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Synchronization of weaning time with peak fruit availability in squirrel monkeys (*Saimiri collinsi*) living in Amazonian Brazil

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Abstract

Many mammals coincide their reproductive activities with factors such as ambient temperature, rainfall, and food availability. In primates that invest immediate food intake into reproduction, the periods of maximum fruit production often coincide with the peak of lactation (to maximize maternal survival) or the occurrence of weaning (to maximize infant survival). This study investigates the relationship between reproductive periods and the availability of ripe fruit in the habitat of a population of wild squirrel monkeys (*Saimiri collinsi*) in Amazonian Brazil. We combine data from several years (2002–2003; 2011–2015) during which we followed the monkeys and quantified the occurrence of matings, gestations, births, and the number of lactating females. We also collected rainfall and plant phenological data for 24 months. Our results confirm that reproductive events are highly seasonal in *S. collinsi*. The period of weaning corresponded to the peak in the abundance of ripe fruits consumed by the monkeys. This indicates that the period of infant nutritional independence is optimally timed to coincide with periods of greater food production in this habitat. We suggest that seasonal breeding in these primates does not necessarily reduce maternal energetic stress, but likely improves infant survivorship.

KEYWORDS

life history, seasonality, squirrel monkey, weaning

1 | INTRODUCTION

Reproductive seasonality, defined as the “temporal clustering of reproductive activity, whether discrete seasons or seasonal peaks” (Lindburg, 1987, p. 167), is a pattern observed in several mammalian taxa (Bronson & Heideman, 1994; Durant, Hall, Cisneros, Hayland, & Willig, 2013; Heideman, Deoraj, & Bronson, 1992; Kenagy & Bartholomew, 1985; Ramos Pereira, Marques, & Palmeirim, 2010; Read, 1990; Van Belle, Fernandez-Duque & Di Fiore, 2016). Environmental cues such as temperature, rainfall, and photoperiod may act as proximate factors controlling seasonal breeding (Blanco, 2011; Fernandez-Duque, Rotundo, & Ramirez-Llorens, 2002; Trevino, 2007; Wolcott, Reitz, & Weckerly, 2015). This life history strategy likely evolved to maximize reproductive success by mitigating the physiological and ecological costs of reproduction, particularly for females

(Gittleman & Thompson, 1988; Koivula, Kosela, Mappes, & Oksanen, 2003; Rocha, Ribeiro, & Marinho-Filho, 2017) who invest more heavily in each reproductive event (Trivers, 1972). Thus, reproducing seasonally may be an important female adaptation, allowing for the timing of especially demanding reproductive phases to coincide with the most favorable ecological and social conditions (Lee, 1996; Tinsley Johnson, Snyder-Mackler, Lu, Bergman, & Beehner, 2018).

Among primates, strict seasonal breeding is common in most lemurs (Rassmussen, 1985; Tecot, Gerber, King, Verdolin, & Wright, 2013; Vasey, 2005; Wright, 1999). For example, Tecot (2010) demonstrated that for the seasonally reproducing red-bellied lemur (*Eulemur fulvus*) the best reproductive strategy was to coincide not lactation but the weaning phase with maximum fruit availability (see also Crockett & Rudran, 1987; Wright, 1999). Infant mortality in the same species increased when the peak ripe fruit season coincided with gestation, rather

than with weaning (Overdorff, Merenlender, Talata, Telo, & Forward, 1999).

Folivorous Asian primates often behave as capital breeders (*sensu* Jonsson, 1997; Stearns, 1992; Stephens, Houston, Harding, Boyd, & McNamara, 2014; Williams et al., 2017): conception occurs during periods of high food abundance, and therefore these primates can rely on stored energy reserves during later, more costly reproductive phases such as lactation (Borries, Suarez, Terranova, & Koenig, 2005; Jin et al., 2009; Koenig, Borries, Chalise, & Winkler, 1997; see also Ogotu, Piepho, & Dublinc, 2014 for a similar pattern in African ungulates). In contrast, Neotropical primates living in predictably seasonal environments usually behave as income breeders. That is, they use immediate energy intake to pay for reproduction (Souza-Alves, Caselli, Gestich, & Nagy-Reis, 2019); their most expensive reproductive phase (gestation or lactation; Fernandez-Duque et al., 2002; Lee, 1987) occurs during the period of maximal rainfall and concurrent food and energy intake. More specifically, in a meta-analysis of seasonally breeding Neotropical primates, Di Bitteti and Janson (2000) argue that the income breeding strategy can be further subdivided into two strategies: (a) coincide weaning with the period of highest food abundance, thus maximizing infant survival (also called “income-I breeders” by Janson & Verdolin, 2005), or (b) time birth and lactation to the period of maximum food availability, thus reducing energetic and nutritional stress on females and maximizing maternal survival (also called “income II breeders” by Janson & Verdolin, 2005).

Squirrel monkeys (genus *Saimiri*) live in large (25–75 individuals; Stone, 2017) multi-male/multi-female groups, and are distributed widely across the Amazon basin with disjunct populations occurring in Central America (Boinski, 1999; Lynch Alfaro et al., 2015). Currently, eight species of squirrel monkeys are recognized (seven in South America and one in Central America; Lynch Alfaro et al., 2015). Habitats used by squirrel monkeys in South America include primary and secondary upland (*terra firme*) forests and flooded (*várzea*) forests (Paim, Chapman, Queiroz, & Paglia, 2017; Stone, 2017). Their diet is composed of ripe fruits, flowers and invertebrates, with the consumption of invertebrates increasing in periods of lower fruit abundance (Lima & Ferrari, 2003; Paim et al., 2017; Stone, 2007; Terborgh, 1983).

Squirrel monkeys show the most pronounced seasonal breeding pattern of any Neotropical primate (Di Bitteti & Janson, 2000). Social groups living within a geographic area and at similar latitudes experience the same 2-month mating season when females are in estrus, followed by a 5-month gestation period and 1–2 months of a birth period when neonates are present (Boinski, 1987; Mitchell, 1990; Stone, 2006). Because of this, squirrel monkeys present a good model to investigate proximate and ultimate factors involved in seasonal reproduction in primates (e.g., Trevino, 2007). In addition, squirrel monkeys show a high degree of maternal investment (Garber & Leigh, 1997; Tardif, 1994), producing large, well-developed neonates (Elias, 1977; Kaack, Walker, & Brizze, 1979; Stone, unpublished trapping data). Lactating females must thus feed, protect and transport expensive infants that continue to grow rapidly within the first 3 months of life, both somatically and

neurologically (Kaplan, 1979; Leigh, 2004; Manocha, 1979). Not surprisingly, squirrel monkey mothers produce milk that is high in energy and fat (Milligan, Gibson, Williams, & Power, 2008).

The purpose of the present study was to investigate the relationship between reproductive periods (mating, gestation, birth, lactation, and weaning) in a population of wild squirrel monkeys and resource availability in their habitat. To do so, we use a data set spanning several years (integrating plant phenology records, field observations and capture-monitor information) from wild *Saimiri collinsi* living in Eastern Amazonia. We predict that the monkeys will follow one of two adaptive strategies: (a) give birth during the period of highest food availability, to minimize female reproductive stress associated with lactation and infant support; (b) wean their infants during the period of greatest food abundance, to enhance the chance of infant survival.

2 | METHODS

All parts of this study complied with protocols approved by the Institutional Animal Care and Use Committee of our respective institutions, by ICMBio in Brazil (permit number 32242-3) and by SisGen in Brazil (protocol numbers AA426B5 and AE85BAE). All procedures reported in this manuscript adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

2.1 | Study area

Data were collected near the community of Ananim, municipality of Peixe-Boi (01°11'S and 47°19'W), 150 km east of Belém, Pará state, Brazil. Mean monthly temperatures range from 26.9°C to 28.8°C (Stone, 2004). The 800-hectare site consists of privately owned properties that include upland primary forest and adjacent secondary forest. We note the presence of fruiting tree species such as *Symphonia globulifera*, *Tapiriria guiananensis*, *Byrsonima amazonica*, *Nectandra* spp. and *Inga alba*, which are abundant and frequently consumed by the monkeys (Stone, 2004). In addition to squirrel monkeys, other nonhuman primates at the site include tamarins (*Saguinus ursulus*), night monkeys (*Aotus infulatus*), and howlers (*Alouatta belzebul*).

2.2 | Study population

We collected data on two social groups of squirrel monkeys: troop A (44 individuals) and troop B (50 individuals). Both groups were well-habituated, as they had been studied from 2002 to 2015 (for approximately 6 years during this period, minimum of 3 months per year), as part of a long-term monitoring project. Group A and Group B ranged in 120 and 150 ha, respectively, with a range overlap of 26 ha; they did not defend territories. The approximate composition of each group was 9–10 adult males; 15–20 adult females; 20 juveniles and infants. Due to the large size of the groups, most

animals were not individually recognizable over the entire study. However, in 2002 and 2003, seven adult females (Group A) and four adult females (Group B) were identified either by having been marked with Nyanzol fur dye (Albanil Dyestuffs International) or by natural characteristics. From 2012–2014, capture and marking was undertaken in this population (Stone, Castro, Monteiro, Ruivo, & Siva Junior, 2015), such that from 2012 to 2015 Group A contained 4 collared adult females and Group B contained 11 collared adult females.

2.3 | Environmental variables and plant phenology

Daily precipitation measurements were taken using a rain gauge during 2 separate years (Year 1: March 2002–February 2003 and Year 2: July 2014–June 2015). We collected monthly plant phenology data during the same 12-month periods, by monitoring 136 and 107 fruiting trees, respectively. These trees represented 36 species within both groups' home range. We sampled only the species (two to three randomly selected individuals per species, located at least 50 m apart) that the squirrel monkeys were known to consume rather than overall habitat productivity, to allow adequate sampling of important species in the monkeys' diet (Doran et al., 2002; Norconk, 1996; Stone, 2007). During later months, additional species were added to the sample if the monkeys were observed feeding on a new species for 5 days or more. During each monthly check, we recorded the presence or absence of flowers, unripe fruit and ripe fruit on trees. To obtain an estimate of the density and abundance of fruiting *Attalea maripa* (Araceae) trees, which are a critical part of both troops' diet (Stone, 2007), the phenological status of an additional 35 mature *A. maripa* trees was recorded monthly along a 0.4 ha transect (400 m by 10 m).

2.4 | Behavioral observations and trapping data

During any given year throughout the study period, both groups were followed for a minimum of 3 months and a maximum of 12 months. The most intensive periods of data collection occurred from March 2002–February 2003 (A. I. S.) and from July 2014–June 2015 (L. V. P. R.), which allowed us to obtain accurate records on the squirrel monkeys' reproductive cycle. Groups were followed for at least 10 days each month (17 ± 4.5 days) from 6:00 to 16:00 hr. During the remaining days, a field assistant followed the groups to note any new fruit species consumed by the monkeys and birth dates.

The groups were followed for approximately 1,300 hr (Group A) and 850 hr (Group B). We used focal animal samples and ad libitum observations (Altmann, 1974) to collect data pertaining to activity budgets, diet and reproductive or social behaviors (e.g., copulations, nursing bouts). Because the groups were intensely followed, we also were able to distinguish reproductive phases, such as the mating season in which males get visibly fattened (DuMond & Hutchison, 1967; Stone, 2014), and determine the number of pregnant and lactating females at any given time. Daily maximum counts of pregnant and lactating females were obtained when multiple females

were in close proximity or crossing canopy gaps, whether they were marked or not. After approximately 6 weeks of gestation, female squirrel monkeys show a visibly distended abdomen. Lactating females were identified by nursing behavior and/or by dark, distended nipples. We defined the start of weaning as the first month that there was a decrease in the number of nursing females and the end of weaning as the month when nursing bouts were no longer observed.

In addition to observational data, the trapping that occurred in November/December 2012, 2013, and 2014 allowed us to confirm whether females were nonreproductive, pregnant, or lactating. Table 1 summarizes the types of data collected each year during the study period.

2.5 | Data analyses

We calculated monthly rainfall (in mm) separately for both Year 1 and Year 2. For each month during those years, we report fruit abundance as (a) the percent of individual trees and (b) percent of species producing ripe fruit. The absolute number of trees and species monitored differed monthly because some additional trees were added later to the sample. We used the Spearman rank correlation coefficient to measure the strength and direction of the relationship between monthly rainfall and fruit availability. Our goal was to identify the lag time (if any) between the peak of rainfall and the peak of fruit availability. To do so, we found the highest correlation between these variables to compute the time between the two peaks. Statistical significance was set at $p = .05$.

Observational and trapping data on the squirrel monkeys were examined to determine the annual reproductive cycle of this population. We then determined the peak birth season and the length of the weaning period based on the number of births and the number of lactating females recorded. Finally, we used the monthly rate of change in number of lactating females to determine whether the

TABLE 1 Summary of types of ecological and behavioral data collected during the study period at the Vila Ananim study site, Eastern Amazonia, Brazil

Year	Rainfall data	Plant phenology data	Behavioral and ecological data on squirrel monkeys	Capture data for squirrel monkeys
2002	X	X	X	
2003	X	X	X	
2011			X	
2012			X	X
2013			X	X
2014	X	X	X	X
2015	X	X	X	

Note: See text for specific months sampled during each year.

peak birth/lactation or the peak weaning period overlapped with periods of greatest abundance of ripe fruit in the monkeys' habitat.

3 | RESULTS

3.1 | Resource availability

The total annual rainfall for Years 1 and 2 at our study site was 2,535 mm and 2,318 mm, respectively (average: 2,426.5 mm; $n = 24$ months). We found that the year at Ananim can be divided into two seasons: the rainy season (January through June; average total rainfall: 2,207 mm) and the dry season (July through December; average total rainfall: 219 mm).

The abundance of fruit was highest during the rainy season, and fruiting peaks during both years occurred approximately 2 months after the peak of rainfall. This was true both when we examined percent trees fruiting, Spearman's correlation coefficient: $r(11) = .74$, $p = .005$ in Y1; $r(11) = .50$, $p = .09$ in Y2, and percent species fruiting, $r(11) = .93$, $p = .0005$ in Y2; $r(11) = .62$, $p = .03$ in Y2. As indicated in Figure 1, the highest availability of ripe fruit at the site occurs from

April to May and the lowest from October to December. In Year 1, fruit diversity was highest in April (76% of species sampled were fruiting; $n = 25$ species sampled) and lowest in December (25% of species; $n = 36$ species). Ripe fruit of the palm *A. maripa* was available during most of the rainy season, with a peak in April (23 fruiting trees/ha) but declined sharply in the dry season, reaching a low in October and November (<5 fruiting trees/ha). In Year 2, fruit diversity was highest in June (59%; $n = 36$ species sampled) and lowest in January (10%; $n = 36$ species).

3.2 | Reproductive events

The mating season in this population occurs from the end of June to the end of August (approximately 8 weeks). Of the 49 copulations observed during the study period, 45 occurred during this 8-week period. In addition, male fattening in this population begins at the end of June and lasts until early September (see also Stone, 2014). Consortships (spatial association of <3 m between a specific male and a female, accompanied by males following females) also were only observed during this period, with males remaining at the periphery of the

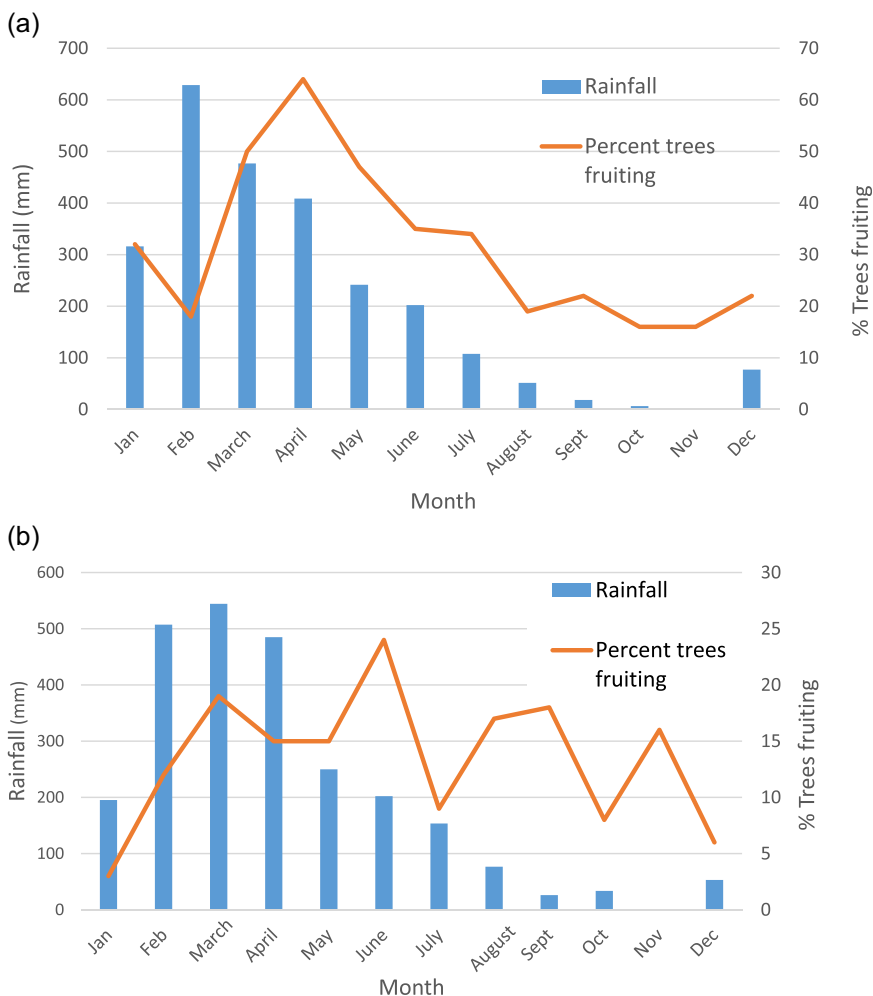


FIGURE 1 Monthly rainfall and ripe fruit availability in Vila Ananim study area. (a) Year 1: 2012–2013 and (b) Year 2: 2014–2015

group during other times of the year. Gestation lasted approximately 5 months. In our population, females were visibly pregnant starting in September, with the peak number of pregnant females seen in November (Figure 2). Thus, gestation took place at the height of the dry season, also the period of lowest fruit availability. Births occurred over an 8-week period in late December to February (Figure 3). In Year 1, 12 infants were born on the night of January 1 and 3 more infants were born in Group A at the end of February. In Year 2, 90% of births ($n = 20$) across both study groups occurred in December and January. The first births for Group A and B occurred on December 25 ($n = 4$) and December 26 ($n = 5$), respectively. By late January, Group A contained at least 9 mother–infant pairs and Group B contained at least 9 mother–infant pairs (two more infants were born in February in Group B). These numbers represent a minimum count, based primarily on the individually recognized females.

Motor development of infants occurred rapidly. Infants were carried continuously during the first 2 weeks, usually by the mother. At 4 weeks of age, infants were able to locomote independently for short distances and crossed short canopy gaps at 6 weeks of age. By the time infants were 5 months old, they were carried mostly during periods of rapid travel; by 6 months of age, observations of carrying

were rare (<10 observations per month). Weaning began when the infants were approximately 4 months old (April–May; Figure 3), with an increased occurrence of weaning conflicts in which the mother bit or grasped the infant's head pelage to terminate the nursing bout (Stone, 2004). In Year 1, the month of highest fruit availability coincided with the first decrease in the number of lactating females, or early weaning (25%, Figure 3a). In Year 2, the fruiting peak coincided with the highest decrease in number of lactating females or later weaning (67%, Figure 3b). Most infants were fully weaned by 6 months, though a few infants continued to nurse intermittently until 8 months of age ($n = 1$ seen in Year 1 and $n = 2$ seen in Year 2; both study groups combined).

4 | DISCUSSION

Our study examined the relationships among the annual pattern of rainfall, fruit availability and reproductive seasonality in a population of squirrel monkeys (*S. collinsi*) living in Amazonian Brazil. We conclude that (a) the availability of fruits consumed by the monkeys at this study site peaks approximately 2 months after maximum rainfall

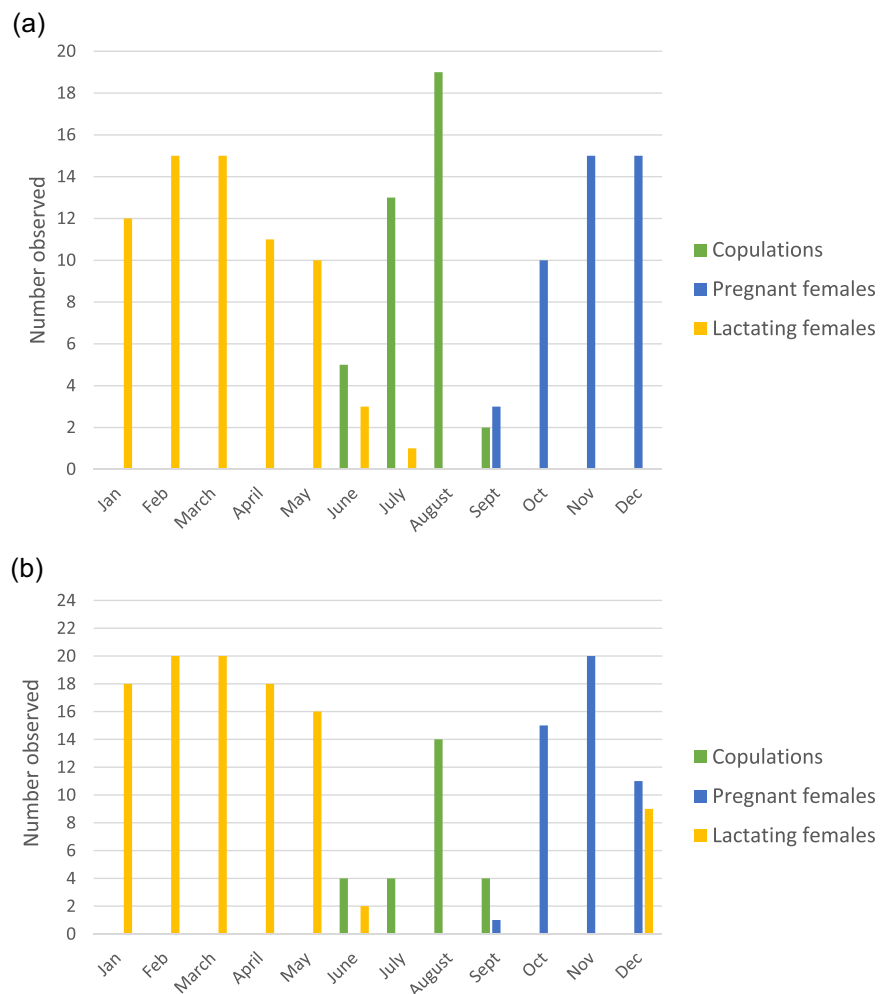


FIGURE 2 Distribution of *Saimiri collinsi* reproductive events per month. (a) Year 1: 2012–2013 and (b) Year 2: 2014–2015

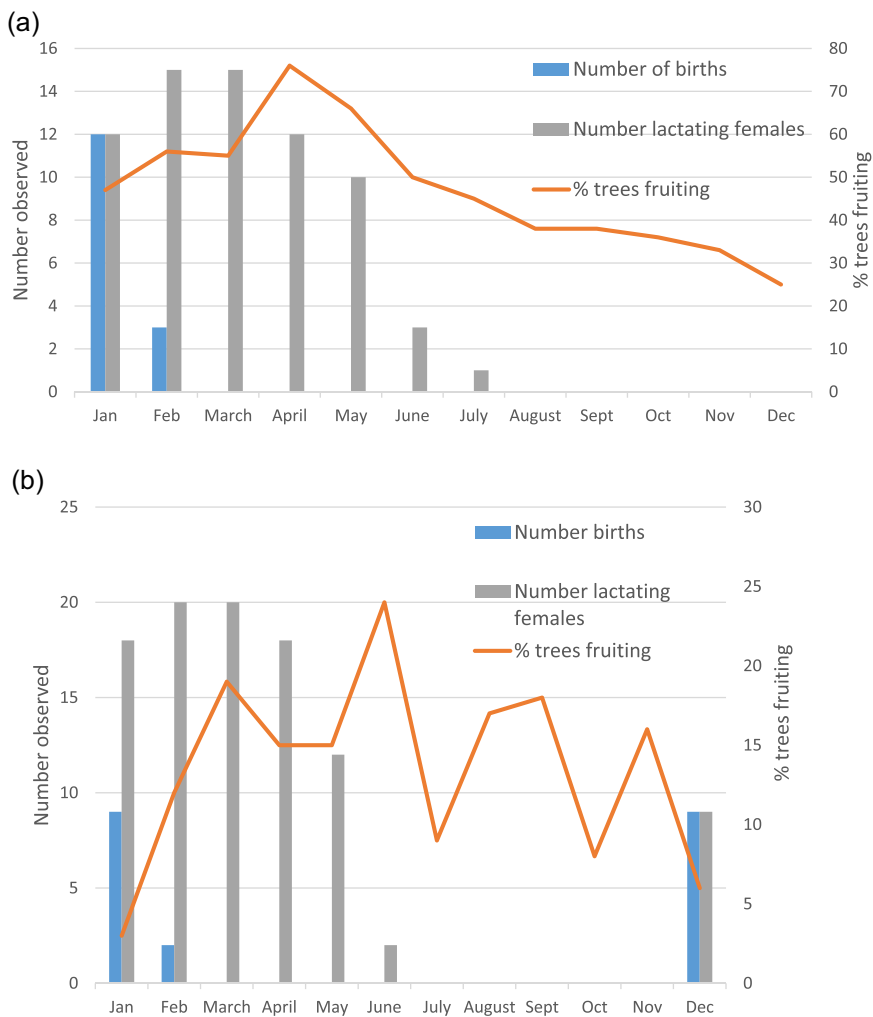


FIGURE 3 Monthly number of births and lactating females for *Saimiri collinsi*, in relation to fruit availability in the study area. (a) Year 1: 2012–2013 and (b) Year 2: 2014–2015

and (see also Mitchell, 1990; Terborgh, 1983); and (b) reproductive phenology of the squirrel monkeys appears strongly influenced by the availability of ripe fruit in their habitat. Seasonally breeding primates are thought to follow one of three alternative strategies (Di Bitteti & Janson, 2000; Janson & Verdolin, 2005): reduce maternal energy stress by timing peak lactation to peak food availability (Carnegie, Fedigan, & Melin, 2011; Souza-Alves et al., 2019); store energy reserves during periods of maximum food availability for later use (Borries et al., 2005); or increase infant survival by weaning infants during the period of greatest food availability (Kowalewski & Zunino, 2004). We found no evidence that squirrel monkeys give birth during the period of the highest food abundance. In addition, similar to other small primates such as callitrichids (Dietz, Baker, & Miglioretti, 1994; Goldizen, Terborgh, Cornejo, Porrás, & Evans, 1988) mating and conception in *S. collinsi* occurred during the early dry season (when fruit availability is declining), indicating that squirrel monkeys do not behave as capital breeders (Janson & Verdolin, 2005). This is perhaps not surprising, given that smaller animals with higher metabolic rates have less capacity for storing energy and therefore are less likely to follow the capital breeding strategy (Williams et al., 2017).

Instead, it appears that *S. collinsi* have adapted to regulate their weaning time to coincide with the period of maximum fruit availability in their habitat. In the two 12-month periods during which plant phenology was monitored, the weaning phase coincided with the months of the highest availability of fruit species in the monkeys' diet. This ensures that infants transitioning to independence will encounter an abundance of ripe fruit to incorporate into their changing diets. The same strategy of reducing energetic stress on weanlings has been observed in lemurs (Overdorff et al., 1999; Tecot, 2010; Wright, 1999). Other authors also have emphasized the importance of "weaning foods," as primate infants become nutritionally self-sufficient (Altmann, 1980; Crockett & Rudran, 1987).

Interestingly, previous work on seasonally breeding neotropical primates suggested that "the weaning strategy" is most often followed by species with a larger body mass (>2 kg) such as capuchins and howlers (Di Bitteti & Janson, 2000). However, despite being under 2 kg, squirrel monkeys also appear to favor a strategy that increases infant survival rather than reduce maternal stress. Below we suggest some reasons why weaning infants during the period of maximum fruit availability would be advantageous for squirrel monkeys. Although squirrel monkeys are characterized by high

maternal investment, most of this investment appears to occur prenatally. Comparative analyses among platyrrhines indicate that *Saimiri* have a relatively long gestation period of 150 days, longer than those of twin-producing callitrichids (Hartwig, 1996), and fast prenatal growth rates (Garber & Leigh, 1997). At birth, infants are large and most of brain growth has been completed in utero (approximately 61%; Elias, 1977). To support such reproductive demands, female *S. collinsi* in our population consume more animal protein than do males, year-round, but particularly during gestation. In addition, during lactation, females cope with the extra energetic requirements by altering their foraging behaviors and activity budgets (Ruivo & Stone, 2017). Therefore, females are able to show behavioral flexibility that likely maximizes maternal survival.

Infant squirrel monkeys in our study groups began exploring and play-foraging at a young age (around 4 weeks). These explorations always were directed at small, soft berries such as those of *Lacistema pubescens* available in February and March (Stone, 2004). Invertebrates comprise the majority of the monkeys' diet at our site (up to 75%; Stone, 2007). Despite the fact that foraging skills for arthropods develop relatively quickly during juvenility, infants younger than 3 months cannot yet capture small prey (especially mobile prey), and foraging success (capture/attempts) does not increase until 6 months of age (Stone, 2006). Another important dietary item for our study groups is fruit of the palm *A. maripa* (covered by a fibrous husk) the most common fruit in the groups' diet (Stone, 2007). Individuals were not able to peel these fruits until at least 1 year of age and relied on scavenging from fruits dropped by adults (Stone, 2006). Therefore, because arthropods and palm fruit are not yet accessible to weanlings, other ripe fruit is likely a critical resource as they begin foraging on their own.

It is noteworthy that, despite general similarity in group size, diet, and habitat use, squirrel monkeys show wide inter-specific differences in certain socioecological and life history traits (Boinski, 1999; Stone, 2004). Do other *Saimiri* species also wean infants during peak food availability? Squirrel monkeys in Peru wean their infants at 18 months, and this process occurs during a period of high fruit availability, in the middle of the wet season (Mitchell, 1990). In the case of Costa Rican squirrel monkeys, births did not coincide with an increase in food availability, but weaning coincided with the periods of high arthropod and fruit abundance (Boinski, 1986, 1987). Finally, we observed that in addition to pronounced seasonal breeding, squirrel monkeys in our population showed high within-group birth synchrony (e.g., in 2003, 80% of births in a group occurred on the same night). In the wild, Costa Rican squirrel monkeys show similar birth synchrony with 64% of births in one group occurring within 8 days (Boinski, 1987), possibly as a response to elevated predation risk for neonates (Boinski, 1987; Di Bitteti & Janson, 2000). In support of this hypothesis, data from our population show that inter-individual distances among adult females decrease during the birth season (Stone, 2004). In contrast, birth synchrony does not seem to occur in captive populations of squirrel monkeys (southern hemisphere: P. Castro, personal communication; northern hemisphere:

L. Williams, personal communication), perhaps due to a relaxation of predation pressure. In other mammals, such tight clustering of births within groups also appears to reduce infanticide risk (Hodge, Bell, & Cant, 2011), facilitate communal nursing (Mennella, Blumberg, McClintock, & Moltz, 1990) and overall maximize female reproductive success (Ims, 1990).

A limitation of the current study is that we did not measure infant survivorship, which is necessary to confirm whether infants born outside of the birth peak (and thus weaned closer to the dry season) experience higher mortality or perhaps slower growth rates. In a wild population of white-faced capuchins (*Cebus imitator*), infant survivorship to 12 months was not affected by whether infants were born within the birth peak or not (Carnegie et al., 2011). However, these primates appear to follow the strategy of maximizing maternal rather than weanling survival; thus, this result is not unexpected. Conversely, Tecot (2010) reported that all infant red-bellied lemurs born outside of the 54-day birth peak died in this seasonally breeding species. Because squirrel monkeys at our site are highly faunivorous (Stone, 2007), another avenue for future research is to investigate whether arthropod biomass fluctuates during the year and, if so, whether its availability has any correlation to *Saimiri* seasonal breeding. Preliminary work at our site has shown that arthropod biomass remains fairly constant over a period of 12 months, although different types of arthropods become more or less available to squirrel monkeys at certain times of the year (Stone, 2004, 2007). One possibility is that the birth/lactation peak occurs at a time of high arthropod abundance (thus maximizing protein intake for lactating females), while infant survival is maximized by timing weaning to the availability of ripe fruit, as shown in our study. If this is the case, then both maternal and infant survival would be optimized.

In sum, our findings show that in this population of squirrel monkeys mating/conception and gestation occur in the dry season (period of lowest fruit abundance), while birth, lactation, and weaning occur in the wet season. These primates exhibit a 2-month birth period, with extremely high birth synchrony within social groups. Although no environmental variables were manipulated in this study, we conclude that *S. collinsi* adaptively tune weaning time (rather than birth peak) to match the highest availability of ripe fruit in the environment. Thus, the species primary reproductive strategy observed with regard to energetics can be characterized as weanling survival or income-I breeders (*sensu* Janson & Verdolin, 2005).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the authors upon reasonable request.

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