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The impact of alpha male replacements on reproductive seasonality and synchrony in white-faced capuchins (*Cebus imitator*)

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Abstract

Objectives: Reproductive seasonality is typically associated with ecological factors, but it can also be related to social factors, such as alpha male replacements (AMR). Such events can produce distinct birth peaks outside of the ecological peak, potentially increasing hardship for mother and infant and ultimately reducing fitness. We examined the impact of AMRs on birth seasonality, birth synchrony, and infant survival in the Santa Rosa population of white-faced capuchins (*Cebus imitator*).

Materials and Methods: We analyzed 33 years of data on seven capuchin groups to test whether AMRs and births occur seasonally and whether birth seasonality changes following AMRs. Using sliding window analysis, we tested whether ecological conditions predict births in future months. We also tested whether birth period affects infant survival and likelihood of infanticide.

Results: AMRs shift birth seasonality from the ecological birth peak in the early wet season (late May–July) to a social birth peak during the late dry season (March–May), but they do not affect synchrony. In addition, we found that being born in the social peak significantly decreases infant survival relative to individuals born in the ecological and nonpeak periods.

Discussion: These findings suggest that Santa Rosa's predictable seasons can provide conception cues for female capuchins, but AMRs disrupt this ecological timing of conceptions. We suggest the increased infant mortality associated with the social birth peak is related to seasonal factors, including water scarcity and varying resource availability, and increased risk of infanticide, as the social birth peak overlaps with the AMR peak.

KEYWORDS
alpha male replacement, birth seasonality, ecological cues, infanticide, reproductive synchrony

1 | INTRODUCTION

Primates display the full spectrum of reproductive seasonality (di Bitetti & Janson, 2001; Heldstab et al., 2021; Janson & Verdolin, 2005), from species that show no breeding seasonality (*Papio ursinus*: Dezeure et al., 2021; some populations of *Pan troglodytes*: Thompson, 2013; Wallis, 1997) to highly seasonal breeders (*Lemur catta*: Cavigelli & Pereira, 2000; *Galago moholi*: Scheun et al., 2016). One common explanation for birth seasonality is that species time their reproductive efforts in a way that takes maximum advantage of predictable ecological conditions, often a period of high food abundance (Heldstab et al., 2021; van Schaik et al., 1999). Other studies on reproductive seasonality in primates have identified additional ecological drivers, including the effects of photoperiod on hormone levels associated with seasonal reproduction (numerous species: Barrett et al., 2017; white-faced capuchins: Schoof et al., 2016), and evasion of seasonal predation pressure (squirrel monkeys: Boinski, 1987; di Bitetti & Janson, 2001).

The related but distinct phenomenon of reproductive synchrony occurs when conceptions and concomitant births within a group occur within the same periods. Synchrony may evolve due to selection to limit paternity skew of dominant males by restricting their ability to mate-guard multiple ovulating females (Barrett et al., 2017; Small & Smith, 1986). The resulting heightened paternity confusion may, in turn, serve as a driver of synchrony by offering protection against infanticide and promoting infant defense and care by both sire and nonsire males (Barrett et al., 2017; Small & Smith, 1986). Although synchrony is often a byproduct of reproductive seasonality, it can also occur aseasonally, often in response to social drivers. For instance, although lions (*Panthera leo*) are not seasonal breeders, male takeovers of a social group often leads to infanticide, which in turn leads to reproductive synchrony amongst the females of the pride (Packer & Pusey, 1983).

If the social causes of reproductive synchrony are themselves seasonal in nature, reproductive seasonality could arise not only because of ecological variables but social ones as well. For instance, male replacements in geladas (*Theropithecus gelada*) occur seasonally and are associated with high levels of infanticide as the new alpha male kills roughly half of unweaned infants (Beehner & Bergman, 2008). In the year following a takeover, reproductive units exhibit a "social birth" season in which 54.4% of gelada infants are born over a 3-month period (December–February). This birth peak is more synchronous than the "ecological birth peak" that occurs in groups not experiencing a takeover, during which 37.4% of infants are born during a different 3-month period (August–October; Tinsley Johnson et al., 2018). Thus, the timing of male takeovers produces reproductive seasonality in geladas through its effects on reproductive synchrony and creates a "social" birth peak that is misaligned with the ecological birth peak.

White-faced capuchins (*Cebus imitator*) living in Sector Santa Rosa (SSR), Área de Conservación Guanacaste, Costa Rica, reside in groups of approximately 20 individuals, with close to twice as many adult females as males in most groups (Fedigan & Jack, 2013; Hogan et al., 2019). Females exhibit philopatry, and males disperse from their natal group around age four and continue to transfer between groups roughly every 4 years (Jack & Fedigan, 2004a, 2004b). Throughout all life stages, males exhibit parallel dispersal in which they disperse in the company of other males or join a group that contains former group mates, some of which are relatives (Jack & Fedigan, 2004a, 2004b; Perry et al., 2012; Wikberg et al., 2014). This frequent movement of males between groups leads to alpha male replacements (AMRs) approximately every 3 years, though alpha male tenures within groups can range from 2 months to 15 years in the Santa Rosa population (Jack & Fedigan, 2018). Although all males mate with group females, paternity data indicate that reproductive skew is high in this species as the alpha male sires the majority of group infants (Godoy et al., 2016; Jack & Fedigan, 2006; Muniz et al., 2006, 2010; Wikberg et al., 2017). Like geladas, this population of white-faced capuchins have AMRs that are seasonal (53% occurring January through April; Fedigan, 2003). AMRs in white-faced capuchins are also strongly associated with high infant mortality (55% infant mortality in association with AMRs vs 24% mortality during times of social stability; Brasington et al., 2017; Fedigan et al., 2021). Thus, these seasonal AMRs and associated infant deaths have the potential to influence reproductive synchrony and reproductive seasonality.

SSR's capuchins are moderately seasonal breeders, with 44% of births occurring during a 3-month period from May to July (Carnegie, Fedigan, & Ziegler, 2011). Previous studies indicate that this birth season coincides with the highest number of capuchin fruit-food species at their fruiting peak (Carnegie, Fedigan, & Melin, 2011). This time period also marks the return of regular rain following the dry season, a potentially important factor as white-faced capuchins require near-daily water consumption (Campos & Fedigan, 2009). White-faced capuchins require a narrower range of temperature conditions than several other Mesoamerican species—black howler monkeys (*Alouatta pigra*), brown howler monkeys (*A. palliata*), and black-handed spider monkeys (*Ateles geoffroyi*)—suggesting that capuchin habitat suitability may be related to thermoregulatory stress (Johnson & Brown, 2018). Interestingly, the combination of low temperatures and high rainfall appear to be an important determinant of white-faced capuchin habitat, as they are found primarily in habitats in which at least 500 mm of rain falls during the coldest 3-month period of the year, indicating that this species could be considered a climate niche specialist (Johnson & Brown, 2018). If AMRs shift the timing of births, the misalignment with the "ecological" birth season may have considerable consequences for infant survival.

Here, we investigated the impact of AMRs on reproductive seasonality and synchrony in white-faced capuchins using a long-term data set from the Santa Rosa capuchin population. Due to the moderately seasonal nature of AMRs and the moderate birth seasonality displayed by white-faced capuchins, we predicted that AMRs will produce a social birth peak (a peak that results from social drivers, like AMRs) distinctive from the ecological birth peak (a peak that results from ecological drivers, like photo period and food abundance) in the year following their occurrence. To test this prediction we (1) analyzed whether infant conceptions and births during periods of group stability occur seasonally, and whether there are climatic predictors (i.e., temperature and rainfall) of this "ecological" birth peak. Similarly, (2) we evaluated AMR seasonality and assessed whether AMR events lead to a "social" birth peak, and evaluated how this differs from the ecological peak. Finally, (3) we compared the survivorship of infants born within the ecological peak to those born outside of it to determine how detrimental it is to give birth outside of the ecological peak.

2 | MATERIALS AND METHODS

2.1 | Study site

SSR has predictable seasonal weather patterns (Figure 1), with a long wet season from mid-May to mid-November (heaviest rains are typically in October, >400 mm monthly total rainfall on average), followed by a long dry season (mid-November to mid-May) during which little to no rainfall occurs (Campos, 2018; Campos et al., 2015). The difference in rainfall between the wet and dry seasons is more extreme than the vast majority (98.9%) of terrestrial locations on Earth, while mean monthly temperature varies by less than 5°C between the coldest and warmest months, making the seasonal temperature variation smaller than 95% of terrestrial habitats (Campos, 2018). The hottest temperatures occur in April or early May (mean temperatures ~30°C), and October and November are the coldest months (mean temperatures ~26°C; Campos, 2018).

2.2 | Study population

The study population of white-faced capuchins in SSR has been the focus of near continuous study since 1983 (Fedigan & Jack, 2012). All research conducted for and reported in this article was authorized by the Costa Rican Ministry of the Environment, Energy and Technology, and complied with protocols approved by the Life and Environmental Sciences Animal Care Committee of the University of Calgary (AC20-0148) and Tulane University's Institutional Animal Care and Use Committee (Protocol ID: 810). We analyzed demographic data from seven groups of SSR capuchins over a 33-year timespan (Table 1).

The interbirth interval for female capuchins is relatively long (mean IBI = 1.89 years) and infant survival to 1 year is the strongest predictor of subsequent interbirth interval length (mean IBI is 2.25 years when the prior infant lives; 1.05 when a prior infant dies; range: 0.67–5.58 years; Fedigan, 2003; Fedigan et al., 2008). The female ovarian cycle (i.e., days between progesterone surges) is 13–26 days in this population, and females cycle asynchronously and

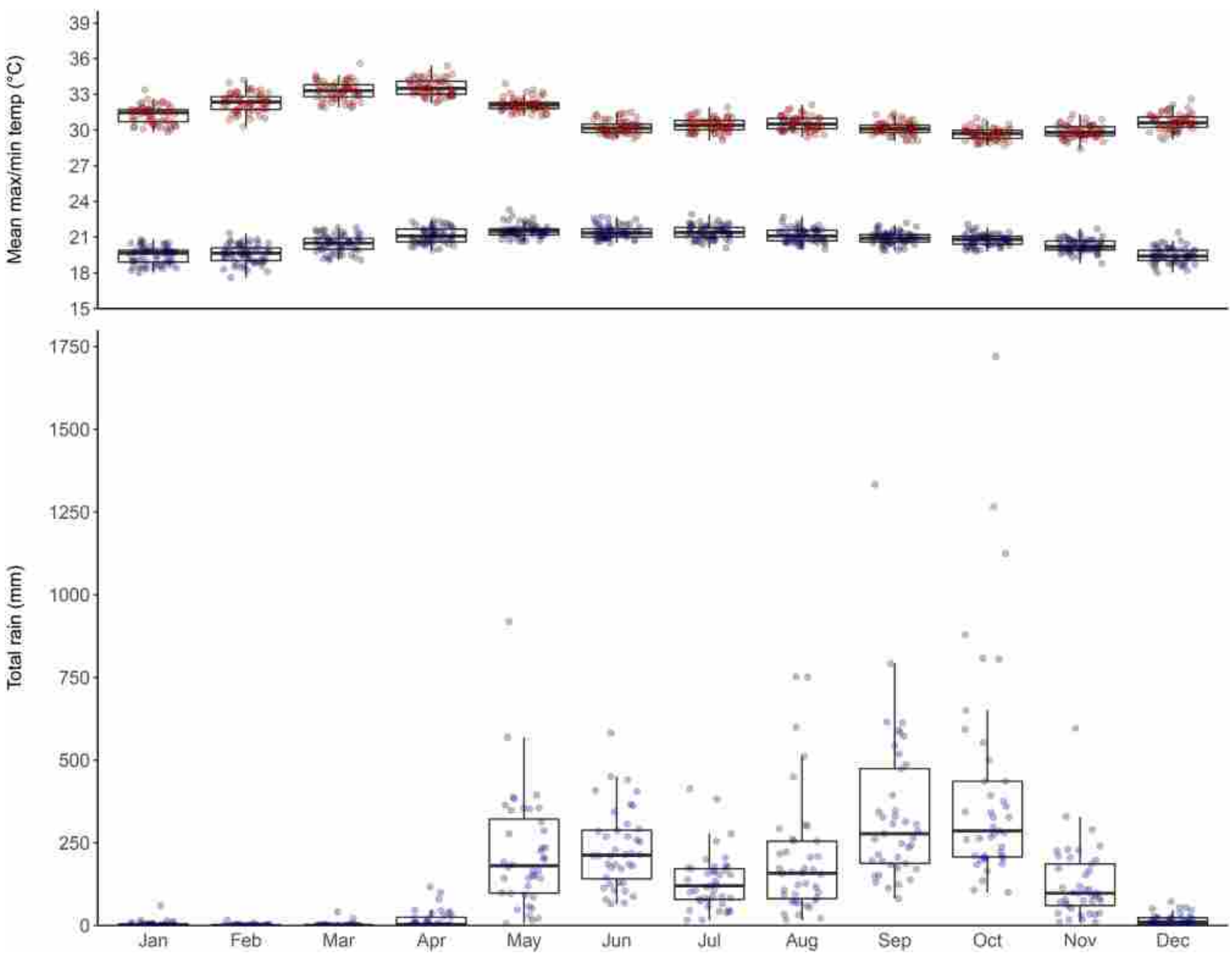

FIGURE 1 Boxplots of the mean monthly minimum and maximum temperatures and total rainfall recorded for Sector Santa Rosa (SSR). Temperature data were obtained from the TerraClimate dataset and represent data from 1958 to 2019. Rainfall data is from the Santa Rosa capuchin project, and was collected between July 1979 and December 2020. Each colored point represents 1 month of data from a year in the respective datasets

TABLE 1 The Santa Rosa capuchin study groups observed for this project, and the timeframe within which they were studied. CPAD and CPRM are the products of a fission of CP

Group	Start date	End date	Years observed
CP	1986	2012	16
CPAD	2013	2020	8
CPRM	2013	2020	8
EX	2007	2016	10
GN	2007	2020	14
LV	1990	2020	31
SE	1986	1993	7

conceive throughout the year when they are not pregnant or nursing young infants (Carnegie et al., 2006; Schoof, Jack, & Ziegler, 2014; Schoof, Wikberg, et al., 2014). Infanticide is common within this population, especially in the context of AMRs (Brasington et al., 2017). On several occasions we have directly observed males attacking and killing infants, or have recovered the body of young infants with visible canine punctures (Brasington et al., 2017; Fedigan et al., 2021; Nishikawa et al., 2020). Due to the heightened risk of infanticide for infants that experience an AMR between conception and age 1 year (Kalbitzer et al., 2017), we consider any infant lost during an AMR period to have likely died via infanticide, although it is important to note that other mortality factors remain.

2.3 | Ecological predictors and birth peaks

Rainfall data in SSR was recorded daily using a rain gauge throughout the study period. Temperature data was obtained from the TerraClimate data set, which has global monthly mean and max temperature data dating back to 1958 with a grid spatial resolution of approximately 4 km^2 (Abatzoglou et al., 2018). We use a single-grid sample of temperatures centered on the Casona historical building in the middle of SSR as a reference landmark. TerraClimate data was available through December 2019 at the time of this study.

To determine whether the ecological birth peak can be predicted by seasonal climatic conditions, we use the climwin package (Bailey & van de Pol, 2016) in R (v. 3.6.2; R Core Team, 2018) to conduct sliding window analyses. The "slidingwin" function of climwin allows us to test every combination of monthly climate data leading up to an infant's conception to determine which climate variables, if any, are the best predictors of a future birth, and for which months those variables are important. This function conducts model selection by comparing each monthly climate model to a null model without any climate predictors. Climwin allows for testing any permutation of windows prior to the outcome event. A female capuchin can only influence the birthdate of her offspring by altering her conception date (because gestation length is essentially fixed within a tight range; (Carnegie, Fedigan, & Melin, 2011), therefore we only investigate climate data for the months prior to conception (i.e., 5–12 months prior to birth) for each infant. Because social births are influenced by non-climatic events, we excluded them from this analysis.

Our baseline model was a negative binomial generalized linear mixed model, with the number of infants born per study group per month as the outcome variable, and social group and year included as random effects. Mean monthly maximum and minimum temperatures and rainfall volumes were included as potential climate predictor variables and were z-transformed for better model fit. Although these variables are highly collinear, we conducted modeling independently for each, and therefore interpretation should not be affected. To ensure that significant results were not spurious due to the large number of models run for each combination of window length and climate variable, climwin offers a function called "randwin," which we used to simulate the null models for each climate variable to then compare to the AICc values of the climate model to the null. Generalized linear mixed models within each sliding window analysis were conducted using the lme4 package (Bates et al., 2015).

Births in this population were recorded during study group censuses which were conducted at least twice monthly or more often during periods of intensive behavioral observations. Infant conception dates were back-calculated from their birth date using the known median gestation length (158 ± 8 days; (Carnegie, Fedigan, & Melin, 2011). Because there are a small number of data gaps of up to 6 months in length in our earlier census records, we only include infants with birth dates that can be ascertained within a 30-day certainty window.

In order to determine whether ecological and social birth peaks were present, and, if so, whether they were different from each other, following Trébouet et al. (2021), we measure birth seasonality in two ways: (1) calculating "peaks" via circular statistics, which are appropriate because of the nonlinear nature of a calendar year (Batschelet, 1981) and (2) assigning "seasons" using van Schaik et al. (1999) categorizations of seasonality (based on the proportion of infants born in the peak 3-month season: <⅓: no seasonality, ⅓–⅔: moderate seasonality, >⅔: high seasonality). Circular statistics were conducted using the "circular" package (v. 0.4–93, Lund et al., 2017) in R. Conception dates were back calculated from birth dates, converted to "day of the year", then into radians, and divided into two groups based on the context of an infant's conception: those that occurred 0–12 months following an AMR (AMR conceptions), and those that did not (stable conceptions). We conducted Rayleigh tests for both birth types independently (Batschelet, 1981; Landler et al., 2018) and generated 95% confidence intervals of the mean direction and concentration parameter for a von Mises distribution of the data via maximum likelihood bootstrapping (reps = 1000). A von Mises distribution is the circular equivalent of a normal distribution for linear data, and is similarly described using the mean (0-2π) and variance (concentration parameter; Batschelet, 1981). Finally, because Rayleigh tests estimate a singular peak (with a confidence interval of that peak) from our birth records, and primate birth seasonality is likely targeted toward a much wider range of ecological conditions that exist for an extended period, we also determined the 3-month (13-week) window associated with the most social and ecological births following van Schaik et al. (1999). For these birth seasons, we calculated the percentage of infants born within the 3-month periods to identify the degree of capuchin birth seasonality.

2.4 | AMR seasonality

All capuchin groups in our study population are observed at least twice per month. We recorded the onset of an AMR based on field observations of behavioral changes within a study group. Specifically, in aggressive AMRs, intense fighting occurs between males often causing wounding, and females become aggressive toward the incoming alpha. In peaceful AMRs, female group members will engage in unique and obvious affiliative behavior toward a new alpha male (including distinct "gargle" vocalizations), and males assuming an alpha role will become more central and aggressive. The specific "start date" of an AMR is not exact, and is best considered to be an estimate with accuracy levels of weeks rather than days.

2.5 | Social birth peaks

Infant conception dates were back-calculated from their birth date using the known median gestation length (158 ± 8 days; Carnegie, Fedigan, & Melin, 2011). Because there are several data gaps of up to 6 months in length in our earlier census records taken when the field project began, we only include infants with birth dates that can be ascertained within a 30-day certainty window (Table 2). Any infant conceived 0–12 months following an AMR was considered an "AMR conception." While previous research on this population found a rise in conceptions in the 3–6 months following an AMR (Fedigan, 2003), the extended time frame used here enables us to include conceptions that occur following infanticide (or infant disappearance) in association with an AMR. A longitudinal analysis on this population has demonstrated that infants born within the 5.5 months following an AMR (i.e., they were not sired by the new alpha male and were not yet born at the time of AMR) are at even higher risk of infanticide (63% mortality) than infants present at the time of the AMR (45% mortality; Brasington et al., 2017). Given the extended period of residual infertility in capuchins following the birth or weaning of an infant (~7 months, based on captive *S. apella*; Recabarren et al., 2000), this extended time-frame for post-AMR conceptions enables us to capture a greater number of births that resulted from the changeover in a group's alpha male. For example, an infant sired by the previous alpha male could be born 5 months after an AMR. This infant would be at heightened risk of infanticide, and if it died, its mother may experience up to 7 months of residual infertility (Recabarren et al., 2000). This female would then conceive with the new alpha male 12 months after the AMR. To help better identify the timing of conceptions after AMRs, we also examined the number of days elapsed between an AMR and an infant's conception for all infants conceived <1 year following an AMR (AMR conceptions).

2.6 | Costs of birth timing

Using the lme4 package in R we created three binomial linear mixed-models to test whether infant survival to age two differed for infants born in one of four predefined birth periods: (1) the ecological peak, (2) social peak, (3) birth valley, and (4) a time outside of these windows ("off-peak") under three different conditions (Table 2). A birth was considered to be in the ecological or social peak if it occurred within the 95% confidence interval of our von Mises analyses for these birth types regardless of the infant's conception context (i.e., ecological infants can and are born in the "social" birth peak), and in the "birth valley" if it occurred during the 7-week period with the fewest births. We analyzed all infants (i.e., those conceived after AMRs and those conceived during stable periods) together because we were interested in understanding if there was a cost associated with being born at a certain time of year, regardless of the conception conditions. For the first model, the predictor variable was birth period while birth year and mother's identity were included as random effects. We included all infants born during the study whose fate up to 2 years of age could be known (i.e., a birth date prior to October 2019). Following the rationale of Tinsley Johnson et al. (2018) we selected survival to 2 years because it represents the end of weaning for capuchins (range 14–23 months; Sargeant et al., 2015).

To determine whether differences in survival could be attributed to ecological conditions, we ran a second model with the same structure as our survival model but using only data for infants not suspected to be killed by infanticide (i.e., those born during periods of group stability). Finally, our third model tested the infanticide risk of infants born within each birth period by using the binomial metric "disappeared, infanticide suspected" as our response variable. Infants

TABLE 2 Description, parameters, and sample sizes used for our three binomial mixed models testing how birth season affects survival and infanticide risk

Analysis description	Response variable	Predictor variable	Number of infants
Survival, all infants with >2 years postbirth data	Survived 2 years (Y/N)	Birth season	258
Ecological risk by birth season (excludes infanticide deaths)	Survived 2 years (Y/N)	Birth season	205
Infanticide risk by birth season (all infants >1 year postbirth data)	Disappeared, infanticide suspected (Y/N)	Birth season	282

Note: Mother ID and birth year were included in all three models as random effects.

that disappeared before age 1 year were presumed dead because no individuals younger than 20 months old have been confirmed to have dispersed in this species (Jack & Fedigan, 2004a). Infants that experienced an AMR between their conception and reaching 1 year of age were considered to be at heightened risk of infanticide, and they were assumed to have died via infanticide if they disappeared in this context. Infants that disappeared but did not experience an AMR between conception and age 1 were assumed to have died due to other causes. Because infanticide is a risk primarily for infants less than 1 year old, only infants with a full year of data available were included in this model (i.e., born before July 2020).

3 | RESULTS

3.1 | Ecological predictors and birth peaks

Sliding window analysis revealed that the mean monthly maximum and minimum temperatures and rainfall were all significant predictors of births per study group/census month and all greatly outperformed the null baseline model (Table 3). In general, decreasing maximum temperatures and increasing monthly rainfall in the months before conception were predictive of future births. All three climate variables outperformed null random models as determined via ΔAICc (Table 3).

This population exhibited a moderate birth season for infants born outside the context of AMRs: 42% of ecological births (i.e., conceptions not influenced by AMRs; 80/180) occurred in May–July. We determined that ecological births have a statistically significant peak (calculated via Rayleigh tests; Table 4, Figure 2b,c), and found the 95% confidence interval of the mean direction of ecological births (1.99–2.67; births late April to early June).

3.2 | AMR seasonality

AMRs in our study population were moderately seasonal (following van Schaik et al. (1999) definition), with 41% occurring between February and April (15/37). Rayleigh testing supports this conclusion (Table 4; Figure 2a).

3.3 | Social birth peaks

We found that 46% of infants conceived following an AMR (social births; 56/121) were born in March–May (social birth season), indicating that these births exhibit a moderately seasonal pattern, like the ecological births. Social births also have a statistically significant peak (calculated via Rayleigh tests; Table 4; Figure 2b,c). The social and ecological birth seasons (as measured using the van Schaik 3-month peak) overlapped but are distinct, and the 95% confidence intervals of the mean direction of births from social (1.13–1.79 radians; births mid-March to early April) and ecological births (1.99–2.67; births late April to early June) do not overlap. We also found that infant conceptions following an AMR were widely distributed from within days of an AMR to nearly a year after an AMR, with a mean of 172 days and a median of 169 days, with first and third quartiles of 85–241 days (Figure 3). Sixty-five percent of these conceptions occurred within the first 7 months following an AMR (Figure 3).

A birth valley was also evident for August–October, during which only 10% of infants were born during the 3-month window (29/301), and this is true for both AMR and stable conceptions. The 7-week window of fewest births (8/301) in this time-period occurred from early September to mid-October.

TABLE 3 Results of sliding window analysis of how climate variables predict future births

Climate variable (monthly mean)	ΔAICc	Optimum window (months prior to birth)	Effect estimate	Standard error	*p*-value
Temp max	−15.57	9–7	−0.45	0.11	<0.0001
Temp min	−11.29	5–5	−0.34	0.09	<0.0001
Rainfall	−20.54	12–8	+0.68	0.14	<0.0001

Note: All three climate variables were significantly predictive of future births, but maximum temperature and rainfall were better predictors than minimum temperature and shared a similar window of effect. Generally, births are predicted by a period of decreasing temperature and increasing rainfall occurring in the months immediately before conception (9–7 and 12–8 months, respectively).

TABLE 4 Results of Rayleigh tests and bootstrapping confidence intervals of the von Mises distribution for alpha male replacements (AMRs), and social and ecological births

Event type	Mean direction (radians)	rho	*p*-value	Mean direction (95% CI)	Concentration parameter (95% CI)
Alpha male replacements	1.11	0.31	0.03	0.39–1.45	0.22–1.16
Social births	1.45	0.39	<0.0001	1.13–1.79	0.58–1.14
Ecological births	2.34	0.31	<0.0001	2.00–2.66	0.42–0.99

Note: AMRs, social and ecological births are significantly asymmetrically clustered, indicating all three are seasonal events. The peaks and confidence intervals for the two distinct birth seasons are nonoverlapping (social birth peak occurs ∼8 weeks earlier), while the peak AMR period overlaps strongly with the social birth peak.

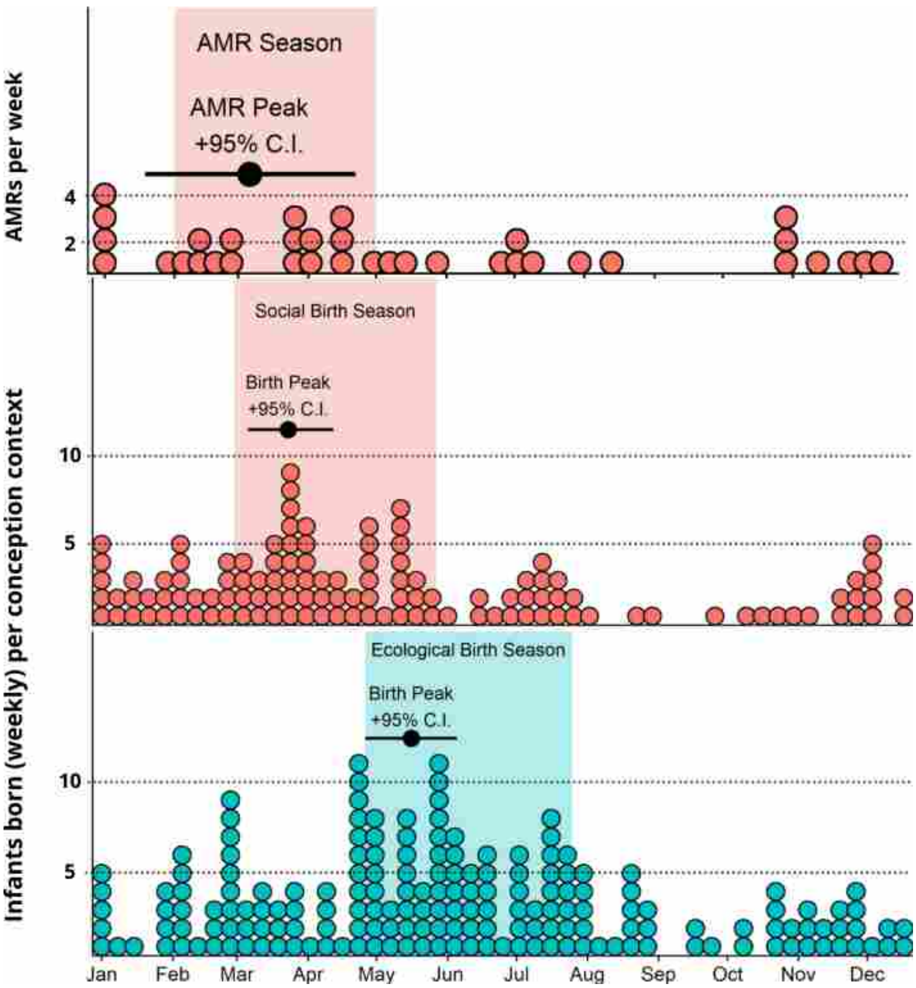

FIGURE 2 The weekly number of (a) alpha male replacements (AMRs), births resulting from (b) social (AMR), and (c) ecological (stable) conceptions for our capuchin study population over a 33-year period, with mean circular peaks (black point) and bootstrapped 95% confidence intervals and the 13-week birth season (shaded region) arising from each conception type. Social conceptions are defined as those that result from infants conceived within 12 months of an alpha male replacement, ecological conceptions result from infants conceived outside of these periods. Alpha male replacements, social and ecological peaks are all significant, and the peak AMR period overlaps considerably with the peak social birth period. The 95% confidence intervals for the social and ecological peaks do not overlap

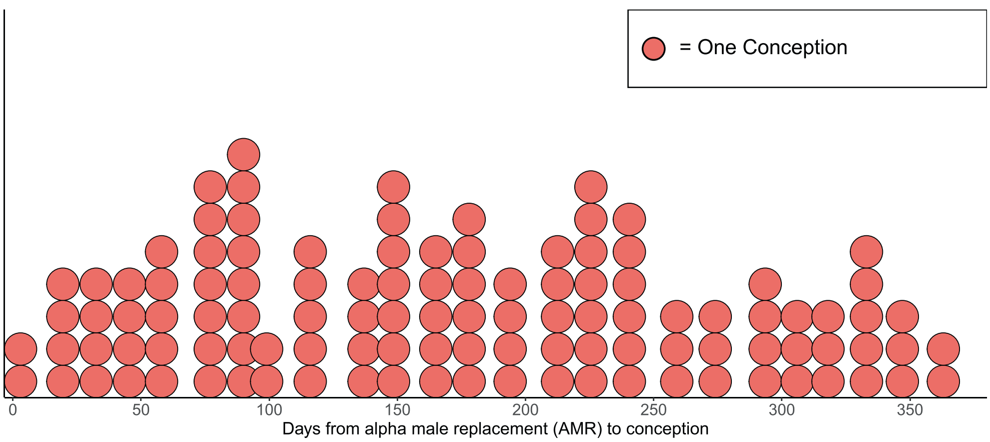

FIGURE 3 Dot plot of the number of days elapsed between an alpha male takeover (AMR) event and an infant's conception for all infants in our sample which were conceived <1 year following an AMR (AMR conceptions). Each circle represents one conception, data are binned in 10-day intervals

3.4 | Costs of birth timing

Infants born in March to mid-April, (coinciding with the social birth peak) were less than half as likely to survive as infants born in any other time of the year (estimate: −0.88, standard error: 0.42, *z*: −2.10, *p*: 0.03). Infants born during any other time period had no significant survival differences relative to each other (Figure 4a, Supplemental Data). Controlling for infanticide risk, we found no significant differences in mortality risk for any birth period (Figure 4b, Supplemental Data), while the risk of infanticide was significantly higher for infants born in the "social" birth window (estimate: 0.92, standard error: 0.44, *z*: 2.11, *p*: 0.04, Figure 4c, Supplemental Data). Full model outputs for all three models and birth seasons can be found in Supplemental Data 1. Infants born in the March to mid-April "social

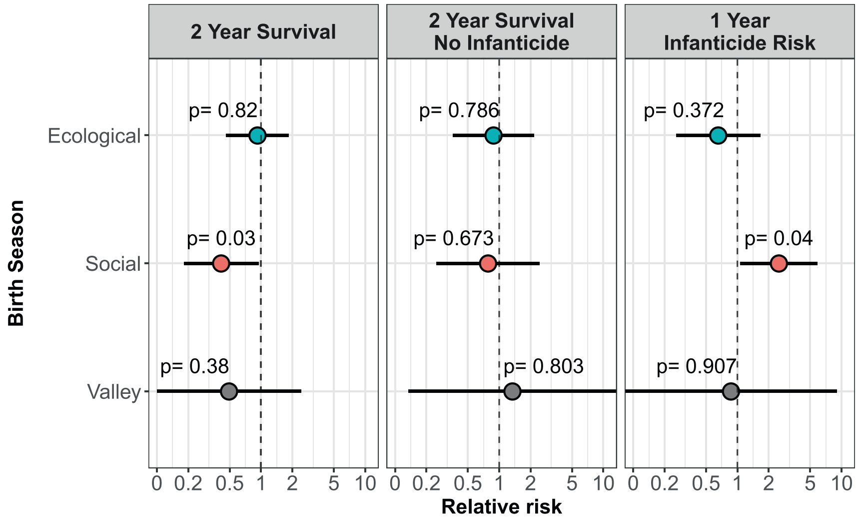

FIGURE 4 The odds ratios (with 95% confidence intervals) of an infant that is born in one of the three defined birth periods (social peak: March to May, ecological peak: Late May to July, and birth valley: August to October) relative to infants born outside of any of the three periods: (a) surviving to 2 years of age; (b) surviving to 2 years of age if infants killed by infanticide are excluded; and (c) dying from infanticide. An odds ratio of 0.5 indicates a 50% reduction in the likelihood of occurrence for the predictor variable (surviving to 2 years or being killed by infanticide, depending on the model), while odds ratio of 5.0 suggests a 500% increased likelihood of occurrence relative to the "out of peak" infants in the dataset

peak" are less than half as likely to survive to 2 years of age when all mortality is considered, and are over twice as likely to die from infanticide than infants born at other times. There is no difference in survival for infants of any birth period when infanticide is controlled for (i.e., infants suspected to have been killed by infanticide are excluded).

4 | DISCUSSION

4.1 | Ecological predictors and birth peaks

Our results support the conclusion that Santa Rosa white-faced capuchins are moderately seasonal breeders, which was previously suggested to be an adaptive strategy for timing an infant's peak lactational demands (first 8 weeks after birth, when they are still fully dependent and their growth rate is highest; McCabe & Fedigan, 2007) to a period of peak fruit abundance (Carnegie, Fedigan, & Melin, 2011). Our sliding window analysis (Table 3) suggests that female capuchins utilize ecological cues (declining temperatures and increasing rainfall) to conceive in a period that will lead to giving birth in late May/June, which is typically the early part of the wet season. Resource availability, specifically water and caterpillars, may cause this window to be the ideal birthing window for capuchins. The dry season is marked by drought and very few standing water sources in Santa Rosa, so female capuchins may avoid dehydration by not having to nurse during a time when water sources are scarce (Bergstrom et al., 2017; Campos & Fedigan, 2009; McCabe & Fedigan, 2007). Likewise, the most energetically expensive period of reproduction, early lactation, coincides with a sharp increase in caterpillar abundance (*Lepidoptera* larvae) and consumption in the early wet season (late May to mid-July; Bergstrom et al., 2019; Carnegie, Fedigan, & Melin, 2011; Janzen, 1988a; McCabe & Fedigan, 2007; Mosdossy et al., 2015). Consumption of caterpillars during the early weeks of nursing may provide females with an ideal food source to meet these increasing energetic demands: high-protein, rich fatty acids, high water content, easily obtained and quickly consumed (Bergstrom et al., 2018; Bergstrom et al., 2019; McCabe & Fedigan, 2007).

From August to October very few infants were born (<10%; "birth valley") under both social (AMR) and ecological (stable) conception conditions. A similar birth valley has been documented by Perry et al. (2012) in the nearby Lomas Barbudal population of white-faced capuchin monkeys, with no births having been observed to occur in October over two decades of research. It is possible that ecological factors drive this pattern, as September and October have the highest monthly rainfall and the lowest mean monthly temperature at Santa Rosa (Campos, 2018). Dietary analyses (Bergstrom et al., 2017, 2019; Bergstrom et al., 2018) indicate that fruit and invertebrates consumed by the capuchins are readily available during these colder, wet months, so it appears this birth valley may be better explained by the weather itself, and not food availability. Interactions between temperature and other climatic features have been shown to drive birth seasonality in other primate species. For example, the interactive effect of temperature and photoperiod has been found to influence birth seasonality in golden snub-nosed monkeys (*Rhinopithecus roxellana*: Xiang et al., 2017). Likewise, the effects of low temperature on female reproduction in geladas are thought to be compounded by the low oxygen conditions at high altitudes (Tinsley Johnson et al., 2018). While September and October may be a poor time for infant births, it may be conducive to heightened female fertility, as the seasonal precipitation that occurs mid September–mid November may serve as a predictor of fruit abundance or as a means for replenishing water sources for the future dry season (Johnson & Brown, 2018). In addition, the availability of food and water during this period might positively impact female fertility and contribute to the timing of the ecological (stable) conception peak. Conceptions for births that occur during the birth valley (early September through mid October) would occur between mid March and early May. This conception window covers the hottest and driest time of the year. If we are correct in our suggestion that the colder and wetter months are related to enhanced female fertility, then perhaps it is also true that the hot, dry season could be related to decreased fertility. The conception window for the birth valley also may be related to social factors. Mid March to early May overlaps with the end of the AMR season, and it is possible that this social stress could lead to stress-induced anovulation (Berga & Loucks, 2019). Future studies should focus on the impacts of the social and ecological factors on female fertility.

4.2 | AMR seasonality

We found that AMRs were moderately seasonal (41% occurred between February and April), and our findings align with a previous report noting that the majority of AMRs occur during the dry season between January and April (Fedigan, 2003). The seasonal nature of AMRs has several possible triggers. Seasonal leaf abscission occurs in approximately 80% of the Santa Rosa tree species (Frankie et al., 1974; Gillespie et al., 2000; Janzen, 1988b), leading to significantly higher visibility in the forest, providing more opportunities for groups to detect each other and perhaps gather information leading to a decision to instigate a takeover. Similarly, water becomes a range-restricting feature in Santa Rosa in the later months of the dry season as groups will increasingly spend time near and defend the remaining surface water patches (Campos & Fedigan, 2009). These factors could lead to increasing frequency of intergroup encounters, spurring more takeover attempts (Schoof & Jack, 2013). Finally, male dispersal between groups may be triggered by female infertility within their group (Schoof et al., 2016; Young et al., 2019) and/or attraction to fertile females in neighboring groups. We found that 65% of the conceptions following AMRs occur before the end of the ~7 month period of residual infertility that would be expected following infant loss or weaning (i.e., if an infant was killed by the new alpha male; Figure 3). These data provide strong evidence that males are joining groups with at least some immediate reproductive opportunities and that AMRs impact female fertility patterns. Future studies should track female fertility patterns in association with AMRs.

4.3 | Social birth peaks

Beyond the effect of ecological conditions, the timing of capuchin births appears to be driven by the occurrence of AMRs, which produces a social birth peak that does not overlap with the ecological peak. The social birth peak occurs during the dry season months of March to May, roughly 12–14 months following AMRs. This social peak may be driven by the broad range of conception timing following an AMR (Figure 3). This large variation in conception timing is likely related to differences in female reproductive status. For example, females that have older or no offspring would be expected to conceive soon after an AMR. On the other hand, females that are pregnant or have young infants would be expected to have a longer delay before they are able to conceive because both gestation and intense nursing cause ovarian cycling to cease. In addition, conception may be further delayed because infanticide may be delayed following an AMR (mean of 46 days post-AMR for confirmed infanticide cases; Jack & Fedigan, 2018) because females avoid the new alpha following an AMR (Fedigan & Jack, 2013; Jack & Fedigan, 2018) and/or an increase in alpha male testosterone may be delayed in the case of coresident AMRs (Schoof et al., 2011). A delay in conceptions after an AMR may also occur in fully cycling females due to stress-induced anovulation (Berga & Loucks, 2019), as observed in geladas (Lu et al., 2021).

AMRs did lead to slightly higher synchrony in the timing of infant births, with 46% of social births occurring in the 3-month season, compared with 42% of ecological births. Females may benefit from further delaying conception following an AMR in order to time births based on ecological conditions. However, given the frequency of AMRs (groups experience one every 3 years on average; Fedigan, 2003) and the extensive energetic and fitness costs losing an infant poses to females (Fedigan et al., 2021), there may be greater fitness incentive for females to conceive as soon as possible to maximize the chances that their infant is independent enough to escape infanticide when the next AMR occurs. Thus, variation in conception times may create a broader distribution when social births occur, reducing observed synchrony from the levels we would expect. Conceptions may also be less likely to occur during the hottest, driest months, leading to avoid the August–October birth valley. Our modeling indicates poor infant survival during this time, although this result was nonsignificant due to the large confidence intervals, which we attribute to small sample size of infants born in the birth valley (Figure 4a).

4.4 | Costs of birth timing

The existence of an ecological birth peak (late May to July) and the presence of predictable climatic cues occurring immediately before the corresponding conception window suggests some benefit to being born in the ecological birth peak (and, from the adult female's perspective, to timing your births to occur in this season). While no significant benefit of being born between late May and July was detected, we found that being born in the social peak (March to May) negatively impacted infant survival and was associated with an increased likelihood of infanticide. March through May is the hottest and driest time of the year and in the middle of the AMR peak, putting infants born in this window at considerable risk of starvation, dehydration, and infanticide. The fact that infants born between March and May, the majority of which were conceived following an AMR the previous year, are at increased risk of infanticide death is surprising, but AMRs are independent events, and it is not uncommon for a group to experience multiple AMRs over consecutive years. For instance, if an AMR occurs in the late dry season (as is typical for this population) and infanticide follows, the females that lose their infants would experience some degree of postpartum amenorrhea and/or fail to mate with the new male for a period of time. These females would then conceive (likely in the second half of the wet season), and after 5.5 months of gestation, they would give birth in the subsequent dry season when there is again increased risk of AMRs and infanticide. Thus, an infant born in between March and May may simply have unlucky timing and have been sired by a male that is unable to retain his alpha status throughout the infant's first years of life.

Being born March to May, as opposed to late May to July, may have a cost for the mother as well as the infant. White-faced capuchins have previously been described as income II breeders that prioritize maternal survival (Carnegie, Fedigan, & Melin, 2011). It is likely that lactating during the time of greatest heat and water stress (Campos & Fedigan, 2009) would be more difficult for the mothers of newborn infants, as they nurse the most intensively for the first 8 weeks after birth (McCabe & Fedigan, 2007; Milligan et al., 2008). It is also possible that the costs of reproduction occurring outside of the late May to July time period are incurred by the mother with regard to her relative energy expenditure or lifetime reproductive success. Future research will attempt to determine if there is a measurable effect on female reproductive fitness in the form of longer interbirth intervals or fewer subsequent offspring.

5 | CONCLUSIONS

Santa Rosa capuchins are moderately seasonal breeders, with an "ecological" birth season from May to July. However, AMRs, which are seasonal themselves, alter the timing of births, with most infants conceived following an AMR arriving earlier the subsequent year (March to May) in a distinct "social" birth period. This change in birth seasonality did not confer a change in birth synchrony, thus, AMRs appear to drive aspects of reproductive seasonality, but not synchrony in white-faced capuchins. Being born during the social peak negatively affects infant survival. We suggest that this is due to several factors, including increased risk of infanticide and the various risks that are associated with Santa Rosa's distinct seasons (e.g., reduced water availability, varying resource availability, and so forth). In addition to infant mortality being affected by birth timing, costs may be absorbed by the capuchin mother, and further investigation into the lifetime fitness effects of repeated AMR exposure and birth timing may prove illuminating. These results suggest that presence and timing of AMRs exert a selective pressure on the timing of conceptions and births following an AMR, thus expanding our understanding of the impacts that seasonal male social behavior can have on female reproductive success. By evaluating the impact of AMRs on birth seasonality, birth synchrony, and infant survival in an evolutionary framework, these results provide unique insights to the energetic tradeoffs and complex interplay between social and ecological variables impacting the evolutionary trajectory of this species. These results add to the rich documentation of primate reproductive strategies and adaptations, enabling crossspecies comparisons for evaluating patterns of biological and social variation in the order.

AUTHOR CONTRIBUTIONS

Lauren F. Brasington: Conceptualization (lead); formal analysis (equal); writing – original draft (lead); writing – review and editing (lead). **Nelle K. Kulick:** Formal analysis (equal); writing – review and editing (equal). **Jeremy D. Hogan:** Data curation (equal); formal analysis (lead); methodology (equal); visualization (lead); writing – review and editing (lead). **Linda M. Fedigan:** Data curation (equal); funding acquisition (lead); project administration (lead); writing – review and editing (equal). **Katharine M. Jack:** Conceptualization (equal); data curation (equal); funding acquisition (lead); project administration (lead); supervision (lead); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available from the University of Calgary PRISM Dataverse at https://doi.org/10.5683/SP3/BLGTNF.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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