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Reproductive seasonality in two sympatric primates (*Ateles belzebuth* and *Lagothrix lagotricha poeppigii*) from Amazonian Ecuador

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Abstract

With their large body size and "slow" life histories, atelin primates are thought to follow a risk-averse breeding strategy, similar to capital breeders, in which they accumulate energy reserves in anticipation of future reproductive events such as gestation and lactation. However, given the paucity of longitudinal data from wild populations, few studies to date have been able to compare the timing of reproductive events (e.g., copulations, conceptions, and births) in relation to shifting resource availability over multiple years. We examined the reproductive patterns of two atelin species—white-bellied spider monkeys (*Ateles belzebuth*) and lowland woolly monkeys (*Lagothrix lagotricha poeppigii*)—in relation to habitat-wide estimates of fruit availability at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador. Our sample included 4 years of data on births ($N = 36$) and copulations ($N = 170$) for *Lagothrix*, 10 years of data on births ($N = 35$) and copulations ($N = 74$) for *Ateles*, and 7 years of data on ripe fruit availability. Reproductive events were distinctly seasonal. For both species, births were concentrated between May and September, a time period in which ripe fruit was relatively scarce, while inferred conceptions occurred between September and January, when ripe fruit availability was increasing and maintained at high-levels throughout the forest. Interannual variation in births was relatively stable, except for in 2016 when twice as many infants were born following a strong El Niño event that may have led to unusually high levels of fruit productivity during the 2015 breeding season. Although copulations were observed year-round, an overwhelming majority (>90% for *Lagothrix* and >80% for *Ateles*) took place between August and February when females were most likely to conceive. Collectively, these data follow the reproductive patterns observed in other atelin primates, and, as proposed by others, suggest that atelins may follow a risk-averse breeding strategy.

KEYWORDS
capital breeding, life history, reproduction, spider monkeys, woolly monkeys

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1 | INTRODUCTION

Most wild populations of primates demonstrate some degree of reproductive seasonality (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005; Lancaster & Lee, 1965; Lindburg, 1987). The strength of reproductive seasonality, that is, how clustered similar reproductive events are in time, is often correlated with the level of intra-annual environmental fluctuation, most notably in rainfall and food availability (Di Bitetti & Janson, 2000). This pattern arises, in part, because the optimal timing of conceptions and births is likely to be dependent on the balance between food availability and the energetic and nutritional demands of mothers and infants during gestation, lactation, and weaning (Crockett & Rudran, 1987; van Schaik & van Noordwijk, 1985).

The timing of reproductive events in relation to food availability has been frequently characterized using the income-capital breeding framework (Brockman & van Schaik, 2005; Carnegie et al., 2011; Di Bitetti & Janson, 2000; Janson & Verdolin, 2005, Lewis & Kappeler, 2005a, 2005b; Richard et al., 2000). In its current form, the model can be viewed as a continuum of solutions differentiated by the degree to which an organism relies on stored energy to finance reproductive costs (Jönsson, 1997; Stephens et al., 2009). Marking the extreme ends of the continuum, an “income” breeder is one that uses current food intake as a cue to initiate reproductive events (mating, conception, and the onset of gestation), whereas a “capital” breeder builds up and stores energy reserves to then draw from during later phases of reproduction (e.g., maintenance of pregnancy and lactation) (Stearns, 1992). Although few species are purely income or capital breeders, testing predictions about the timing and frequency of reproductive events in relation to seasonally fluctuating resources may allow the classification of individuals as more representative of one strategy than the other (Brockman & van Schaik, 2005; Stephens et al., 2009).

Among nonhuman primates, income breeders, also known as “classic” breeders, are generally smaller-bodied species (e.g., those <3 kg), with shorter life spans, that rely on high quality, seasonal resources like fruits and insects. Their reproductive biology is predicted to include: (1) a conception window heavily influenced by exogenous factors, such as photoperiod or rainfall, (2) little to no fat accumulation during pregnancy, (3) low prenatal mortality rates, and (4) little to no interannual variation in birth rates, but (5) high interannual variation in the rate of infant mortality (Brockman & van Schaik, 2005). Income breeders generally reproduce once per year and often show a narrow birth peak, with births timed just before or during peak food availability (Brockman & van Schaik, 2005; Janson & Verdolin, 2005). In highly seasonal environments, some income breeders, typically those >3 kg, may conform to a strategy that improves maternal survival by timing infant births to occur up to several months before peak food availability. This form of income breeding ensures that infants will be of an appropriate size for weaning during peak food abundance and in turn decrease maternal energy stress during the most energetically costly part of reproduction (i.e., mid to late lactation; Altmann, 1980; Brockman & van Schaik, 2005; Bronson, 1989; Janson & Verdolin, 2005). Thus, income breeding strategies are thought to (a) decrease maternal energy stress during the most energetically costly part of reproduction (Altmann, 1980; Brockman & van Schaik, 2005; Bronson, 1989; Janson & Verdolin, 2005) and/or (b) improve infant survival by reducing the energetic stress that infants experience during weaning (Altmann, 1980; Crockett & Rudran, 1987). In turn, infant survivorship is expected to be higher for infants born during the birth window that permits weaning to occur during periods of greatest food availability compared with infants born outside of that window (Di Bitetti & Janson, 2000).

For primates living in environments with unpredictable peaks in food availability, or for those with relatively long interbirth intervals, the timing of reproductive events may be dependent principally on maternal body condition needed to support cycling and gestation rather than on food availability at either the time of infant weaning or of peak lactational stress for mothers. Such females have been called “capital” breeders, as they seem to follow a strategy of accumulating and storing energy reserves for future reproductive events such as gestation and lactation (Stearns, 1992; van Schaik & van Noordwijk, 1985). Although no primates seem to follow a capital breeding strategy to the same extent as some other mammals, (e.g., pinnipeds, where females rely exclusively on their fat reserves to sustain both the infant and the mother through weaning), a number of large-bodied species do exhibit a risk-averse breeding strategy (Emery Thompson, 2013) in which maternal body condition acts as a cue that the mother will be able to afford the costs of both gestation and lactation regardless of future food availability. As such, the reproductive responses of primate capital breeders are predicted to include: (1) a variable conception window that is cued endogenously through individual condition thresholds or energy balance, (2) accumulation of fat reserves throughout pregnancy, (3) high prenatal mortality rates, (4) high interannual variation in birth rates, and (5) low variation in infant mortality rates (Brockman & van Schaik, 2005). If capital breeders mate throughout the period of increasing food availability but only conceive once their body condition reaches an adequate threshold, then their births are predicted to occur after the mean peak in food abundance by a period of time equal to the delay in conception plus gestation length (Janson & Verdolin, 2005).

In an influential review of the timing of births in Neotropical primates, Di Bitetti and Janson (2000) found that, across species, births tend to occur before the peak in food availability. They argue that, for small-bodied species, this pattern would allow peak lactation to occur during peak food availability, while for larger species, it would allow weaning of offspring to occur before the start of the next lean season. However, the atelins—spider monkeys (genus *Ateles*), muriquis (genus *Brachyteles*), and woolly monkeys (genus *Lagothrix*)—which are the largest (>7 kg) of the New World primates, do not neatly conform to this pattern. Instead, despite living in climatically different environments, atelins tend to give birth when preferred resources, such as new leaves for muriquis (*Brachyteles arachnoides*) and ripe fruits for woolly monkeys (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.), are relatively scarce (Nishimura, 2003). Given their large body size and long period of infant dependency (Table 1), it is unlikely that atelins would be strict income breeders, but rather should fall towards the other end of the income-capital

TABLE 1 Weights and reproductive/life-history parameters of wild *Ateles belzebuth* and *Lagothrix lagotricha* spp

Parameter	*Ateles*	*Lagothrix*
Adult female body weight (g)	8,744 ± 858 (*N* = 7)[a]	6,089 ± 574 (*N* = 7)[a]
Age of dispersal from natal group (years)	5.9 ± 0.4 (*N* = 13)[b]	6.0 ± 0.4 (*N* = 5)[c]
Age of first parturition (years)	8.8 ± 1 (*N* = 5)[b]	9.0 ± 0.8 (*N* = 4)[c]
Female cycle length (days)	NA[d]	22.9 ± 2.7 (*N* = 8)[e]
Gestation length (days)	229 ± 3[f]	220 ± 5[f]
Interbirth interval (months)	44.2 ± 7.8 (*N* = 21)[b]	36.7 ± 6.7 (*N* = 6)[a]

[a] This study.

[b] Link et al. (2018).

[c] La Macarena, Colombia (Nishimura, 2003).

[d] Data not available for *A. belzebuth*, but Campbell et al. (2001) estimates cycle length of 20–24 days for *Ateles geoffroyi*.

[e] Abondano unpublished data, calculated from ovulation events of 26 consecutive cycles across eight females at the Tiputini Biodiversity Station.

[f] Hartwig (1996).

breeding continuum, that is, unable to conceive and successfully gestate until they reach an adequate body condition (Nishimura, 2003; Strier & Ziegler, 1997; Strier, 1996).

Observational data, coupled with physiological data, support the notion that atelin primates may be capital breeders and follow a risk-averse breeding strategy. For example, although spider monkeys and woolly monkeys are both observed to copulate year-round, births are reported to only occur during 8–9 months out of the year in spider monkeys (reviewed in Shimooka et al., 2008) and during ~6 months out of the year in woolly monkeys (Nishimura, 2003), and among muriquis matings are rarely observed during the dry season, when preferred resources are most scarce (Strier, 1996). Thus, if a female muriqui fails to conceive by the end of the wet season, when preferred resources are abundant, she will potentially experience a full year delay in reproduction, waiting until the next rainy season to recommence sexual activity (Strier, 1996). Finally, most multiparous atelins exhibit several months of ovarian cycling before conception is achieved, also suggesting that maternal body condition may be critical for successful conception (Campbell et al., 2001; Nishimura, 2003; Strier & Ziegler, 1997).

While the observations noted above support the view that atelin reproductive strategies may be constrained by female body condition, few studies to date (e.g., Campbell & Gibson, 2008; Nishimura, 2003; Symington, 1987a) have explicitly examined whether and how reproductive behavior and births are related to temporal variation in resource availability at a given site over the long term. In this paper, we aim to fill this gap by presenting long-term data on the timing of reproductive events for two sympatric atelin primates—white-bellied spider monkeys (*Ateles belzebuth*) and lowland woolly monkeys (*Lagothrix lagotricha poeppigii*)—at the Tiputini Biodiversity Station (TBS) in Amazonian Ecuador. Specifically, we present data on the distribution of observed copulations, inferred months of conception, births, and infant survivorship in both species over multiple years and then examine how these are related to seasonal patterns of ripe fruit availability, the preferred food source for both species. We also compare the degree of reproductive seasonality observed at TBS to that observed among atelin taxa at other sites.

If these two atelin primates are capital breeders, with conception and maintenance of gestation conditional on the maternal state, we would expect spider monkeys and woolly monkeys at TBS to exhibit comparable reproductive timing given that they are feeding, primarily, on very similar resources (see Dew, 2005). Specifically, under a capital breeding model, we would predict that matings in both species would become more common as fruit becomes more abundant and that conception will occur when maternal body condition is adequate (most likely during or right after the mean peak in fruit availability), with births following 7–7.5 months later. We would also expect to see high variation in interannual birth rates, but low variation in infant mortality. Furthermore, previous comparisons of phenological patterns between TBS and other field sites inhabited by similar taxa (e.g., Manu, Peru and La Macarena, Colombia), suggest that fruit availability at TBS is less variable across the annual cycle than in other lowland tropical forests (Di Fiore, 1997; Link, 2011). If so, this raises the possibility that spider monkeys and woolly monkeys at TBS may be less constrained than other atelin taxa living in more seasonal habitats, and, as such, may exhibit less reproductive seasonality with a wider birth window compared with other atelin populations (Di Bitetti & Janson, 2000; Janson & Verdolin, 2005).

2 | METHODS

2.1 | Ethics statement

This study complied with protocols approved by the institutional animal care and use committee (IACUC) at the University of Texas at Austin, adhered to Ecuadorian legal requirements, and adhered to the American Society of Primatologists' Code of Best Practices in Field Primatology.

2.2 | Study site

Research was conducted at the TBS in the Yasuní Biosphere Reserve of Ecuador. Adjacent to Yasuní National park (982,000 ha), TBS encompasses ~650 ha of largely undisturbed primary moist tropical rainforest with an annual rainfall of >2800 mm (Blake et al., 2010; Di Fiore et al., 2009). Although there is not a pronounced dry season, rainfall can vary dramatically between months. March through July are consistently the wettest months of the year with ≥250 mm of rain falling each month, while August and September tend to be drier, with rainfall increasing again in October, peaking in November, then drying off again for December and January (Snodderly et al., 2019). Still, there is a considerable interannual variation that muddies this pattern (Snodderly et al., 2019). Because of its location near the equator, photoperiod is consistent throughout the year, although the timing of sunrise may vary as much as 30 min during a biannual cycle. Sunrise occurs slightly earlier in May and November and slightly later in February and August (Snodderly et al., 2019). The field site hosts an intact predator community (Blake et al., 2012) as well as 10 different species of nonhuman primates (Di Fiore et al., 2017).

2.3 | Subjects

Three groups of spider monkeys range at least partially within the 650 ha TBS trail system, and one of these groups (MQ-1) has been monitored regularly since August 2006, with only two periods of observer absence exceeding 2 months (January 2007 through May 2007 and September 2015 through June 2016) between 2006 and 2017. Over that time, MQ-1 has ranged in size between 23 and 37 individuals, with an average of 6 adult males and 10 adult females, and 11 immatures (Link et al., 2018). At least eight social groups of woolly monkeys have been identified to range within the same study area. Groups vary in size from 14 to 40 individuals, with a typical composition including 2–5 adult males, 4–10 adult females, and 5 or more immatures. For this study, we relied on behavioral data collected on several groups of woolly monkeys over a 4-year period. Specifically, data were collected on two groups (C and G) in 2013 and on four groups (C, D, G, and P) between 2014 and 2016. All groups followed during these study periods were habituated to observer presence, and most group members could be recognized individually based on unique facial markings, pigmentation of the anogenital region, and/or other distinct features such as broken fingers and scars. Given that this was a longitudinal study, we have had numerous observers assist in the data collection of atelin behavior. To ensure interobserver reliability, data were only included from observers with ≥2 months of training.

2.4 | Data collection

2.4.1 | Behavioral data

For both species, behavioral data were recorded using a combination of instantaneous and continuous samples taken during the context of focal animal follows (Altmann, 1974). With multiple observers in the field and an opportunistic schedule of rotation among focal individuals, we ensured that all adults and subadults were sampled and accounted for in group demography at least once per month. Contact hours with *Ateles* averaged 148.5 ± 93.9 h per month, and contact hours with *Lagothrix* averaged 324.4 ± 267.1 h per month. Observations of rare events such as copulations and solicitations between nonfocal individuals were recorded ad libitum. Copulations were defined as mounting behavior between male and female subjects in which the observer could visibly confirm intromission, or, after dismount, could visually confirm that ejaculate was present. In woolly monkeys, copulations are frequently interrupted by juveniles, and, on occasion, by harassing females (Di Fiore & Fleischer, 2005). Therefore, copulations in which a male or female terminated copulation due to harassment, but then immediately resumed copulating once a harassing individual was chased away or reprimanded, were considered a single event.

2.4.2 | Birth and conception data

The presence of newborn infants in each of the focal groups of spider and woolly monkeys was recorded opportunistically during group follows. While several infant births could be assigned to an exact day, the majority of infants born during the study were born outside of a specific follow. In these cases, infant birth dates were assigned to the midpoint of the month in which the infant was first seen, unless the infant's appearance (i.e., hair color and size) suggested to an observer familiar with the development process that they were born 1–2 months prior. Infant birth dates that could not be estimated in this manner to within two months were not included in seasonality analyses; by this criterion, we excluded eight woolly monkey infants born in *Lagothrix* groups D and P between May and October of 2016, a time period in which these two groups were not followed consistently. Birth dates for some spider monkeys infants born early in the study were further corroborated through videos and photos collected from 1 to 2 camera traps monitoring a mineral lick in the group's home range that was visited frequently (Galvis et al., 2014; Link et al., 2011). The month of conception for each infant was then estimated by subtracting the average gestation length, which has been estimated to be between 7 and 7.5 months, or 229 ± 3 days in spider monkeys and 220 ± 5 days in woolly monkeys (Hartwig, 1996), from the infant's assigned birth month. Based on birth records and estimated dates of conception, we scored each woolly and spider monkey female as either "gestating" or "not gestating" during each month and then calculated the total number of gestating females per species per month.

2.4.3 | Fruit availability

Biweekly estimates of fruit availability at TBS have been collected regularly since September 2006. Following methods outlined in Stevenson (2004), we surveyed nearly 9 km of transects spread throughout the TBS trail system. During each survey, we recorded all trees whose crown overlapped the phenological transect and was bearing ripe fleshy fruit. Fruiting trees were marked with an identification tag and entered into our long-term phenological database, where upon first occurrence, we recorded the species (or morphospecies), diameter at breast height (DBH), and distance of the trunk to the center of the transect; for lianas, the DBH and distance to transect of the main supporting trunk was measured. The basal area,$\pi\left(\frac{\mathrm{DBH}}{2}\right)^2$, was then calculated as a proxy index of ripe fruit production for that tree or liana (Chapman et al., 1992; Stevenson, 2004) and the effective width of the phenological transects sampled was calculated as the average distance from all fruiting trees to the center of the transects. The area sampled during each monitoring period—calculated as the effective transect width *x* total transect length—was 5.25 ha. For trees and lianas that produced fruits in more than one biweekly period, we assigned ripe fruit production during each period to be a proportion of the tree's basal area following the coefficients of Pascal's triangle. For example, if a tree had a basal area of 100 cm^2 and produced fruit during four subsequent monitoring periods, we would distribute our basal area index of ripe fruit production among those four periods using Pascal's coefficients of 1:3:3:1, resulting in scores of 12.5, 37.5, 37.5, and 12.5 cm^2, for the same respective periods. We chose this model because a weighted distribution of fruit productivity determined by Pascal's triangle showed the best fit to actual fruit productivity (as monitored using fruit traps) at another diverse, lowland rainforest site at La Macarena, Colombia (Stevenson, 2004). To estimate habitat-wide fruit availability for a given biweekly monitoring period, we summed these portions of the basal area of each tree and liana producing ripe fruits to obtain the total basal area of plants bearing ripe fleshy fruits that period and divided that by the total area monitored (5.25 ha) to yield an estimate of production per hectare.

We included in analyses of temporal variation in fruit availability only those years of phenological monitoring that were missing data from five or fewer biweekly surveys ($N = 7$, years: 2008, 2011–2016). For these years, a small number of missing biweekly values ($N = 10$ out of 168 potential values, or 6% of data set) were imputed using the package MICE (Multivariate Imputation via Chained Equations; van Buuren & Groothuis-Oudshoorn, 2011) in R version 3.6.1 (R Core Team, 2019). Five different imputed data sets were created using predictive mean matching, and the average of these data sets were used to represent a final data set of monthly mean basal area of plants bearing ripe fruit per hectare.

2.5 | Data analysis

We used circular statistics to determine if annual fruit availability and reproductive events for each species could be classified as seasonal. Circular statistics are useful when the distribution of data can be plotted along a circular scale such as compass directions or time (e.g., months of the year, hours of the day, etc.). For our study, we considered the total length of the circular axis to be one year, with each month represented by 30° (or 1/12th) of that axis. We then converted observations of births, inferred conceptions, and total sum of fruit basal area per hectare per month to a vector in which vector length, *l*, was equal to the cumulative number of events observed that month and the vector angle, *a*, was equal to the midpoint of that month's 30° section (i.e., January = 15°, June = 165°, and December = 345°; see Figure 1). The subsequent vectors were then compared with those of a uniform distribution using Rayleigh's test of uniformity (Batschelet, 1981). The resulting value is a mean vector length, *r*, which ranges in values between 0 and 1.0, with 0 indicating an equal distribution of events along the circular axis, and 1.0 indicating an extremely high clustering of events where all events occur during the same interval. Statistical analyses were executed in the circular statistics program for Windows, Oriana v.4 (Kovach, 2011).

To better understand the seasonal distribution of observed copulations, we calculated the frequency of copulations observed each month as the number of copulations observed divided by the total number of hours that observers followed focal groups that month, and we express the frequency of copulations as the number of copulations per 100 observer-hours. We attempted to remove duplicate observation hours in which multiple observers were following the same subgroup (animals within a minimum distance threshold of <30 m for spider monkeys and <100 m for woolly monkeys). However, this was not always possible for woolly monkeys as groups of this species often range in a dispersed pattern, and observers could be >100 m from one another viewing different animals and yet still be part of the same subgroup (Ellis & Di Fiore, 2019). In these cases, we included both observers' hours in the denominator, which means that calculated rates may somewhat underestimate actual copulation rates in woolly monkeys.

To assess the relationship between fruit production and reproductive events we used a series of generalized linear mixed-effects models (GLMMs). Models incorporating count data as the response variable (e.g., number of births, number of conceptions, and number of gestating females each month) were fit with a Poisson error distribution and a log link function. For the model evaluating copulation rates, the response variable was set as the number of copulations in relation to the total number of observation hours collected during that month and was fit with a binomial error distribution and a logit link function. Fruit availability was set as a fixed effect in all models. Given that our calculations of fruit production are only a subsample of what is available to the primates of TBS, we broadly categorized each month as falling into a high or low period of fruit availability (i.e., above or below the overall average). Additionally, given the variation in sampling from year to year (including change in observers and number of groups studied), we chose to incorporate year as a random effect in all models. Each model was fit with the *glmer* function in the R package "lme4" (Bates et al., 2015). To determine model significance, we compared each model to the null model (containing random effects only) using log-likelihood ratio tests (LRT) calculated using the *ANOVA* function in R version 3.6.1 (R Core Team, 2019).

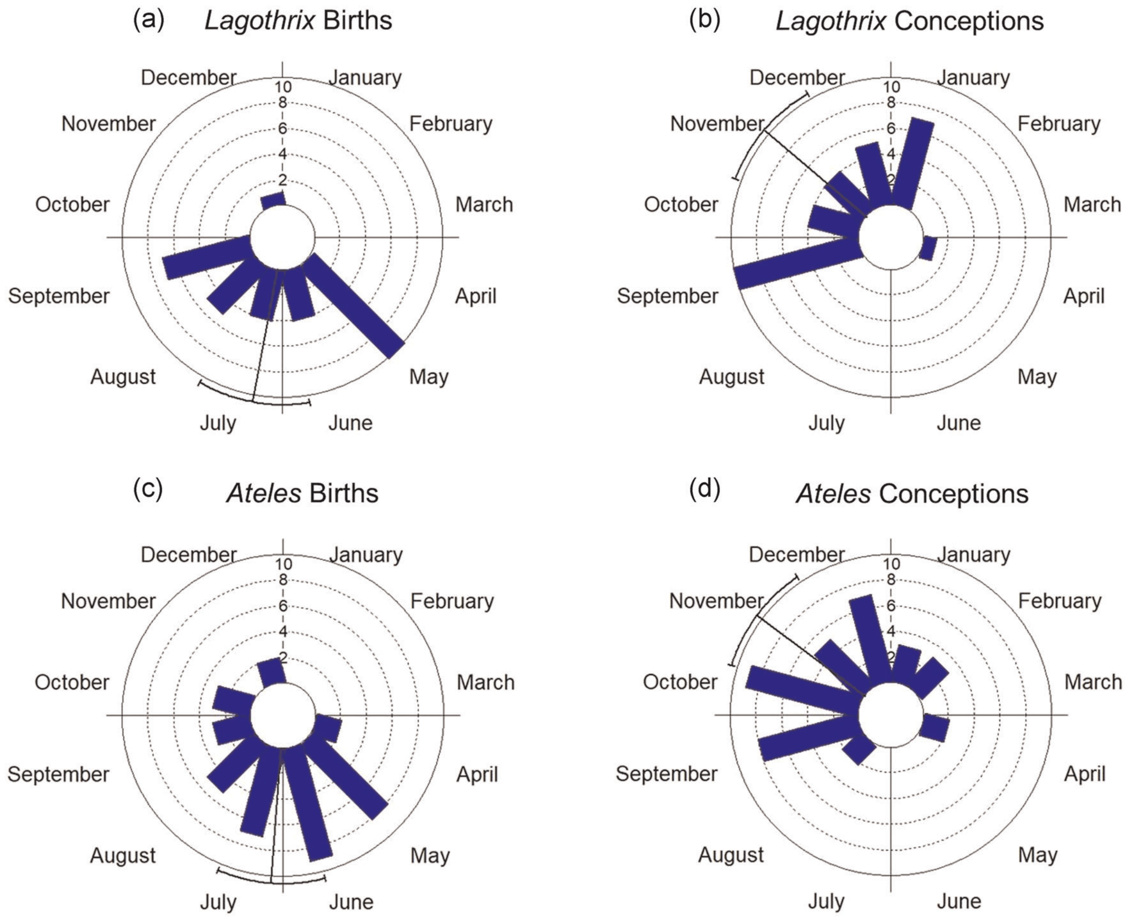

FIGURE 1 Circular plot showing the distribution (blue bars) and mean ± 1 SD (black line) of (a) woolly monkey births and (b) conceptions from 2013 to 2016 ($N = 31$) and of (c) spider monkey births and (d) conceptions from 2006 to 2012 ($N = 35$) at the Tiputini Biodiversity Station in Ecuador. The timing of births/conceptions across months is significantly different from a uniform distribution in both woolly monkeys ($Z = 13.308$, $p < .001$) and spider monkeys ($Z = 12.542$, $p < .001$). For both species, the mean month for births in July and the mean month for conceptions in November

3 | RESULTS

3.1 | Woolly monkeys

Between January 2013 and December 2016, 36 woolly monkeys were born in our four focal groups. All woolly monkey infants with assigned birth months ($N = 31$) were born between May and September, with one exception, a male born in December of 2016 (Figure 1). The monthly distribution of woolly monkey births, collated across years, differed significantly from a uniform distribution (Rayleigh test: $r = .636$, $Z = 12.542$, $p < .001$). May had the highest number of births followed by another small peak in September.

While there was little interannual variation in the number of infant births between the years of 2013 and 2015, 2016 was an exception, with twice as many infants born that year in comparison to the previous 3 years (Table 2). During the 4 years of study, only two woolly monkey infants disappeared before reaching 2 years of age. One infant, born in September 2013, disappeared with his mother between January and March 2015; we do not know if this disappearance represents a dispersal event or a fatality. A second infant, born September 2014, was no longer seen after we found his mother deceased of unknown causes in September of 2015.

We calculated the month of conception for each woolly monkey infant by subtracting the mean gestation length of 220 days from the assigned month of birth. All infants were conceived between October and February, except for the one infant born in December 2016, which would have to have been conceived in May. October was the month with the highest number of inferred conceptions, followed by February.

Since January 2013, we have observed 170 woolly monkey copulations (Table 3). Over 90% of these occurred between August and February, with the frequency of copulations per 100 observation hours peaking in November. Copulations were rarely observed between April and July.

For nine individually recognized woolly monkey females who gave birth between the start of 2013 and end of 2016, the mean number of months between parturition and the first recorded observation of resumed sexual activity was 20.1 months (range: 13–27 months).

	Group C		Group D		Group G		Group P		Group totals	
Year	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
2013	1	1	1		2			1	4	2
2014				2	3	1	1	1	4	4
2015	1	1	1				2	1	4	2
2016	2		2	1	3	3	3	2	10	6
Total	4	2	4	3	8	4	6	5	22	14

TABLE 2 Number of male and female woolly monkeys born each year to four different study groups (C, D, G, and P)

Mothers of male infants had significantly longer periods of postpartum sexual inactivity (23.3 ± 5.7 mo, $N = 4$) compared with mothers of female infants (17.6 ± 4.5 mo, $N = 5$; two-sample $t = 2.83$, df = 7, $p < .05$). With a small sample size, however, these results should be taken with caution. For five of these females, we could also calculate the length of time between the first observation of resumed sexual activity and successful conception, which averaged 6.4 months, with a range between 2 and 17 months ($N = 5$).

3.2 | Spider monkeys

Similar to woolly monkeys, the distribution of spider monkey births across the annual cycle also differed significantly from a uniform distribution (Rayleigh test: $r = .617$, $Z = 13.308$, $p < .001$). Since 2006, over 65% of spider monkey births ($N = 35$) occurred between the months of May and August, and no births were recorded between January and March. Overall, June was the mean peak birth month for spider monkeys.

TABLE 3 Total number of observation hours and the number of observed copulations for each month in spider monkeys from 2007 to 2017 and in woolly monkeys from 2013 to 2016

	Observed copulations *Ateles*			Observed copulations *Lagothrix*		
Month	Contact hours	No.	No./ 100 h	Contact hours	No.	No./ 100 h
January	1475.5	4	0.271	1413.7	8	0.566
February	1795.6	11	0.613	1264.3	19	1.503
March	1285.5	4	0.311	812.3	3	0.369
April	1380.5	2	0.145	1142.9	0	0.000
May	1637.8	3	0.183	916.0	4	0.437
June	1462.7	1	0.068	1490.4	2	0.134
July	1735.9	2	0.115	2421.6	6	0.248
August	1598.6	10	0.626	1659.0	13	0.784
September	1308.6	7	0.535	805.5	25	3.104
October	1384.2	8	0.578	1237.0	24	1.940
November	1259.6	18	1.429	1045.6	50	4.782
December	774.6	4	0.516	1037.6	16	1.542
Total	17099.1	74	0.433	15246.0	170	1.115

On average, three infants were born into the *Ateles* MQ-1 group each year, but as with woolly monkeys, nearly twice as many infants were born in 2016 ($N = 7$) than were seen in any other previous year (range: 1–4 for years 2006–2015; Table 4). Six known infants (three males and three females) have died or disappeared since 2006. All were born between May and August, and a majority of them ($N = 4$) were only a few weeks old when they vanished. In two cases, both the mother and infant disappeared simultaneously. The death of one male infant in August of 2010 was attributed to suspected infanticide (Alvarez et al., 2015).

Counting back 229 days from the month of birth, we estimated the month of conception for these same 35 infants. Most inferred conceptions (over 65%) occurred between September and December, with the highest number found in October. No conceptions occurred between May and July.

Due to the formation of consortships in spider monkeys, mating behavior can be difficult to detect by observers (Campbell & Gibson, 2008). Thus, despite a much longer period of investigation and a larger number of contact hours compared with the woolly monkeys, we have only seen about a third as many copulations ($N = 74$; Table 3). Although copulations were observed year-round, a large

TABLE 4 Number of male and female spider monkeys born each year across 13 females in MQ-1

Year	No. of males	No. of females	No. of unknown
2006	1	2	
2007	1	2	
2008	1		
2009	2	3	
2010	1	2	
2011		3	
2012	3	1	
2013		2	
2014	2		
2015		1	1
2016	4	3	

majority (over 80%) occurred between August and February. As for woolly monkeys, November was the month with the greatest number of copulations seen per 100 observation hours, and very few copulations were observed between April and July.

Spider monkey females resumed sexual activity following parturition later than woolly monkey females. Excluding events in which a previous infant died ($N = 1$) and instances where no copulations were seen before conception ($N = 1$), spider monkey females took, on average, 29.5 months after parturition to be observed to resume mating (range: 17–37 months, $N = 8$ infants involving seven different females). Given that these females all had female infants, we were unable to test for significant differences in the length of postpartum sexual inactivity between mothers of female infants compared with mothers of male infants. Once a female resumed copulating, it then took between 1 and 20 months for her to conceive (average: 7.8 months, $N = 6$). Interestingly, of the three females still present in the group after the death or disappearance of their infant, two who lost their offspring during the same month in which they were born were able to conceive 1 and 3 months after parturition, respectively; a third female, whose infant was between 3 and 9 months old when it disappeared, conceived 16 months after parturition.

3.3 | Fruit availability

Monthly fruit availability did not follow a uniform distribution ($r = .163$, $Z = 5.416$, $p = .004$). The highest estimates of fruit abundance were typically observed between December through March and the lowest estimates of fruit availability extended from May to August (Figure 2). January was the mean month of peak fruit availability, with the highest estimates of fruit abundance, while May often had the lowest estimates of fruit abundance.

3.4 | Reproductive events in relation to relative fruit abundance

In both species, births were significantly more common during periods of low fruit availability (woolly monkeys: $\beta = 1.153$, $Z = 2.536$, $p = .011$, model fit LRT full vs. null: $\chi^2 = 7.880$, $p = .005$; spider monkeys: $\beta = 1.599$, $Z = 2.563$, $p = .010$, model fit LRT full vs. null: $\chi^2 = 9.146$, $p = .002$; Tables S1 and S2), with a threefold and fivefold increase in the number of births expected for woolly monkeys and spider monkeys, respectively, during months with lower than average fruit availability compared with months with higher than average fruit availability. For both species, the number of births peaked in May and June when the abundance of ripe fruit was rather scarce compared with other months of the year (Figure 3). Spider monkeys are significantly less likely to be gestating during periods of lower-than-average fruit availability ($\beta = -0.465$, $Z = -2.943$, $p = .003$, model fit LRT full vs. null: $\chi^2 = 8.689$, $p = .003$; Tables S1 and S2), with a 63% decrease in the number of gestating females observed during periods of low fruit availability. However, we found no significant relationship between high and low fruit availability and the number of woolly monkeys gestating each month ($\beta = -0.152$, $Z = -1.08$, $p = .277$, model fit LRT full vs. null: $\chi^2 = 1.176$, $p = .278$; Tables S1 and S2). Although only one conception occurred for each species between April and July, a period with very low fruit availability, our model did not detect a significant relationship between high versus low fruit availability and the number of conceptions observed for either species (woolly monkeys: $\beta = -0.198$, $Z = -0.525$, $p = .599$, model fit LRT full vs. null: $\chi^2 = 0.275$, $p = .600$; spider monkeys: $\beta = -0.810$, $Z = -1.728$, $p = .084$, model fit LRT full vs. null: $\chi^2 = 3.157$, $p = .076$; Tables S1 and S2). Finally, we found a significant relationship between high versus low levels of fruit

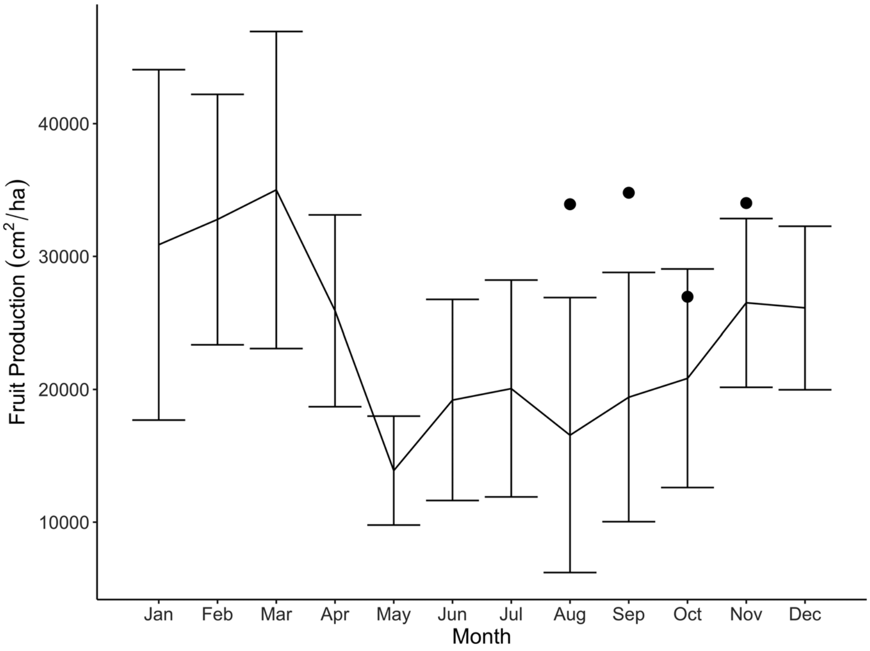

FIGURE 2 Average monthly estimates of fruit production (measured as the proportion of the basal area (cm^2/ha) of plants bearing ripe fruits) at the Tiputini Biodiversity Station, Ecuador over 7 years (2008, 2011–2016). The solid line and error bars represent mean ± 1 *SD* monthly production of ripe fruit. Solid circles represent unusually high estimates of ripe fruit availability observed between August and November of 2015, during an El Niño event

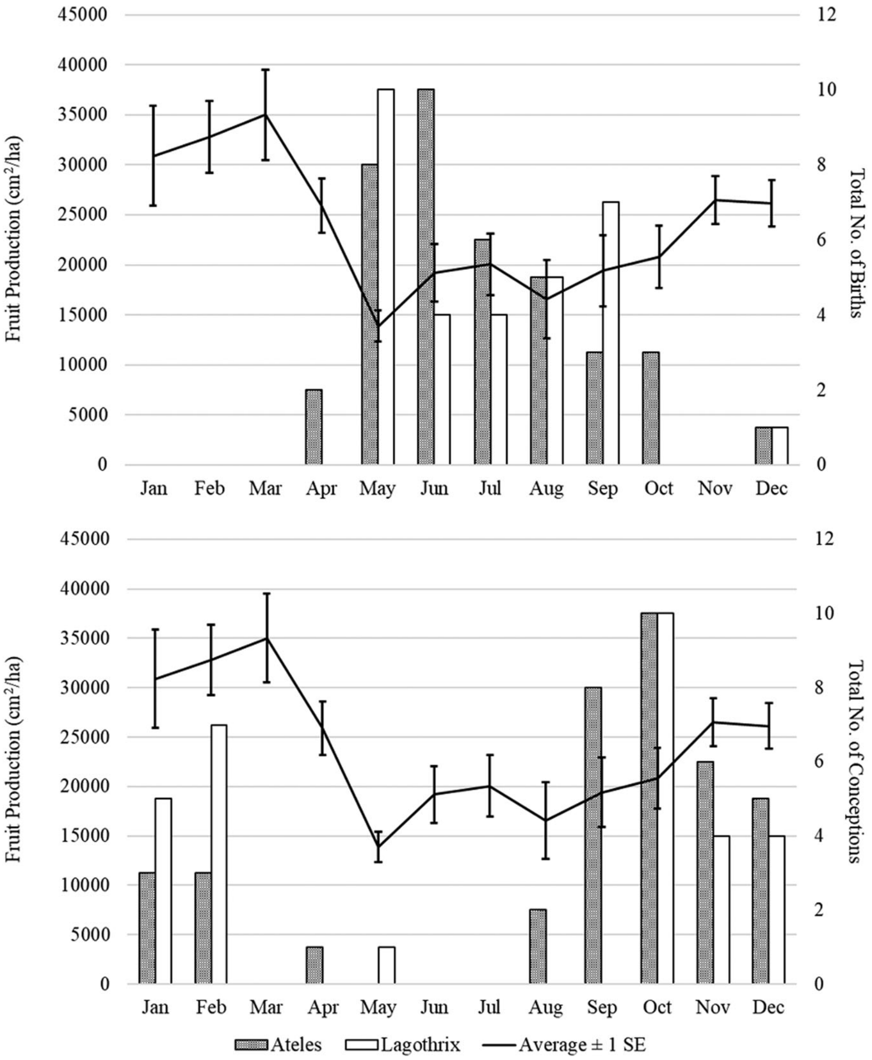

FIGURE 3 The number of woolly and spider monkey births and conceptions between January 2011 and December 2016 in relation to average monthly estimates of fruit abundance (measured as the proportion of the basal area (cm^2/ha) of plants bearing ripe fruits) at the Tiputini Biodiversity Station, Ecuador. Significantly more births occurred during periods of low fruit availability (woolly monkeys: $\beta = 1.153$, $Z = 2.536$, $p = .011$, model fit $\chi^2 = 7.880$, $p = .005$; spider monkeys: $\beta = 1.599$, $Z = 2.563$, $p = .010$, model fit $\chi^2 = 9.146$, $p = .002$). Despite few conceptions occurring during the leanest part of the year (April–July), we found no effect of fruit availability on the number of conceptions observed each month (woolly monkeys: $\beta = -0.198$, $Z = -0.525$, $p = .599$, model fit $\chi^2 = 0.275$, $p = .600$; spider monkeys: $\beta = -0.810$, $Z = -1.728$, $p = .084$, model fit $\chi^2 = 3.157$, $p = .076$). The solid line and error bars represent mean ± 1 *SE* production of ripe fruit each month, the bars represent the total number of reproductive events for each species, with spider monkeys shown in shaded bars, and woolly monkeys shown in white bars. *SE*, standard error

availability and monthly copulation rates observed for each species, although in different directions (woolly monkeys: $\beta = .370$, $Z = 2.018$, $p = .044$, model fit LRT full vs. null: $\chi^2 = 4.013$, $p = .042$; spider monkeys: $\beta = -0.789$, $Z = -2.769$, $p = .005$, model fit LRT full vs. null: $\chi^2 = 7.640$, $p = .006$; Tables S1 and S2). In woolly monkeys, copulations were 44% more likely to be observed during periods of low fruit availability, while for spider monkeys, the chances of observing copulations during low fruit availability decreased by 45%. This discrepancy may be due to interannual variation of fruit productivity and a relatively shorter sampling period for woolly monkeys (4 years) compared with spider monkeys (10 years).

3.5 | Degree of seasonality compared with atelins at other field sites

Although our study site is located very near the equator and shows less variation in fruit availability across seasons when compared with other sites inhabited by atelin taxa, woolly monkeys and spider monkeys at TBS showed slightly higher degrees of reproductive seasonality, as measured by Rayleigh's test for uniformity (*r*), than reported elsewhere (Table 5). Comparatively, both species in the current study had very similar *r* values (in both food availability and births) to those calculated for muriquis (*Brachyteles*) from Caratinga, Brazil, a site located 19°50′S from the equator.

TABLE 5 Seasonality in fruit availability and births as measured by Rayleigh's test of uniformity (*r*) among several atelin primates

Species	Site	Latitude	*r* fruit	*r* births	No. births	*p*	References
Ateles belzebuth	La Macarena, Colombia	2°40′N	0.489	0.491	6	NS	Klein (1971)
A. belzebuth	TBS, Ecuador	0°40′S	0.163	0.617	35	<.001	This study
Ateles geoffroyi	BCI, Panamá	9°9′N	0.225	0.539	18	<.005	Milton (1981)
Ateles paniscus	Manu, Perú	11°55′S	0.283	0.370	46	<.005	Symington (1987a,b)
Brachyteles arachnoides	Caratinga, Brazil	19°50′S	0.211	0.629	57	<.001	Strier (1996), Strier et al. (2001)
Lagothrix lagotricha lugens	La Macarena, Colombia	2°40′N	0.489	0.589	20	<.001	Nishimura et al. (1992)
Lagothrix lagotricha poeppigii	TBS, Ecuador	0°40′S	0.163	0.636	31	<.001	This study

Note: Values of *r* range between 0 and 1.0, with 0 indicating an equal distribution of events, and 1.0 indicating an extremely high clustering of events (Batschelet, 1981).

4 | DISCUSSION

Based on long-term demographic, behavioral, and phenological data on wild populations of woolly and spider monkeys at TBS, we found that reproductive events of these two atelin primates were distinctly seasonal. Births for both species were concentrated between the months of May and September, a time period in which fruit availability at the site is, historically, at its lowest. In turn, most conceptions occurred between September and January, when fruit availability tends to be increasing or is maintained at a high level throughout the forest. The frequency of observed copulations also increased during this period, suggesting that copulations most often occur when females are more likely to conceive (between August and February, for both species), although we should note that female reproductive hormone profiles are necessary to more precisely identify the timing of ovulation and conception. While some females took just over a year to resume copulating postparturition, others were not observed to copulate for more than 2 years after giving birth, with the larger-bodied spider monkeys taking ~8 months longer to resume copulating than woolly monkeys. Once females resumed sexual activity, woolly monkeys took, on average, more than 6 months—and spider monkeys nearly 8 months—to conceive.

4.1 | Are spider monkeys and woolly monkeys capital breeders?

Without direct measures of female body condition and how that changes (or not) seasonally, we cannot confidently classify the atelins of TBS as capital breeders. However, some of our results do offer support that spider monkeys and woolly monkeys follow a risk-averse breeding strategy. First, despite the variation in body size between spider monkeys and woolly monkeys, both species exhibited a clear clustering of births during the same time interval (May to September), with the peak number of births for each species each year usually falling in May and June. Second, sexual activity was rarely observed between April and July, a period in which fruit availability rapidly declines from peak levels. As fruit slowly became more abundant, typically in August and September, the number of copulations observed per month began to increase. Conceptions did not coincide with or immediately follow the mean annual peak in fruit availability. Instead, conceptions occurred as fruit availability is increasing habitat-wide, but before availability peaks, often by a couple of months. This suggests that females are becoming pregnant partway through a several month-long period of generally higher fruit abundance, with the potential to continue accumulating fat stores throughout the early months of gestation. Indeed, woolly monkeys have been reported to undergo substantial seasonal variation in weight gain, forming large fat deposits throughout the months of greatest fruit availability (Peres, 1991, 1993). Moreover, in the Ecuadorian Amazon, indigenous hunters report that they prefer to hunt woolly monkeys between May and August, during the "season of fat monkeys," when the monkeys are found pregnant and at their "fattest" (i.e., more yellow fat is present and the meat is more palatable; Rival, 2005, p. 98). Such a seasonal pattern of weight gain has not been reported for spider monkeys, but given that their diets are comparable to woolly monkeys (e.g., Dew, 2005), spider monkeys could plausibly be undergoing similar changes in body condition. Finally, along with investigating when conceptions do occur, we can also consider when they do not occur (Symington, 1987a). Both spider monkeys and woolly monkeys experience a period of nonconception between April and July, when fruit production is rapidly declining and stays at low levels in the forest for several months. This pattern of not conceiving when fruit availability is at its lowest has been observed in several spider monkey species and may reflect a decrease in female reproductive condition or changes in ovarian cycling that reduce the chances of conception (Campbell & Gibson, 2008; Symington, 1987a).

In this study, the number of births did not vary substantially between years, except in 2016, when both woolly and spider monkeys experienced twice as many births as recorded in several preceding years. Interestingly, this spike in births followed an exceptionally strong El Niño event (Climate. gov, 2017), which may have created climatic conditions favorable to fruit production (Wright et al., 1999). In 2015, the abundance of ripe fruit increased in August, several months sooner than seen in previous years and was maintained at exceptionally high levels for several months (Figure 2). Such a prolonged period of fruit productivity may have provided a greater opportunity for some females to improve body condition before conception, making it more likely for them to conceive and to lay down additional energy reserves during early gestation. Indeed, some of the shortest interbirth intervals in both species were observed following this period. For example, one woolly monkey female that had given birth in June 2014 was able to conceive for the next time ~10 months earlier than expected (February 2016), reducing her interbirth interval to 27 months. At least two other woolly monkey females who gave birth in 2014 likely achieved similarly reduced interbirth intervals; however, because these females belonged to *Lagothrix* group D and the birth of their successive infants were not recorded precisely, we can only crudely estimate that the interbirth intervals of these two females were between 24 and 30 months. For spider monkeys, two females who gave birth in 2013 and then again in 2016 had interbirth intervals of 37 and 38 months, respectively, roughly 7 months earlier than the average interbirth interval observed at our site over a 12-year period (Link et al., 2018). Higher birth rates and shorter interbirth intervals following periods of high fruit availability are not uncommon among primates that follow a capital breeding pattern (e.g., *Macaca fuscicularis* [van Noordwijk & van Schaik, 1999; van Schaik & van Noordwijk, 1985] and *Pongo pygmaeus* [Knott, 1998, 2001]), suggesting that successful female reproduction may indeed be tied to body condition.

In contrast to income breeders whose infant survival rates tend to plummet when infants are born outside of the window for optimal food conditions (e.g., *Lemur catta* [Gould et al., 2003], *Eulemur rubriventer* [Tecot, 2010]), capital breeders do not depend on increased food availability during lactation for infant survival, but rather on their own accumulated energy reserves before and during pregnancy, resulting in relatively low infant mortality. Following the expectations of a capital breeding pattern (Brockman & van Schaik, 2005; Di Bitetti & Janson, 2000; Janson & Verdolin, 2005), the atelins of TBS experienced low overall infant mortality. Only two of 36 woolly monkey infants disappeared over the 4-year period, and over the course of 10 years only six of 35 spider monkey infants died or disappeared. In spider monkeys, the two females who lost their infants within the first few weeks and remained in the group were able to conceive between 1 and 3 months later, while one female, whose infant disappeared after 3 months, had to wait an entire year before she could conceive again. Such observations may indicate that females who lose infants within the first few months still retain enough energy reserves to successfully conceive and support gestation, while females who lose infants after several months may have depleted their energy reserves further than can be replenished either in time to conceive or to successfully carry a pregnancy to term that year, driving them to forego reproduction until the next breeding season.

Low infant mortality rates in capital breeders may be linked to higher rates of prenatal mortality. Because capital breeders rely on energy stores acquired during pregnancy to support lactation later on, females who are unable to procure sufficient energy reserves to continue their current reproductive effort may be forced to abandon their pregnancies in early to mid-gestation (Brockman & van Schaik, 2005). In captive primates, capital breeders are known to experience higher rates of fetal loss in early pregnancy than other breeding patterns (Brockman & van Schaik, 2005; Hendrickx & Nelson, 1971; Hendrie et al., 1996). Although data on prenatal mortality are incredibly difficult to obtain for wild populations, hormonal profiles of female spider monkeys in Panama showed that some females do experience spontaneous abortion (Campbell et al., 2001), and, based on the examination of the reproductive organs of wild-caught female woolly monkeys (*Lagothrix poeppigii*) in Peru, Bowler et al. (2014) were able to estimate that embryo mortality may be as high as 33%.

For capital breeders, the degree of reproductive seasonality is often reduced in captivity (Brockman & van Schaik, 2005). Because captive animals are fed a relatively nutritious and consistent diet, their body condition likely remains stable and above the minimum threshold necessary to successfully conceive and gestate, regardless of the time of year. Woolly monkeys and spider monkeys in captivity certainly follow this pattern, giving birth throughout the year when held in captivity (Chapman & Chapman, 1990; Mooney & Lee, 1999), while this study and others clearly show reproductive seasonality in the wild. Given that seasonal variation in fruit production at TBS is less pronounced than at other tropical sites located farther from the equator, one might expect the degree of reproductive seasonality to be weaker in our atelin populations than at other field sites. However, this was not the case. Contrary to expectations, woolly and spider monkeys at TBS were characterized by somewhat higher degrees of reproductive seasonality than reported elsewhere for their respective genera (Table 5). The reason behind such a trend is not clear at this time, although it may be due to the limited sample size (Janson & Verdolin, 2005). We look forward to seeing if the pattern holds as more long-term data accumulate.

4.2 | Resumption of reproductive activity

After giving birth, spider monkey females took an average of ~8 months longer than woolly monkey females to resume copulating. This should not be surprising given that spider monkey females are both larger than woolly monkey females and exhibit longer periods of infant dependency. During a 23-month investigation of atelin juvenile development at TBS, Schmitt (2009) documented significantly more nursing bouts per focal sample between spider monkey females and their juvenile offspring than between woolly monkey females and their juvenile offspring, perhaps suggesting a longer period of milk dependency in spider monkeys. If the period of lactation is indeed extended for spider monkeys, then spider monkey females may take longer to recuperate lost energy reserves, and correspondingly, may refrain longer from sexual activity, until their body condition reaches a minimum critical threshold.

Among woolly monkeys, females who gave birth to a son took nearly 6 months longer to resume copulating than females who gave birth to a daughter. Such a pattern could indicate that male infants place greater energetic demands on their mothers than female infants, or it could represent a mother's differential investment in male versus female offspring. Given that woolly monkeys are among the most sexually dimorphic platyrrhine primates (with males being 25%–30% larger than females and with even greater dimorphism in canine length: Di Fiore et al., 2014), differences in male and female growth trajectories may lead to unequal energetic demands on the mother, whether through lactation effort and milk production or the cost of transporting a heavier infant. Longer durations and greater energetic costs of postnatal maternal care for sons compared with daughters have been observed in a number of primates, including spider monkeys (Chapman & Chapman, 1990; Symington, 1987b), chimpanzees (Nishida et al., 2003), mountain gorillas (Eckardt et al., 2016), and hanuman langurs (Ostner et al., 2005).

4.3 | Conclusions and future directions

At TBS, spider monkey and woolly monkey conceptions were tied to periods of increasing fruit availability, allowing females to accumulate and store energy reserves throughout gestation. As habitat wide fruit availability declined, so did the likelihood of conception and/or potentially the ability to accrue enough energy capital to successfully carry a pregnancy to term, as evidenced by the lack of births between November and February, 7–7.5 months later. Coupled with low rates of infant mortality and interannual variation in birth rates skewed by extreme fruiting events, the woolly monkeys and spider monkeys of TBS appear to follow a risk-averse breeding strategy typical of capital breeders.

Finally, due to the “slow” life histories of atelin primates, important reproductive parameters, such as age of first reproduction and interbirth intervals, can be extremely difficult to estimate in the absence of long-term data. We view this paper as a first step towards providing some of these important data and towards understanding the reproductive patterns of the atelin primates at TBS. Given that female body condition likely plays an important role in atelin reproduction, we believe a productive area for future research will involve regular, noninvasive tracking of female body condition, reproductive function, and fecundity using physiological markers (e.g., fecal progesterone to monitor a female's reproductive state and urinary c-peptide to monitor body condition [reviewed in Behringer & Deschner, 2017]), particularly in relation to fruit availability. It will also be informative to investigate further the influence of infant sex on maternal investment and energetic expenditure.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study may be made available by the corresponding author upon reasonable request.

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REFERENCES

Altmann, J. (1974). Observational study of behavior: Sampling methods. *Behaviour*, *49*(3), 227–266. https://doi.org/10.1163/156853974X00534

Altmann, J. (1980). *Baboon mothers and infants*. Harvard University Press.

Alvarez, S., Di Fiore, A., Champion, J., Pavelka, M. S., Páez, J., & Link, A. (2015). Male-directed infanticide in spider monkeys (Ateles spp.). *Primates*, *56*(2), 173–181. https://doi.org/10.1007/s10329-014-0454-y

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Batschelet, E. (1981). *Circular statistics in biology*. Academic Press.

Behringer, V., & Deschner, T. (2017). Non-invasive monitoring of physiological markers in primates. *Hormones & Behavior*, *91*, 3–18. https://doi.org/10.1016/j.yhbeh.2017.02.001

Blake, J. G., Guerra, J., Mosquera, D., Torres, R., Loiselle, B. A., & Romo, D. (2010). Use of mineral licks by white-bellied spider monkeys (*Ateles belzebuth*) and red howler monkeys (*Alouatta seniculus*) in eastern Ecuador. *International Journal of Primatology*, *31*(3), 471–483. https://doi.org/10.1007/s10764-010-9407-5

Blake, J. G., Mosquera, D., Loiselle, B. A., Swing, K., Guerra, J., & Romo, D. (2012). Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. *Ecotropica*, *18*, 137–146.

Bowler, M., Anderson, M., Montes, D., Pérez, P., & Mayor, P. (2014). Refining reproductive parameters for modelling sustainability and extinction in hunted primate populations in the Amazon. *PLOS One*, *9*(4), e93625. https://doi.org/10.1371/journal.pone.0093625

Brockman, D. K., & van Schaik, C. P. (2005). Seasonality and reproductive function. In D. K. Brockman, & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 269–306). Cambridge University Press.

Bronson, F. H. (1989). *Mammalian reproductive biology*. University of Chicago Press.

Campbell, C. J., & Gibson, K. N. (2008). Spider monkey reproduction and sexual behavior. In C. J. Campbell (Ed.), *Spider monkeys: Behavior, ecology, and evolution of the genus Ateles* (pp. 266–287). Cambridge University Press. https://doi.org/10.1017/CBO9780511721915.010

Campbell, C. J., Shideler, S. E., Todd, H. E., & Lasley, B. L. (2001). Fecal analysis of ovarian cycles in female black-handed spider monkeys (*Ateles geoffroyi*). *American Journal of Primatology*, *54*(2), 79–89. https://doi.org/10.1002/ajp.1014

Carnegie, S. D., Fedigan, L. M., & Melin, A. D. (2011). Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. *International Journal of Primatology*, *32*(5), 1076–1090. https://doi.org/10.1007/s10764-011-9523-x

Chapman, C. A., & Chapman, L. J. (1990). Reproductive biology of captive and free-ranging spider monkeys. *Zoo Biology*, *9*(1), 1–9. https://doi.org/10.1002/zoo.1430090102

Chapman, C. A., Chapman, L. J., Wrangham, R., Hunt, K., Gebo, D., & Gardner, L. (1992). Estimators of fruit abundance of tropical trees. *Biotropica*, *24*, 527–531.

Climate.gov. (2017). El Niño & La Niña (El Niño-Southern Oscillation)| NOAA Climate.gov. [online]. https://www.climate.gov/enso Accessed April 1, 2017.

Crockett, C. M., & Rudran, R. (1987). Red howler monkey birth data I: Seasonal variation. *American Journal of Primatology*, *13*(4), 347–368. https://doi.org/10.1002/ajp.1350130402

Dew, J. L. (2005). Foraging, food choice, and food processing by sympatric ripe-fruit specialists: Lagothrix lagotricha poeppigii and Ateles belzebuth belzebuth. *International Journal of Primatology*, *26*(5), 1107–1135. https://doi.org/10.1007/s10764-005-6461-5

Di Bitetti, M. S., & Janson, C. H. (2000). When will the stork arrive? Patterns of birth seasonality in Neotropical primates. *American Journal of Primatology*, *50*(2), 109–130. https://doi.org/10.1002/(SICI)1098-2345(200002)50:23.0.CO;2-W

Di Fiore, A. (1997). *Ecology and behavior of lowland woolly monkeys (Lagothrix lagotricha poeppigii, Atelinae) in Eastern Ecuador* (unpublished doctoral dissertation). University of California—Davis.

Di Fiore, A., & Fleischer, R. C. (2005). Social behavior, reproductive strategies, and population genetic structure of *Lagothrix poeppigii*. *International Journal of Primatology*, *26*(5), 1137–1173. https://doi.org/10.1007/s10764-005-6462-4

Di Fiore, A., Schmitt, C. A., & Fernandez-Duque, E. (2014). *Morphometrics of wild woolly monkeys: Implications of sexual dimorphism in body and canine size. American Journal of Physical Anthropology*. 83rd Annual Meeting of the American Association of Physical Anthropologists, April 2014, Calgary, Canada S58 (106).

Di Fiore, A., Link, A., Schmitt, C. A., & Spehar, S. N. (2009). Dispersal patterns in sympatric woolly and spider monkeys: Integrating molecular and observational data. *Behaviour*, *146*(4), 437–470.

Di Fiore, A., Fernandez-Duque, E., Link, A., Schmitt, C., Porter, A., Álvarez, S., Abondano, L., & Ellis, K. (2017). Estudios de primates en la Estación de Biodiversidad Tiputini. In D. Romo, D. Mosquera, K. Swing, A. Di Fiore, J. G. Blake, B. Loiselle, T. B. Ryder, S. de la Torre, T. Erwin, N. Pitman, D. F. Cisneros-Heredia, C. C. Voigt, R. J. Burnham, H. Alvarez, G. Vinueza, L. Abondano, S. Álvarez, E. M. Bruna, R. Durães, K. Ellis, E. Fernandez-Duque, S. J. Ghanem, J. Guerra, J. Hidalgo, C. Jenkins, A. Link, E. Maehr, F. Paniagua, A. Porter, M. Rodríguez, C. Schmitt, L. Seales, C. Snowdon, G. Stocks, W. P. Tori, J. Widmer, P. Yépez, & L. Zamorano (Eds.), *Los secretos del Yasuní: Avances en investigación en la Estación de Biodiversidad Tiputini, Universidad San Francisco de Quito* (pp. 73–83). Editorial USFQ.

Eckardt, W., Fawcett, K., & Fletcher, A. W. (2016). Weaned age variation in the Virunga mountain gorillas (*Gorilla beringei beringei*): Influential factors. *Behavioral Ecology and Sociobiology*, *70*(4), 493–507. https://doi.org/10.1007/s00265-016-2066-6

Ellis, K., & Di Fiore, A. (2019). Variation in space use and social cohesion within and between four groups of woolly monkeys (*Lagothrix lagotricha poeppigii*) in relation to fruit availability and mating opportunities at the Tiputini Biodiversity Station, Ecuador. In R. Reyna-Hurtado, & C. Chapman (Eds.), *Movement ecology of neotropical forest mammals* (pp. 141–171). Springer.

Emery Thompson, M. (2013). Reproductive ecology of female chimpanzees. *American Journal of Primatology*, *75*, 222–237. https://doi.org/10.1002/ajp.22084

Galvis, N., Link, A., & Di Fiore, A. (2014). A novel use of camera traps to study demography and life history in wild animals: A case study of spider monkeys (Ateles belzebuth. *International Journal of Primatology*, *35*(5), 908–918. https://doi.org/10.1007/s10764-014-9791-3

Gould, L., Sussman, R. W., & Sauther, M. L. (2003). Demographic and life-history patterns in a population of ring-tailed lemurs (Lemur catta) at Beza Mahafaly Reserve, Madagascar: A 15-year perspective. *American Journal of Physical Anthropology*, *120*(2), 182–194. https://doi.org/10.1002/ajpa.10151

Hartwig, W. C. (1996). Perinatal life history traits in New World monkeys. *American Journal of Primatology*, *40*(2), 99–130. https://doi.org/10.1002/(SICI)1098-2345(1996)40:23.0.CO;2-V

Hendrickx, A. G., & Nelson, V. G. (1971). Reproductive failure. In E. S. E. Hafez (Ed.), *Comparative reproduction of nonhuman primates* (pp. 403–425). CC Thomas Publishers.

Hendrie, T. A., Peterson, P. E., Short, J. J., Tarantal, A. F., Rothgarn, E., Hendrie, M. I., & Hendrickx, A. G. (1996). Frequency of prenatal loss in a macaque breeding colony. *American Journal of Primatology*, *40*(1), 41–53. https://doi.org/10.1002/(SICI)1098-2345(1996)40:13.0.CO;2-0

Janson, C., & Verdolin, J. (2005). Seasonality of primate births in relation to climate. In D. K. Brockman, & C. P. van Schaik (Eds.), *Seasonality in primates: Studies of living and extinct human and non-human primates* (pp. 307–350). Cambridge University Press.

Jönsson, K. I. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*, *78*, 57–66. https://doi.org/10.2307/3545800

Klein, L. L. (1971). Observations on copulation and seasonal reproduction of two species of spider monkeys, *Ateles belzebuth* and *A. geoffroyi*. *Folia Primatologica*, *15*(3), 232–248. https://doi.org/10.1159/000155382

Knott, C. (2001). Female reproductive ecology of the apes: Implications for human evolution. In P. T. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 429–463). Walter de Gruyter Publishing.

Knott, C. D. (1998). Changes in orangutan diet, caloric intake and ketones in response to fluctuating fruit availability. *International of Primatology*, *19*, 1061–1079. https://doi.org/10.1023/A:1020330404983

Kovach, W. L. (2011). *Oriana–circular statistics for windows, ver. 4*. Kovach Computing Services.

Lancaster, J. B., & Lee, R. B. (1965). The annual reproductive cycle in monkeys and apes. In I. De Vore (Ed.), *Primate behavior: Field studies of monkeys and apes* (pp. 486–513). Holt Rinehart and Winston.

Lewis, R. J., & Kappeler, P. M. (2005a). Are Kirindy sifaka capital or income breeders? It depends. *American Journal of Primatology*, *67*(3), 365–369. https://doi.org/10.1002/ajp.20190

Lewis, R. J., & Kappeler, P. M. (2005b). Seasonality, body condition, and timing of reproduction in *Propithecus verreauxi verreauxi* in the Kirindy Forest. *American Journal of Primatology*, *67*(3), 347–364. https://doi.org/10.1002/ajp.20187

Lindburg, D. G. (1987). Seasonality of reproduction in Primates. In G. Mitchell, & J. Erwin (Eds.), *Comparative primate biology, vol. 2B: Behavior, cognition and motivation* (pp. 167–218). Alan R. Liss.

Link, A. (2011). *Social and ecological determinants of "fission-fusion" sociality and grouping strategies in the white bellied spider monkey (Ateles* *belzebuth belzebuth) in a lowland rainforest in Western Amazonia* (unpublished doctoral dissertation). New York University.

Link, A., Milich, K., & Di Fiore, A. (2018). Demography and life history of a group of white-bellied spider monkeys (*Ateles belzebuth*) in western Amazonia. *American Journal of Primatology*, *80*(8), e22899. https://doi.org/10.1002/ajp.22899

Link, A., Galvis, N., Fleming, E., & Di Fiore, A. (2011). Patterns of mineral lick visitation by spider monkeys and howler monkeys in Amazonia: Are licks perceived as risky areas. *American Journal of Primatology*, *73*(4), 386–396. https://doi.org/10.1002/ajp.20910

Milton, K. (1981). Estimates of reproductive parameters for free-ranging *Ateles geoffroyi*. *Primates*, *22*, 574–579. https://doi.org/10.1007/BF02381250

Mooney, J. C., & Lee, P. C. (1999). Reproductive parameters in captive woolly monkeys (*Lagothrix lagotricha*). *Zoo Biology*, *18*(5), 421–427. https://doi.org/10.1002/(SICI)1098-2361(1999)18:53.0.CO;2-6

Nishida, T., Corp, N., Hamai, M., Hasegawa, T., Hiraiwa-Hasegawa, M., Hosaka, K., Hunt, K. D., Itoh, N., Kawanaka, K., Matsumoto-Oda, A., Mitani, J. C., Nakamura, M., Norikoshi, K., Sakamaki, T., Turner, L., Uehara, S., & Zamma, K. (2003). Demography, female life history, and reproductive profiles among the chimpanzees of Mahale. *American Journal of Primatology*, *59*(3), 99–121. https://doi.org/10.1002/ajp.10068

Nishimura, A. (2003). Reproductive parameters of wild female *Lagothrix lagotricha*. *International Journal of Primatology*, *24*(4), 707–722. https://doi.org/10.1023/A:1024681703616

Nishimura, A., Wilches, A. V., & Estrada, C. (1992). Mating behaviors of woolly monkeys, *Lagothrix lagotricha*, at La Macarena, Colombia (III): Reproductive parameters viewed from a long-term study. *Field Studies of New World Monkeys, La Macarena, Colombia*, *7*, 1–7.

Ostner, J., Borries, C., Schulke, O., & Koenig, A. (2005). Sex allocation in a colobine monkey. *Ethology*, *111*(10), 924–939. https://doi.org/10.1111/j.1439-0310.2005.01102.x

Peres, C. A. (1991). Humboldt's woolly monkeys decimated by hunting in Amazonia. *Oryx*, *25*(2), 89–95. https://doi.org/10.1017/S0030605300035122

Peres, C. A. (1993). Notes on the primates of the Juruá River, western Brazilian Amazonia. *Folia Primatologica*, *61*(2), 97–103. https://doi.org/10.1159/000156735

R Core Team (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org

Richard, A. F., Dewar, R. E., Schwartz, M., & Ratsirarson, J. (2000). Mass change, environmental variability and female fertility in wild *Propithecus verreauxi*. *Journal of Human Evolution*, *39*(4), 381–391. https://doi.org/10.1006/jhev.2000.0427

Rival, L. (2005). The growth of family trees: Understanding Huaorani perceptions of the forest. In A. Surrallés, & P. G. Hierro (Eds.), *The land within: Indigenous territory and the perception of the environment* (pp. 90–109). IWGIA.

Schmitt, C. A. (2009). *Comparative behavior, development and life history of wild juvenile atelin primates (Ateles belzebuth and Lagothrix poeppigii)* (unpublished doctoral dissertation). New York University.

Shimooka, Y., Campbell, C., Di Fiore, A., Felton, A., Izawa, K., Link, A., & Wallace, R. (2008). Demography and group composition of spider monkeys. In C. J. Campbell (Ed.), *Spider monkeys: The biology, behavior and ecology of the genus Ateles* (pp. 329–348). Cambridge University Press.

Snodderly, D. M., Ellis, K. M., Lieberman, S. R., Link, A., Fernandez-Duque, E., & Di Fiore, A. (2019). Initiation of feeding by four sympatric Neotropical primates (Ateles belzebuth, Lagothrix lagotricha poeppigii, Plecturocebus (Callicebus) discolor, and Pithecia aequatorialis) in Amazonian Ecuador: Relationships to photic and ecological factors. *PLOS One*, *14*(1), e0210494. https://doi.org/10.1371/journal.pone.0210494

Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.

Stephens, P. A., Boyd, I. L., McNamara, J. M., & Houston, A. I. (2009). Capital breeding and income breeding: Their meaning, measurement, and worth. *Ecology*, *90*(8), 2057–2067. https://doi.org/10.1890/08-1369.1

Stevenson, P. R. (2004). Phenological patterns of woody vegetation at Tinigua park, Colombia: Methodological comparisons with emphasis on fruit production. *Caldasia*, *26*(1), 125–150.

Strier, K. B. (1996). Reproductive ecology of female Muriquis (Brachyteles arachnoides). In M. A. Norconk, A. L. Rosenberger, & P. A. Garber (Eds.), *Adaptive radiations of neotropical primates* (pp. 511–532). Springer US. https://doi.org/10.1007/978-1-4419-8770-9_29

Strier, K. B., & Ziegler, T. E. (1997). Behavioral and endocrine characteristics of the reproductive cycle in wild muriqui monkeys, *Brachyteles arachnoides*. *American Journal of Primatology*, *42*(4), 299–310. https://doi.org/10.1002/(SICI)1098-2345(1997)42:43.0.CO;2-S

Strier, K. B., Mendes, S. L., & Santos, R. R. (2001). Timing of births in sympatric brown howler monkeys (Alouatta fusca clamitans) and northern muriquis (Brachyteles arachnoides hypoxanthus). *American Journal of Primatology*, *55*(2), 87–100. https://doi.org/10.1002/ajp.1042

Symington, M. M. (1987a). *Ecological and social correlates of party size in the black spider monkey, Ateles paniscus chamek* (unpublished doctoral dissertation) Princeton University.

Symington, M. M. (1987b). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioral Ecology and Sociobiology*, *20*(6), 421–425. https://doi.org/10.1007/BF00302985

Tecot, S. R. (2010). It's all in the timing: Birth seasonality and infant survival in Eulemur rubriventer. *International Journal of Primatology*, *31*, 715–735. https://doi.org/10.1007/s10764-010-9423-5

van Buuren, S., & Groothuis-Oudshoorn, K. (2011). Mice: Multivariate imputation by chained equations in R. *Journal of Statistical Software*, *45*(3), 1–67. https://doi.org/10.18637/jss.v045.i03

van Noordwijk, M. A., & van Schaik, C. P. (1999). The effects of dominance rank and group size on female lifetime reproductive success in wild long-tailed Macaques, Macaca fascicularis. *Primates*, *40*(1), 105–130. https://doi.org/10.1007/BF02557705

van Schaik, C. P., & van Noordwijk, M. A. (1985). Interannual variability in fruit abundance and the reproductive seasonality in Sumatran long-tailed macaques (*Macaca fascicularis*). *Journal of Zoology*, *206*(4), 533–549. https://doi.org/10.1111/j.1469-7998.1985.tb03557.x

Wright, S. J., Carrasco, C., Calderón, O., & Paton, S. (1999). The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, *80*(5), 1632–1647.

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