

## Reproductive Seasonality in Female Capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica

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Received: 24 January 2011 / Accepted: 22 March 2011 / Published online: 3 May 2011  
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**Abstract** The income-capital breeding model was developed to explain birth seasonality and reproductive strategies in female animals in relation to the abundance of food energy in the environment. An income breeder uses currently available energy and acts so as to maximize either maternal survival or weanling survival, depending on the relationship between timing of births and abundance of food energy. A capital breeder stores energy reserves for future reproductive use. Here we examined energetic influences on reproductive seasonality in a population of female white-faced capuchins (*Cebus capucinus*) living in a seasonal dry forest in Costa Rica. Our objectives were to determine: 1) the degree of fruiting seasonality in capuchin food trees and 2) the temporal relationship between capuchin births/conceptions and fruit abundance. Our sample included 25 yr of birth data ( $N=100$  births), 4 yr of capuchin fruit tree phenology data, and 18 mo of ovarian hormone data, which we used to calculate gestation lengths and estimate conception dates. Using circular statistics, we found that the mean peak in fruit abundance occurs in June, and that this population of capuchins reproduces seasonally, with 44% of births occurring within a 3-mo period (May to July, mean month=May). We propose that white-faced capuchins can be generally classified as income breeders that maximize maternal survival instead of weanling survival and that they time infant births such that the most energy expensive period of reproduction, mid-to-late lactation, occurs during the mean peak in fruit abundance.

**Keywords** Breeding patterns · Fruit abundance · Maternal survival · Reproductive strategies

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## Introduction

The degree of seasonality in the reproductive patterns of primates and other mammals is generally agreed to be a direct consequence of the strength of seasonal variation in ecological variables such as food and rainfall (Crockett and Rudran 1987; Di Bitetti and Janson 2000; van Schaik and van Noordwijk 1985). Most primates show some sort of birth seasonality because food abundance usually cycles in predictable ways (Brockman and van Schaik 2005), but the degree of that seasonality can vary depending on the climatic factors, e.g., rainfall and photoperiod, that affect productivity patterns (van Schaik and Pfannes 2005). Van Schaik *et al.* (1999) defined highly seasonal breeders as those wherein >67% of births are concentrated in a single 3-mo period, and moderately seasonal breeders as those wherein 33–67% of births occur in a 3-mo period. Natural selection is expected to favor reproductive patterns that time births or weaning periods to the optimal period of energy availability, thus maximizing survival for the mother and the weanling.

The income-capital breeding model, which was first developed to explain breeding patterns in birds (Drent and Daan 1980), has more recently been used to characterize reproductive patterns in nonhuman primates (Brockman and van Schaik 2005; Janson and Verdolin 2005; Lewis and Kappeler 2005; Richard *et al.* 2000). An income breeder is described as one that uses current energy intake and other proximal cues, e.g., photoperiod, rainfall, to initiate reproductive events. In contrast, a capital breeder is one that builds and stores energy reserves for future use during reproduction and draws from those reserves during gestation (Stearns 1992).

Attempts to classify nonhuman primates into one or the other of the income-capital breeding categories have been difficult for several reasons. First, most primates have reproductive cycles that are longer than the annual cycle of resources within their habitats, whereas the original income-capital terminology was applied to animals whose reproductive cycle was only as long as their annual resource cycle (Brockman and van Schaik 2005; Drent and Daan 1980). Second, it is important to be clear as to what stage of the cycle, e.g., conception, gestation, lactation, weaning, is being modeled when predicting a reproductive pattern for any single species within the income-capital framework (Janson and Verdolin 2005; Lewis and Kappeler 2005). Consequently, various meta-analyses have attempted to identify the predictors that explain the diversity of seasonal birth patterns seen among primates by modifying the original dichotomous income-capital model (Brockman and van Schaik 2005; Di Bitetti and Janson 2000; Janson and Verdolin 2005).

According to Janson and Verdolin (2005), nonhuman primates that are considered income breeders generally can be divided into 2 categories: Income-I and Income-II breeders (Table I). Income-I breeders are characterized by small body mass (<3 kg) and low adult survival and they depend on highly seasonal food resources such as insects, new leaves, or fruits. They also consistently time births such that infant weaning will coincide with the peak in food abundance, or the period of time with the greatest abundance of food or nutrients. Income-I breeders have adopted a reproductive strategy to maximize infant survival by reducing energetic stress on infants during weaning. Di Bitetti and Janson (2000) predicted that infant survivorship would be greater for infants that are born during the mean peak in

**Table 1** Derived hypotheses and predictions explaining the reproductive seasonality in primates with regard to births, conceptions, and infant survival

Hypotheses	Predictions <sup>a</sup>
1. Weanling survival (Income-I)	Janson and Verdolin (2005): <ul style="list-style-type: none"> <li>• Births occur during the mean peak in food abundance.<sup>b</sup></li> <li>• Low adult survival, i.e., short life span.</li> </ul> Di Bitetti and Janson (2000): <ul style="list-style-type: none"> <li>• Infant survival will be higher for infants born during the mean peak in fruit abundance.</li> </ul>
2. Maternal survival (Income-II) or (Relaxed Income)	Janson and Verdolin (2005) and Brockman and van Schaik (2005): <ul style="list-style-type: none"> <li>• Births occur before the mean peak in food abundance.</li> <li>• Long adult lifespan.</li> </ul>
3. Maternal condition (Capital)	Janson and Verdolin (2005): <ul style="list-style-type: none"> <li>• Births occur after the mean peak in food abundance by a period of time equal to the delay in conception plus the gestation length.<sup>c</sup></li> </ul>

<sup>a</sup> Each set of authors elaborates in more detail on each of their set of predictions in their respective studies.

<sup>b</sup> The mean peak in food abundance here refers to the period of the year with the greatest food/nutrient abundance.

<sup>c</sup> Janson and Verdolin (2005) suggest this time period is *ca.* 6 mo for monkeys with 5-mo gestation lengths.

food abundance vs. ones that are not (Altmann 1980; Butynski 1988; Crockett and Rudran 1987). In contrast, Income-II breeders are characterized by a body mass >3 kg and also depend on highly seasonal food resources, but they time births to occur just before the mean peak in food abundance, which allows for the period of mid-to-late lactation to coincide with this peak (Janson and Verdolin 2005). These species have adopted a strategy that maximizes maternal survival by minimizing energetic stress on the lactating mother, because lactation is considered to be the most energetically expensive time of reproduction (Altmann 1980; Bronson 1989; Clutton-Brock *et al.* 1989).

Capital breeding primates store nutrients during the months of high food abundance and then give birth after the mean peak in food abundance by a period of time equal to the delay in conception plus the gestation length (Table 1) (Janson and Verdolin 2005; Stearns 1992). The reproductive strategy for this group is dependent on maternal body condition, in that a certain physical threshold, e.g., body mass, must be reached before ovarian cycling and conception can occur. Capital breeders tend to rely on nutrients stored before and during pregnancy (Brockman and van Schaik 2005; Janson and Verdolin 2005). This strategy is thought to be more prevalent in species living in habitats where peaks in food abundance can be unpredictable and in species with long interbirth intervals, e.g., long-tailed macaques (*Macaca fascicularis*: van Schaik and van Noordwijk 1985), orangutans (*Pongo abelii*: Wich *et al.* 2004), and humans (Seidman *et al.* 1989).

Brockman and van Schaik's (2005) meta-analysis indicated that a modified model was needed to explain the variety of breeding patterns among primates, and they suggested the model instead be viewed as a range of strategies as opposed to 2 strict

classifications, calling their modification the “income-capital continuum model.” Their model is similar to that described by Janson and Verdolin (2005), except that Brockman and van Schaik’s analogous category for Income-II breeders is referred to as “relaxed income breeders” (Table I, hypothesis 2). Species that adopt this relaxed income strategy are characterized by reproductive patterns that overlap those found among income and capital breeders, including conceptions that are cued by exogenous environmental stimuli, e.g., photoperiod, that in turn indicates impending food production, and endogenous maternal condition thresholds (Brockman and van Schaik 2005).

The meta-analysis conducted by Janson and Verdolin (2005) concluded that capuchins, in general, fit the maternal survival strategy (Income-II) because they give birth too late to fit the pattern found for Income-I breeders and they have long adult life spans, suggesting that maximizing maternal reproductive success is important (Janson and Verdolin 2005). However, an earlier meta-analysis by Di Bitetti and Janson (2000) had suggested that capuchins follow the pattern of Income-I breeders or the weanling survival strategy because, even though they tend to give birth shortly before or during the mean peak in food abundance, weaning may not occur until >1 yr after birth; thus weaning is timed to coincide with the mean peak in food abundance for the weanling (Di Bitetti and Janson 2000). Both conclusions may be valid because in all capuchin species, adults have long life spans and weaning can occur from 12 to 15 mo postpartum (Di Bitetti and Janson 2000; Fragaszy *et al.* 2004). The difference between these 2 analyses (Di Bitetti and Janson 2000; Janson and Verdolin 2005) is that each used slightly different approaches to test the relationship between the timing of births and food abundance. Di Bitetti and Janson (2000) reviewed published data on the reproductive patterns of various species, whereas Janson and Verdolin (2005) considered the timing of the solstices in different geographic areas as an indicator of food abundance and then related birth patterns to this timing. Given the poor resolution of these indirect measures, there is a clear need to investigate birth seasonality in primate populations in which long-term birth patterns and accurate phenology patterns of the relevant food sources are known, as noted by the authors of the aforementioned studies. Our current study helps to fill this gap by drawing on birth and capuchin fruit tree phenology data from a long-term study (>30 yr) on white-faced capuchins (*Cebus capucinus*) living in the Santa Rosa Sector of the Area de Conservación Guanacaste, Costa Rica.

We here examine the energetic influences on the reproductive seasonality of female white-faced capuchins. Our main objectives are 1) to determine the degree of fruiting seasonality among capuchin food trees and 2) to determine the relationship between the timing of capuchin births/conceptions and the abundance of fruit on the trees eaten by capuchins in Santa Rosa.

Our specific predictions with regard to seasonality are:

- 1) The timing of the mean peak in fruit abundance differs from a random distribution across the year, and is instead concentrated in certain months.
- 2) The timing of births/conceptions differs from a random distribution across the year, and instead peaks in certain months.

With regard to the hypotheses and predictions derived from the income-capital breeding model (Table I), our predictions are the following:

- 3) Janson and Verdolin (2005) made their prediction for weanling survival based on the timing of weaning, which we are unable to test directly. Because weaning occurs 12–15 mo after birth in this population, we instead make our prediction about birth timing on the assumption that weaning occurs *ca.* 1 yr after birth and in the same season of the year as birth. Therefore, if the reproductive strategy of female capuchins is to maximize infant survival (Income-I breeders), then we predict:
  - a) Births will be timed to occur during the mean peak in fruit abundance so that infant weaning occurs during the annual mean peak in fruit.
  - b) Infant survival will be greater for infants born during or around the time of the mean peak in fruit abundance.
- 4) In this population of capuchins, lactating females' energy intake rates peak *ca.* 8 wk after giving birth, suggesting that the most energetically demanding part of lactation for this species is the period starting on or around 8 wk postpartum (McCabe and Fedigan 2007). If the reproductive strategy of female capuchins is to maximize maternal survival (Income-II breeders/relaxed income breeders), then we predict:
  - a) Births will be timed to occur shortly before the mean peak in fruit abundance to time peak lactation energy needs with the mean peak in energy abundance.
  - b) If the reproductive strategy of female capuchins is based on maternal condition (capital breeder), then we predict:
    - a. Births will occur *ca.* 6–6.5 mo after the mean peak in food abundance, which is the time period equal to the delay in conception plus a gestation length of *ca.* 5.5 mo (*Cebus capucinus*: (Carnegie et al. 2011).

## Methods

### Study Site and Species

We conducted the study in Sector Santa Rosa (SSR), the original sector of the Area de Conservación Guanacaste (ACG). SSR is located in northwestern Costa Rica (10.82049 lat.; 85.62813 long.), the boundaries of which encompass 108 km<sup>2</sup> of dry deciduous forest fragments of semievergreen riparian and regenerating pasture land (Janzen 1983). The forest type is classified as a tropical dry forest, which experiences a distinct dry season when virtually no rain falls (mid-December–mid-May), and a distinct wet season (mid-May–mid-December), when 800–2600 mm of rain can fall annually (Janzen 1983).

White-faced capuchins live in multimale, multifemale groups consisting of immigrant males and natal females and their immature offspring. Females start to show hormonal activity and ovarian cycling at 5 yr of age and can produce their first infant at 6 yr (Carnegie et al. 2005). The interbirth interval for the study population

averages 2.25 yr when the previous infant survives vs. 1.05 yr if the previous infant dies before 12 mo of age (Fedigan *et al.* 2008). Capuchins are omnivores, eating a range of fruit, flowers, seeds, insects, and small vertebrates including birds, bats, squirrels, and coati pups (Fragaszy *et al.* 2004). However, fruit constitutes a large part of their diet, making up 50–80% of what they eat (Chapman and Fedigan 1990; Vogel 2004).

### Focal Sample

The birth data for this study were collected between 1986 and 2010 (25 yr) and fruit abundance data collected between 2006 and 2009 (4 yr). Both groups of data come from L. M. Fedigan's long-term unpublished database. S. D. Carnegie collected ovarian hormone data, used to estimate gestation lengths and conception dates, between May 2005 and November 2006. All individuals can be identified by natural markings such as broken digits, scars, fur coloring, blotches on faces and the brow, and peak shape, i.e., shape of the edge of the black fur cap on forehead.

### Fruit Abundance

In previous studies, researchers used rain as a proxy for food abundance (Fedigan *et al.* 2008), but we used a more direct estimate to assess the seasonality of fruit abundance. From January 2006 to December 2009, we scored monthly  $\leq 43$  different species (*ca.* 430 individual trees in total) of fruit trees eaten by capuchins on: 1) fruit coverage, measured by observing the proportion of the canopy that contained fruit and scored on a 4-point scale from 0 to 100% coverage (Chapman *et al.* 1992); and 2) fruit maturity, also measured on a 4-point scale as the proportion of fruit on the tree at different stages of ripeness: 0% meant none of the fruit was ripe, and 4 meant up to 100% of the fruit was ripe. Using these calculations, we determined the peak month, i.e., the month of greatest fruit production, for each species for each year. This is sometimes preferable to, e.g., scoring the percentage of fruiting trees each month because such data are not independent because the mean fruiting duration is usually longer than the sampling interval used, i.e., 1 mo (Morellato *et al.* 2010). However, to confirm that the statistical method we use in assessing mean peak fruit abundance is also biologically relevant, we also employed directional analysis on the estimates of the mean fruit biomass produced monthly at our site. If peak fruiting is an accurate measure of seasonality in fruit abundance, we anticipate that our fruit biomass data will show a pattern similar to the statistical analysis.

We estimated monthly fruit biomass data based on the size and density of the fruit trees, in combination with the monthly phenological data (Melin 2011). We calculated fruit biomass of a species by summing the fruit biomass of all individual trees of that species located in forest transects (Melin 2011) using the following formula:  $F=47*DBH^{1.9}$  (Peters *et al.* 1988), wherein  $F$ =estimated grams of fruit produced by a given DBH. We then multiplied each species' value by the proportion of individuals of that species containing ripe fruit in the phenology trail each month. We combined the values for all species and divided them by the total transect area to estimate total grams of fruit/hectare (ha) produced each month.

## Birth and Conception Data

Data used to calculate birth and conception seasonality came from 5 different capuchin groups living in Sector Santa Rosa (Table II). Birth dates included in this analyses are certain to  $\leq 30$  d (birth sample= $N_b=100$ ). We used the average gestation length of wild, female capuchins ( $157.83 \pm 8.13$  d) to estimate conception dates for all births used in the sample (Carnegie *et al.* 2011).

## Infant Survivorship

We compared the survivorship of infants that were born  $\leq 1$  mo of the mean peak in fruit abundance (1 mo before, during the peak, and 1 mo after=3-mo range) with those born outside of that 3-mo peak in fruit abundance. We divided infants into those that lived  $>12$  mo and those that lived  $<12$  mo. One year is considered the critical length of survival because the majority of infant deaths occur during the first year of life (Fedigan 2003; Fedigan *et al.* 2008), and because at 1 yr, infants are beginning to be weaned and the loss of an infant at that age would not affect the mother's resumption of cycling or the mother's subsequent IBI (Fedigan *et al.* 2008). We removed 4 infants from the main sample of 100 (infant survivorship sample= $N_{is}=96$ ) because they were known to have died from infanticide, which is not influenced by the abundance of fruit. We conducted several analyses for infant survival. The first one assessed infant survival for infants born in the 3-mo period surrounding the mean peak in fruit abundance—May, June, and July—and a second assessed infant survival for infants born during the entire time of fruit abundance between April and September. We also ran additional analyses after removing infants that died before 3 wk of age, juveniles that died between 12 and 15 mo of age, and infants that were born out-of-season, i.e., May–July; we assume there is increased nutritional stress on mothers during this time.

## Statistical Analysis

We used directional or circular statistics to investigate the degree of seasonality in fruit abundance and reproductive events. Circular statistics allows one to examine

**Table II** Capuchin groups, the number of capuchin-years, and the number of births included in the birth and conception analyses

Groups	Years represented	No. of years	No. of births
Cerco de Piedra (CP)	1986–2010	25	40
Los Valles (LV)	1990–2010	21	34
Exclosure (EX)	2007–2010	4	5
Guanacaste (GN)	2007–2010	4	15
Sendero (SN)	1986–1993	8	6
Total		53	$N_b=100^a$

<sup>a</sup>  $N_b$  refers to the sample that is used for the birth and conception seasonality analysis, which differs from the sample used for the infant survival analysis ( $N_{is}$ ).

the distribution of data that can be plotted on a circular scale such as compass directions or months of a year, where there is no 0 point and the axis is divided equally into angles  $\leq 360^\circ$  (Batschelet 1981; Fisher 1993; Zar 1999). For example, when investigating monthly seasonality, the total length of the circular axis is 1 yr, creating an axis divided into 12 equal sections, with each sector being  $30^\circ$  wide. If the observations are available on a monthly basis, each month is converted to the numeric value of the month of the year, e.g., to a maximum of 12, then converted to an angle that divides the circle into equal sections (Zar 1999). For example, January would be represented at the midpoint of the first section at  $15^\circ$ , February at  $45^\circ$ , and December at  $345^\circ$ .

Each observation, e.g., the number of births in a month, is converted to a vector with an angle,  $a$ , and a length,  $r$ , and analysis of all the vectors, using trigonometric functions (Batschelet 1981; Zar 1999), results in a mean vector angle and a mean vector length of  $r$ . The mean angle can be converted back to a mean date, which provides information on when the variable of interest is most concentrated, e.g., in June. The mean vector length,  $r$ , gives an indication of how closely spaced the observations are on the axis ranging from 0 to 1.0, with 0 meaning there is a perfectly equal distribution around the axis and 1.0 meaning that all observations occurred in the same interval (Morellato *et al.* 2010).

There are some caveats to interpreting the value of  $r$  (Janson and Verdolin 2005; Morellato *et al.* 2010). First, the value of  $r$  is accurate only for unimodal distributions, not for bimodal distributions. However, if the data are arranged symmetrically opposite each other on the circular scale, i.e., bimodal, doubling the angles for each observation can convert the data to unimodal so that  $r$  can be recalculated (Batschelet 1981; Zar 1999). Second, grouped data, such as monthly data, can result in a value of  $r$  that is lower than what the plotted distribution shows, but this is easily fixed by applying a specific correction term to  $r$  (Zar 1999).

We used the circular statistical program Oriana ver. 3 (Kovach 2009) to assess the degree of seasonality and the mean month of the peak in fruit abundance and reproductive events. For count data only, the program calculates Raleigh's Uniformity test to evaluate the probability that the data are distributed uniformly on the circular axis (Batschelet 1981). For linear data, e.g., weighted data, the method can still be applied, but the Rayleigh test is not applicable. The Oriana program also recognizes when grouped data are used and applies the appropriate correction term when calculating the mean vector length,  $r$  (Kovach 2009).

We tested infant survivorship using the Kaplan-Meier SURVIVAL analysis, which accounts for censored events, and performed the analysis via PASW Statistics version 17.01.

#### Ethical Note

All data collection adhered to the legal requirements of Costa Rica and the Sector Santa Rosa, Area de Conservación, Guanacaste, Costa Rica, and complied with the Life and Environmental Science Animal Care Committee (University of Calgary; certification no. BIO8R-03).

## Results

### Fruit Abundance

The distribution of fruit abundance at the Santa Rosa site differs significantly from a random distribution (Rayleigh test:  $Z=22.876$ ,  $p<0.001$ ; Table III). The mean month of the peak in capuchin fruit abundance, averaged over a 4-yr period, is June, and the mean date is June 17 (Fig. 1). However, fruit is readily available to capuchins starting around April and lasting until the end of September. When we subjected the fruit biomass data to directional analysis, the mean angle was  $178.55^\circ$  giving a mean date of *ca.* June 30th, which is very close to that of our analysis of peak fruit abundance based on the peak fruiting month per species (June 17).

### Births and Conceptions

The frequency of capuchin births differs significantly from a random distribution (Rayleigh test: births:  $Z=18.006$ ;  $p<0.001$ ; Table III). Over the 25-yr period evaluated (1986–2010), the mean month of capuchin births is May, with the mean date occurring around May 13 (Fig. 2a). We found that 44% of births occur within the 3-mo period surrounding the mean peak of fruit abundance —May, June, and July— and 80% of births occur during the 6-mo period of February through July.

**Table III** Circular statistics results for the distribution fruit abundance, births, and conceptions

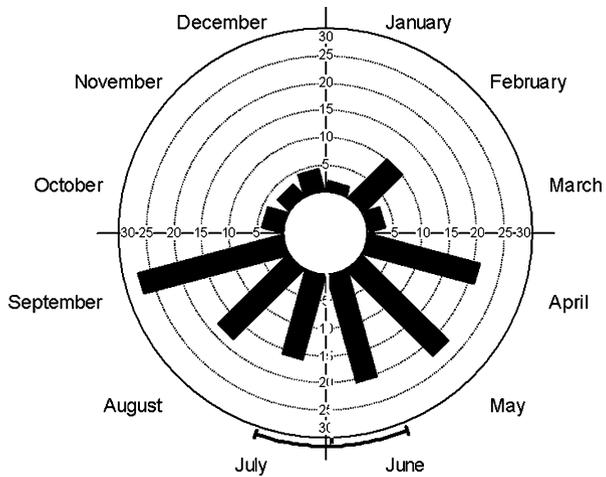
	Fruit abundance	Births	Conceptions
Number of observations	150 <sup>a</sup>	100	100
Group width and number	30° (12)	30° (12)	30° (12)
Mean angle ( $\bar{\alpha}$ )	165.84°	131.17°	332.73°
Mean date <sup>b</sup>	June 17	May 13	December 3
Mean group	June	May	December
Length of mean vector ( $r$ ) <sup>c</sup>	0.391	0.424	0.411
Concentration	0.848	0.937	0.901
Circular std. deviation	78.572°	75.022°	76.424°
Std. error of mean	8.129°	9.419°	9.089°
95% CI for $\bar{\alpha}$ ( $\pm$ )	149.9°/181.77°	113.35°/148.985°	314.262°/351.191°
Rayleigh test ( $Z$ )	22.876	18.006	16.878
Rayleigh test ( $p$ )	<0.001	<0.001	<0.001

<sup>a</sup> Refers to the number of observations of the peak month of fruiting for each species in each year measured (range of tree species is 29–43).

<sup>b</sup> We calculated the mean date according to the following equation: mean date=(365\* $\bar{\alpha}$ )/360° (Zar 1999); this date may vary by one day because of leap years. This date is the time period when the variable of interest is most concentrated (see text).

<sup>c</sup> The mean vector  $r$  gives an indication of the degree of clustering around the mean date on a 0–1 scale, with 0 indicating no clustering and a 1 indicating that all values are the same.

**Fig. 1** Circular histogram illustrating the distribution and the mean in the peak of fruit abundance for capuchin fruit trees in Santa Rosa from 2006 to 2009. Fruit abundance throughout the year differs significantly from a random distribution ( $Z=22.876$ ,  $p<0.001$ ), with June being the mean month of fruit abundance (mean date=June 17), but fruit is available from April to September. We collected phenology data at the beginning of the month.



Births can take place all year round, but there is a clear increase in births starting in February (Fig. 2a), which is 2 mo before the start of the increase in fruit abundance (April); therefore, costs associated with peak lactation occur at the same time as the abundance of fruit begins to increase. This pattern supports the Income-II (maternal survival) hypothesis.

Using 158 d as the average gestation length, we counted back from the day of parturition to estimate a conception date. Not surprisingly, we found that conceptions also differ significantly from a random distribution throughout the year (Rayleigh test:  $Z=16.878$ ,  $p<0.001$ ). The mean month of conceptions is December, with the mean date on December 3 (Fig. 2b).

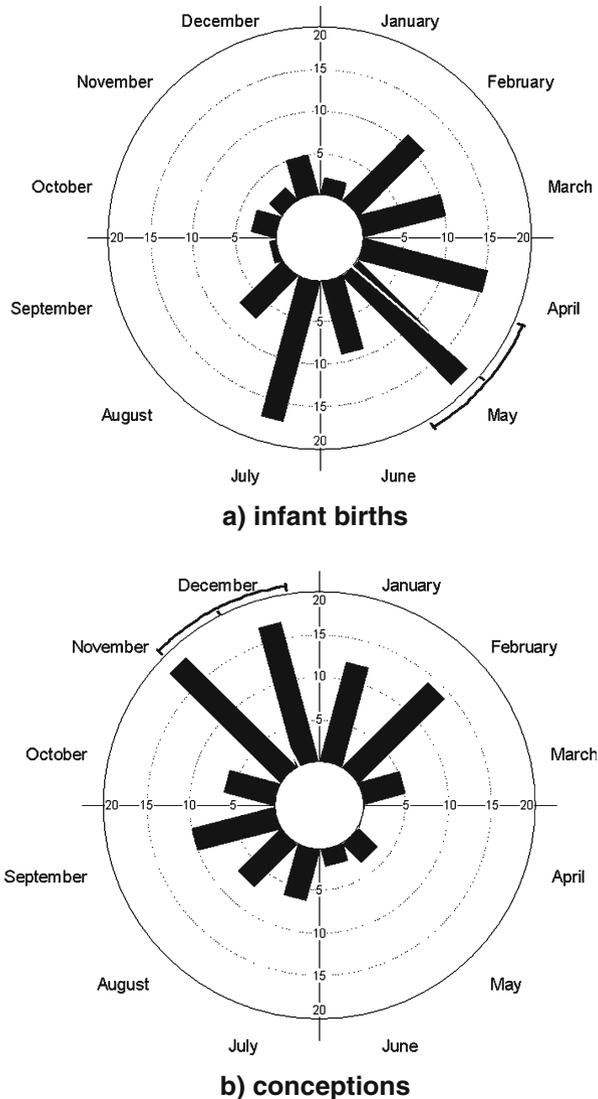
### Infant Survivorship

We found no difference in infant survivorship to 12 mo of age between infants that were born between May to July ( $\chi^2=0.008$ ,  $df=1$ ,  $p=0.928$ ) vs. those that were not. Nor did we find a difference in infant survival between infants born during the entire period of fruit abundance, i.e., April–September; ( $\chi^2=0.628$ ,  $df=1$ ,  $p=0.428$ ), vs. those that were born October–March. There was no difference in survivorship when we removed infants that died before 3 wk of age (5 infants), or that died between 12 and 15 mo of age (4 juveniles). Of the 52 infants born outside the period of mean fruit abundance, only 3 died between the ages of 2 and 5 mo and we found no difference in survival for infants within this age group.

### Discussion

The availability of long-term birth and multiyear fruit abundance data has allowed us to evaluate the pattern of capuchin births in relation to fruit abundance and to test the predictions of the income-capital breeding model as described by Janson and Verdolin (2005) and Brockman and van Schaik (2005). We found that fruit abundance and births do follow a seasonal pattern and that the mean birth peak

**Fig. 2** Circular histograms illustrating the distribution and the mean of **(a)** capuchin infant births and **(b)** conceptions in Sector Santa Rosa ( $N=100$ ). The timing of both births and conceptions differs significantly from a random distribution (births:  $Z=22.876$ ,  $p<0.001$ ; conceptions:  $Z=22.876$ ,  $p<0.001$ ). May is the mean month of births, whereas December is the mean month of conceptions.



occurs slightly before the mean abundance of fruit peaks, but that infant survival is not contingent on being born during this time.

#### Seasonality of Fruit Abundance and Reproductive Events

The seasonal distribution of fruit in Santa Rosa differs significantly from a random distribution, with the mean month of capuchin fruit production occurring in June, although fruit is available to capuchins starting in April and extending through September. In addition, we found that the timing of the mean peak in fruit biomass, our biologically relevant measure, also followed the same pattern (mean peak occurring in June), which supports our statistical findings. In the absence of plant

phenology data in the past, the amount of rainfall had been used as a proxy for general food abundance in this population (Fedigan *et al.* 2008). Rainfall may still be a good general indicator for fruit because the wet season overlaps with the period of fruit abundance, i.e., the rains begin in mid-May and continue to mid-November. However, fruit production actually starts to increase in April, one of the hottest and driest months in the park, and drops sharply at the end of September, well before the rains end in mid-November, so it is not an entirely accurate indicator of fruit abundance. According to van Schaik and Pfannes (2005), rainfall in seasonal climates is a more accurate estimate for the timing of tree flushing, i.e., production of new leaves, rather than for tree fruiting.

A birth peak has always been known to exist in this population, occurring in the late dry/early wet season (Fedigan 2003), but births can also occur year round, leaving the question of whether this population of capuchins could be considered “seasonal breeders or not. Our analysis confirms that 80% of capuchin births occur within a 6-mo period (February–July), with the mean peak in births occurring in May, and that this timing does differ significantly from random, indicating they are seasonal breeders. We also found that slightly over half of these births (44%) occur in the 3-mo period surrounding and including the mean peak in fruit abundance, which according to van Schaik *et al.* (1999), would classify this population as moderately seasonal.

### How Do White-faced Capuchins Fit the Income–Capital Breeding Framework?

According to the predictions of the weanling survival hypothesis (Income-I breeders), we predicted that: 1) capuchins would time births to occur during the mean time of fruit abundance so that weaning would also occur during this period; and 2) infant survival would be greater for infants born during the mean peak in fruit abundance. First, capuchins do appear to time births to correspond with the mean peak in fruit abundance, but births tend to occur somewhat before, as well as during, the mean period of fruit abundance. Because weaning in white-faced capuchins occurs *ca.* 1 yr postpartum, this pattern would suggest that weanling survival may be an important reproductive strategy for capuchins (Janson and Verdolin 2005). However, we also predicted that infant survival would be greater for infants born during the optimal period of fruit abundance (Di Bitetti and Janson 2000), and we found this not to be the case. In testing the survival of infants to 12 mo of age born during the 3 mo surrounding the mean peak of fruit (May, June, July) and during the overall period of fruit abundance (6-mo period) vs. infants that were not born during these optimal periods, there was no difference in survival. This finding is not entirely surprising because thus far, we have only been able to measure the abundance of fruit, but capuchins are known to have a diverse diet that includes seeds, flowers, insects, and small vertebrates (Fragaszy *et al.* 2004). In addition, even though figs, an important capuchin fruit source, peak in production around June/July (Melin *et al.* 2009), they still provide a year-round and consistent source of fruit for capuchins, including weanlings, because individual trees fruit asynchronously throughout year (Janzen 1983).

If the maternal condition hypothesis, i.e., capital breeding pattern, holds for this population of capuchins, we predicted that births would occur after the mean peak in fruit abundance, and as such, conceptions would occur during the mean peak in fruit abundance when females have reached a sufficient body condition that facilitates

reproduction, e.g., body mass (Brockman and van Schaik 2005; Janson and Verdolin 2005; Richard *et al.* 2000). Instead we found that births start to occur before the mean peak of fruit abundance and that conceptions occur well after the mean month of fruit abundance, and *ca.* 2 mo after the overall drop in fruit (September), which does not support the maternal condition/capital breeding hypothesis for this population.

Finally, if the maternal survival strategy (Income-II or relaxed income breeders) holds, for these capuchins, we predicted that: 1) births would be timed to occur shortly before the peak of food abundance so that the peak period of lactation is timed during the abundance of fruit energy. This is exactly what we found. Births were more likely to occur shortly before the mean peak in food abundance: starting in April, and peaking in May, just 1–2 mo before the mean fruit peak in June. Births continue throughout the period of fruit abundance, but drop off substantially just before fruit begins to decline (births drop in August and fruit drops in October). This pattern supports the hypothesis that our focal individuals pursue the strategy of maternal survival; i.e., the most energetically expensive time of reproduction for capuchins, which is 8 wk postpartum lactation, is timed to occur during the mean peak in energy abundance (Brockman *et al.* 1995; Janson and Verdolin 2005). In addition, capuchins have a very long life span, having been known to live in captivity up to 55 yr (Fragaszy *et al.* 2004) and in the wild up to 30 yr (Fedigan, *unpubl. database*). This long life span further suggests that lifetime maternal reproductive success may be more important than weanling survival in this species (Janson and Verdolin 2005).

## Conclusions

White-faced capuchins living in Sector Santa Rosa, Costa Rica exhibit a birth season that extends from February to July, with the mean peak in birth activity occurring in May, and a conception season that peaks in December (late wet season). Their primary reproductive strategy with regard to energetics can be described as maternal survival, and they can be best classified as Income-II breeders as described by Janson and Verdolin (2005), but may also fit into Brockman and van Schaik's (2005) income–capital continuum model as relaxed-income breeders. This continuum model encompasses the variety of reproductive patterns seen in primates by placing them on a scale from strictly seasonal breeders, e.g., *Macaca fuscata* (Fedigan and Griffin 1996), to species that are capable of reproducing throughout the year, but show seasonal peaks in reproductive activity, e.g., white-faced capuchins (this study), to primate species that show no apparent seasonal variation in their reproductive timing at all, e.g., *Pan troglodytes* (Wallis 1997).

**Acknowledgments** We thank the Costa Rican National Park Service and the administrators of the ACG, especially R. Blanco-Seguro, for allowing us to work in Santa Rosa National Park. We thank A. Biasin, G. McCabe, N. Parr, and A. Petrosioniak for their assistance in the field; C. Janson for advice on directional statistics; and D. Wittwer, and S. Jacoris for assistance with laboratory methods. We also thank 2 anonymous reviewers for their constructive comments that helped to strengthen the manuscript. This research was funded by the National Sciences and Engineering Research of Canada (NSERCC) Ph.D. scholarship (S. D. Carnegie, A. D. Melin), the Alberta Ingenuity Scholarship (S. D. Carnegie, A. D. Melin), an International Primatology Society Research Grant (S. D. Carnegie), a Sigma-Xi grant (S. D. Carnegie), an operating grant from NSERCC (L. M. Fedigan), the Canada Research Chair funds (L. M. Fedigan), and The Leakey Foundation General Research Grant (A. D. Melin).

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