997), which corresponds to the onset of weaning in *S. collinsi* (Stone 2006). Due to the high prenatal costs

incurred by squirrel monkey females, it is perhaps surprising that more sex differences in foraging were not *also* seen during pregnancy (dry season), aside for an increase in time spent foraging. Gestation lengths in *Saimiri* (5 months; Mitchell 1990) are nearly a month longer than those of *Aotus* and are similar to those of the larger *Callicebus* and *Cebus* (Hartwig 1996). In addition, despite the production of a single infant, estimated prenatal growth rates in *Saimiri* are high compared to the twin-producing callitrichines (Ross 1991, Hartwig 1996; Garber & Leigh 1997; Leigh 2004). It is possible that the high degree of insectivory required by both males and females in the dry season overrides most sex differences during this period of low-food abundance. Lactating *C. capucinus* females (which also produce large infants) ingest more energy per hour compared to pregnant females (MacCabe & Fedigan 2007). In conclusion, the present study shows that intersex differences in foraging of squirrel monkeys are most pronounced when females are lactating. The pattern of female dominance in this particular species (*S. collinsi*), reinforces these sex differences.

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