



Breeding Seasonality in Female Vervet Monkeys (*Chlorocebus pygerythrus*) Living in an Anthropogenic Landscape

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Abstract

Resource availability is intricately linked to female reproductive success, and poor timing of reproduction can negatively impact maternal and/or infant survival. Thus, females should exhibit flexibility in the timing of reproduction that reflects local conditions. We examined eight years of data on births, conceptions, mating seasonality, and interbirth intervals (IBIs) in relation to food availability, weather, and female dominance rank in three groups of vervets (*Chlorocebus pygerythrus*) living in a forest-agriculture matrix near Lake Nabugabo, Uganda. Births (N = 126) occurred year-round but were moderately seasonal (61.1% of births in October–December). The degree of seasonality varied slightly between groups. However, there was no survival difference for infants born within or outside of birth peaks. Fruit availability did not vary seasonally, nor did feeding on either natural or anthropogenic foods. IBI did not vary between groups but was shorter than those of other



Badge earned for open practices: Open Data. Experiment materials and data are available in the repository at Figshare (reproduction data: <https://doi.org/10.6084/m9.figshare.14866146>, <https://doi.org/10.6084/m9.figshare.19312373>; weather data: <https://doi.org/10.6084/m9.figshare.14847750>; food availability data: <https://doi.org/10.6084/m9.figshare.14847726>; dominance data: <https://doi.org/10.6084/m9.figshare.14866233>). Code is available on Figshare (https://figshare.com/articles/software/Schwegel_et_al_R_scripts/19665339) and on GitHub (<https://mschweg.github.io/VervetBreeding2020/>).

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wild populations, with most females breeding in successive years. Higher-ranking females had shorter IBIs than lower-ranking females. The moderate breeding seasonality and shorter IBIs in the Nabugabo vervets compared with other populations may relate to habitat differences and latitudinally-variable factors. The maintenance of a birth peak despite consistent food availability suggests vervets and other primates may be phylogenetically constrained, which prohibits adapting to changing environmental conditions, such as climate change.

Keywords Female reproductive strategies · Interbirth interval · Income-capital breeding · Maternal investment

Introduction

The timing of reproductive events is an important aspect of mammalian life history shaped by evolutionary and ecological factors (Clauss *et al.*, 2021). Female reproductive strategies involve trade-offs in the size and number of offspring, investment in current and future offspring, and the timing of reproductive events in relation to energy balance (Bronson, 2009; Heldstab *et al.*, 2021; Stearns, 1989, 1992). These strategies vary both between and within species as a means of maximizing fitness in relation to environmental, social, and individual factors (Clauss *et al.*, 2021; Emery Thompson, 2013). Understanding the within-species variation in reproductive parameters in different habitats is critical to understanding the flexibility of reproduction in a changing world (Bronson, 2009).

Primates are highly variable in the degree to which mating, conceptions, and births are seasonal, and to how much mating behaviour and conceptions overlap. Some species have short, overlapping mating and conceptive seasons (e.g., gray mouse lemurs, *Microcebus murinus*; Perret & Aujard, 2001), whereas others exhibit conception seasonality with longer mating periods (e.g., Hanuman langurs, *Semnopithecus entellus*; Borries *et al.*, 2001; white-faced capuchins, *Cebus capucinus*; Carnegie, Fedigan, & Melin, 2011a; northern pig-tailed macaques, *Macaca leonina*; Trébouet *et al.*, 2021). Still other primates, especially those whose interbirth intervals exceed the calendar year, lack reproductive seasonality (e.g., gorillas, *Gorilla gorilla beringei*; Watts, 1998).

The income-capital breeding model proposes different reproductive strategies based on the temporal relationship between energy availability and reproduction (Brockman & van Schaik, 2005; Stearns, 1989, 1992). One strategy is that of capital breeders who rely on energy stores to initiate and maintain reproduction and are thus predicted to depend on internal cues to time reproduction (Brockman & van Schaik, 2005). As such, births tend to occur year-round (i.e., nonseasonal breeding) or following food peaks when body condition exceeds the threshold needed to sustain maternal investment (Brockman & van Schaik, 2005). In contrast, income breeders rely on energy acquired *during* reproduction, and thus, births are timed so that food peaks overlap with peak-lactation or weaning (Brockman & van Schaik, 2005; Stearns, 1992). Income breeders therefore exhibit breeding seasonality and are thought to rely primarily on external cues that are reliable predictors of future

resource availability (Brockman & van Schaik, 2005; Helm *et al.*, 2013). However, the utility of the income-capital model is limited; regardless of breeding strategy, individuals must reach a minimum acceptable body condition threshold to reproduce (Bronson, 2009; Clauss *et al.*, 2021). Many primates also fall on a continuum between the capital and income breeding extremes. These species use a mixed strategy (“relaxed” income breeding) that relies on both internal and external cues (Brockman & van Schaik, 2005).

Regardless of strategy, both food availability and quality are the primary factors that limit female reproduction (Emery Thompson, 2013). In unpredictable or non-seasonal environments, individuals are expected to depend on internal cues to time reproduction, whereas in seasonal environments, individuals are expected to rely on external environmental cues that consistently predict resource availability (Brockman & van Schaik, 2005; Clauss *et al.*, 2021). External cues may include photoperiod (especially further from the equator; Hau, 2001; Rowell & Richards, 1979), temperature, rainfall (Chapman *et al.*, 1999), and/or humidity (Ingraham *et al.*, 1976).

These environmental factors, and consequently resource availability (namely food availability and/or quality), vary across latitudes (Heldstab *et al.*, 2021), as well as over time and small geographic ranges (Cheney *et al.*, 1988). Given the importance of energy in reproduction, these differences in food can affect not only reproductive seasonality, but also other reproductive parameters, such as the interbirth intervals (IBIs). For example, among free-ranging Hanuman langurs, IBIs were longer when food availability was low compared to when food was abundant (Borries *et al.*, 2001). Similarly, mothers of sexually dimorphic species tend to have longer IBIs after birthing a male, because males tend to be more energetically expensive than female infants (Garcia *et al.*, 2009; Smith & Leigh, 1998; but see Maestriperi, 2001). Within groups, dominance rank can influence food access, such that high-ranking females tend to be in better condition and have more energy for reproduction, resulting in higher fitness through improved survival and greater fecundity (Fairbanks & McGuire, 1984; van Noordwijk & van Schaik, 1999). For instance, dominant female vervet monkeys have lower mortality rates during periods of drought (Wrangham, 1981), whereas high-ranking long-tailed macaques (*Macaca fascicularis*) are more likely to give birth in unfavourable conditions (van Noordwijk & van Schaik, 1999). Not all studies find an association between rank and measures of fecundity or reproductive success (Cheney *et al.*, 1988, 2006). This is possibly because the reproductive benefits incurred by dominant females may be countered by predation or infanticide risk (Cheney *et al.*, 2006), or the benefits may primarily exist during periods of resource scarcity. Ultimately, both food availability and accessibility likely influence the timing of reproduction.

The effects of seasonal fluctuations in natural food availability on reproduction may be limited if females supplement their diet with anthropogenic foods (Oro *et al.*, 2013). Such supplementation has been associated with greater body mass across group members, shorter IBIs among adult females, and among younger individuals, earlier age at sexual maturity and increased survival probability, especially past infancy (Altmann & Alberts, 2003; Mori, 1979; Schmitt *et al.*, 2020; Sugiyama & Ohsawa, 1982). Therefore, quantifying the potential impacts of anthropogenic food

on reproduction requires an understanding of the relationship between reproductive parameters and resource availability.

Vervet monkeys are omnivorous generalists (Struhsaker, 1967a) found in a range of habitats throughout sub-Saharan Africa (Isbell & Jaffe, 2013). They are characterized by female philopatry and male-biased dispersal (Isbell *et al.*, 2009), and have been variously characterized as having sex-specific dominance hierarchies, where the dominance hierarchies function separately in terms of access to resources (Lancaster, 1971; Struhsaker, 1967b), and as having codominant hierarchies, where males are not always dominant to females (Bramblett *et al.*, 1982; Young *et al.*, 2017). Previous studies found that vervets do not conceive at peak food availability (Lee, 1987), and female dominance rank does not influence IBI (Cheney *et al.*, 1988), suggesting that vervets tend toward income breeding (Brockman & van Schaik, 2005). Wild vervets appear to have higher breeding seasonality (*sensu* van Schaik *et al.*, 1999, with >67% of births within three consecutive months) and highly variable weaning age (9-21 months, Cheney *et al.*, 1988; Whitten, 1982) compared to captive vervets (Table I). Relative to wild vervet populations, captive populations tend to have longer breeding seasons (i.e., moderate seasonality, with 33-67% of births within 3 months), shorter IBIs, and earlier weaning (~6 months, Fairbanks & McGuire, 1984) (Table I; Brockman & van Schaik, 2005).

We studied an equatorial population of vervets along the shores of Lake Nabugabo, Uganda. Unlike most vervets studied to date, this population lives in a human-modified, forest-agriculture matrix and supplements their natural omnivorous diet with anthropogenic foods by crop foraging and eating food refuse and tourist handouts (Chapman *et al.*, 2016). Previous analyses of births in one group suggested that, relative to other wild vervets, the Lake Nabugabo vervets breed less seasonally, and have IBIs more similar to those recorded in captive populations (Table I; Schoof *et al.*, 2015). We aimed to characterize the reproductive seasonality of the Nabugabo vervets using eight years of data from three groups while considering external cues that may be used to time reproduction, how food availability may affect body condition, and how dominance influences female reproduction. Given the influence of energy availability in female mammalian reproduction, we hypothesized that the Nabugabo vervets would be classified as relaxed income breeders (Brockman & van Schaik, 2005) due to their equatorial location and access to anthropogenic foods. We predicted that these vervets:

- 1) will be seasonal breeders that use external cues to time reproduction such that mating and/or conceptions will be predicted by environmental cues, and lactation and/or weaning will coincide with high food availability;
- 2) will have longer birth peaks and shorter IBIs than other wild populations;
- 3) will have differential survival of infants born within and outside the birth peak;
- 4) will not differ between groups in their reproductive parameters;
- 5) will have shorter IBIs among high-ranking females due to priority of access to food resources compared to lower-ranking females.

Table 1 Reproductive parameters for wild and captive vervet monkey (*Chlorocebus pygerythrus*) populations

Site	Coordinates	Groups (N)	Births (N)	Wild/ captive	Birth season	Mating season	Breeding sea- sonality	IBI (mo)	Sources
Kampala, Uganda	0°20' N 32°33' E	1	9	Captive	Jan-July	n/a	Moderate (45.5%)	10.9	BS/IBI: Rowell, 1970
Institute of Primate Research, Kenya	1°21' S 36°42' E	(28 females)	n/a	Captive	Year-round (Nov-Feb peak)	n/a	Moderate		BS: Else, 1985, as cited in Else <i>et al.</i> , 1986
Austin, Texas, USA	30°17' N 97°44' W	1	38	Captive	Year-round (except Nov)	n/a	Moderate (47.4%)	11.3	BS/IBI: Bramblett <i>et al.</i> , 1975
Lolui Island, Uganda	0°05' S 33°42' E	n/a	n/a (>200)	Wild	Apr-Sept	Oct-May			BS/MS: Gartlan, 1969
Segera Ranch, Laikipia, Kenya	0°15' N 36°50' E	2	40	Wild	Jan-Mar	all months but Jan, Mar, Apr (peak: Jun-Oct)	High (75%)	13.3	BS/MS: Isbell & Jaffe, 2013; IBI: Isbell <i>et al.</i> , 2009
Lake Nabugabo, Uganda (2012-2019) (2012-2014)	0°22' S 31°54' E	3	126	Wild	Oct-Dec	all months	Moderate (61%)	11.5* (11.3-11.9)	Current study
Samburu-Isiolo Reserve, Kenya	0°30' N 37°30' E	2	16	Wild	Nov-Dec	all months	Moderate (46%)	11.7	BS/MS/IBI: Schoof <i>et al.</i> , 2015
Amboseli National Park, Kenya	2°41' S 37°10' E	3	75	Wild	Oct-Dec	Mar-June	High (93.75%) (Oct-Dec)	20.1	BS/MS: Whitten, 1983; IBI: Whitten, 1982
						Apr-Oct (May-Jun primarily)	High (87%)	17.1 (13.8-21.3)	BS/IBI: Cheney <i>et al.</i> , 1988; BS/MS: Lee, 1984; MS: Andelman, 1987

Table 1 (continued)

Site	Coordinates	Groups (N)	Births (N)	Wild/ captive	Birth season	Mating season	Breeding seasonality	IBI (mo)	Sources
Masai-Amboseli Game Reserve, Kenya	2°45' S 37°15' E	4	15	Wild	Oct-Mar (Nov peak)	May-mid/late Oct			BS/MS: Struhsaker, 1967a
Zambezi River, Zambia	17°55' S 25°51' E	1	14	Wild	late Oct-Jan	n/a			BS: Lancaster, 1971
Soetdoring Nature Reserve, South Africa	28°50' S 26°02' E	1	15	Wild	Oct-Nov	Mar-Jun	High (93.3%)		BS/MS: Blaszczyk, 2018
Samara Private Game Reserve, South Africa	32°22' S 24°52' E	2	65	Wild	Nov-Jan	Apr-June		21 (17.9 - 24)	BS/MS: McFarland <i>et al.</i> , 2014; IBI: Pasternak <i>et al.</i> , 2013
Windy Ridge Game Park, South Africa	38°35' S 31°46' E	1	8	Wild	Oct-Dec	Apr-Jun	High (87.5%)		BS/MS: Baldellou & Adan, 1997

BS: Birth season; MS: Mating season; IBI: Mean interbirth interval in months for all groups, where the range represents mean IBIs from individual groups studied (where available); n/a: not available. Breeding seasonality is categorized based on van Schaik *et al.* (1999): the percentage is the proportion of all births that occurred within a 3-month birth peak. Moderate seasonality indicates 33-67% of births occurred within a 3-month peak; high seasonality shows >67% occurred in that period. Adapted from Schoof *et al.* (2015)

*Two upper outliers in interbirth interval were omitted (698 and 1412 days)

Methods

Study Site, Subjects, and Data Collection

We collected data on three neighbouring groups (M, HC, and KS) of free-ranging, habituated vervet monkeys near the shores of Lake Nabugabo, Uganda (0°22' S, 31°54' E; Chapman *et al.*, 2016). We began studying M group in June 2011, and HC and KS groups in January 2016. Our team could individually identify monkeys within six months of initial observation, thus we included data starting in January 2012 for M group and July 2016 for HC and KS. The groups' ranges are within and adjacent to the village of Bbaale (approximately 50-100 households). The area is a human-modified matrix of grasslands, forest patches, regenerating vegetation, and small agricultural plots (Chapman *et al.*, 2016). The region experiences two wet (March-May, September-December) and two drier seasons (January-February, June-August; see below).

We collected scan sampling data at 30-minute intervals from 2011 to 2015 and at 15-minute intervals from 2016 onward. These data consisted of the activity of five juveniles, subadults or adults of either sex, of which we only used female data. To avoid spatial and temporal autocorrelation, we haphazardly sampled non-interacting individuals spread throughout the group and avoided sampling the same individuals in two consecutive scans. Groups consisted of a mean of 35 individuals (range: 17-50) with 10 adult females (range: 5-15). We conducted scans in two teams between 7:30 am and 4:00 pm for 18 days per month (six days per week for three weeks, followed by one week off), rotating between study groups. We supplemented scans with *ad libitum* agonism data and recorded all births, deaths, and dispersals.

Reproductive Seasonality

For the birth season analysis, we included all dates of birth (DOBs) accurate to within one month from July 2012 (M group) and July 2016 (HC and KS) until June 2020. These ranges ensured each month was sampled eight times (M) and five times (HC and KS) during the study. Likewise, we examined conception seasonality by subtracting 163 gestation days from DOBs (range: 157-168 days; Kavanagh *et al.*, 2011) to obtain estimated conception dates (Andelman, 1987; Bramblett *et al.*, 1975) and binned both births and conceptions ($N = 126$) into months. We also considered mating seasonality by extracting the monthly proportion of scans in which we observed a copulation/mount. For analyses on the influence of weather and food availability, we approximated peak-lactation as beginning 60 days following DOBs (based on time spent suckling; Hauser, 1994) and estimated weaning date as starting 180 days following DOBs (based on the cessation of breastfeeding; Fairbanks & McGuire, 1984). To account for variability, we binned peak-lactation and weaning according to the month, and we used a 2-month buffer in our calculations such that we analyzed peak-lactation between 60- and 120-days postpartum, and weaning between 180- and 240-days postpartum. We chose the weaning date to begin when captive vervets are weaned because a previous study of the Nabugabo vervets indicated they have shorter IBIs than most wild populations (Schoof *et al.*, 2015).

Because we relied on scan data, we were unable to better estimate the timing of peak-lactation and weaning for our groups.

To investigate the fitness consequences of seasonal breeding, we examined whether infants born during the birth peak had a survival advantage over those born outside the peak. We identified the birth peak as the 3 months in which most births occurred year after year (*sensu* van Schaik *et al.*, 1999). Because survivorship of the Nabugabo vervets plateaued around one year of age (unpublished data) and vervet infants tend to associate closely with their mothers until one year of age (Hauser, 1993), we defined survival as living to at least 365 days. We included the same births from the breeding analysis, except we only used births until June 2019, because the infants had to survive a minimum of one year.

Food Availability

From June 2011 to January 2020, we conducted monthly surveys of food trees, vines, and shrubs and recorded a phenology score (0-4, where 0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%) for flowers, young leaves, mature leaves, ripe fruit, and unripe fruit (Chapman *et al.*, 2016). Between June 2011 and July 2018, we sampled on average 72 individual trees and/or shrubs per month from up to 34 species. In August 2018, we expanded our sampling effort to 137 individuals per month from a total of 40 species. Previous work on the Nabugabo vervet population found that 69% of feeding bouts consisted of ripe and unripe fruits, whereas insects made up the next highest proportion of feeding bouts at 10.6% (Chapman *et al.*, 2016). Given we have not collected data regarding the availability of insects year-round, we limited our evaluation of food availability to fruit abundance. We analyzed fruit availability for all plants combined, as well as for the top five most consumed plant species individually: *Pseudospondias microcarpa* (8.9%), *Lantana camara* (7.7%), *Maesopsis eminii* (6.3%), *Ficus natalensis* (5.2%), and *Pycnanthus angolensis* (4.5%) (Chapman *et al.*, 2016). For each tree, we calculated a monthly fruiting score by adding the ripe and unripe fruit scores (Chapman *et al.*, 2005; Schoof *et al.*, 2015). Then, we averaged those scores across all trees sampled to generate a total monthly fruit availability score, treating all food species equally. To examine the potential role of crop foraging on breeding seasonality, we calculated the monthly proportion of scans in which vervets were in agricultural plots or observed feeding on anthropogenic foods relative to the total number of feeding scans.

Weather Data

We extracted weather data from June 2011 to June 2020, namely average daily maximum temperature (T_{\max}), mean humidity, and monthly rainfall from World Weather Online for the two weather stations nearest Lake Nabugabo: Entebbe International Airport (0°03' N, 32°28' E; World Weather Online, 2020a) and Mbarara (0°36' S, 30°40' E; World Weather Online, 2020b). We used the inverse distance weighting (IDW) method to interpolate weather conditions at Nabugabo (Teegavarapu &

Chandramouli, 2005). We omitted photoperiod since our study population lives $<1^\circ$ from the equator, where maximum photoperiod variation was only 3 minutes.

Interbirth Interval

We calculated interbirth intervals (IBIs) for all consecutive infants of multiparous females whose DOBs were accurate to within 15 days ($N = 83$). This inclusion criterion was based on the field team's schedule of rotating between groups such that there was a maximum of 15 consecutive days during which a specific group was not followed. We calculated IBIs by taking the infant DOB (i_{n+1}) minus the DOB of the previous infant (i_n). We distinguished IBIs by whether the previous infant (i_n) survived to 6 months of age, at which time maternal investment decreases significantly (Fairbanks & McGuire, 1987). In examining factors that influence IBI, we only included those IBIs in which the prior infant (i_n) survived beyond 6 months of age ($N = 65$). Based on a boxplot interquartile range outlier analysis, we excluded two of three statistical upper outlier IBIs (698 and 1412 days), because these outliers are likely the result of undetected pregnancies and miscarriages. We maintained the third statistical outlier (491 days) since it was not a biologically significant outlier. For analyses relating dominance rank and IBI, we excluded two entries in which the corresponding female had not engaged in any agonistic interactions at the time of conception.

Dominance Rank

We extracted all dyadic female-female agonistic interactions from the scan and *ad libitum* data, recording the winner (i.e., the individual directing aggression without receiving retaliation) and the loser (i.e., the individual submitting). We recorded a draw if both individuals directed and received aggression during the agonistic bout. We defined a bout as any agonistic interactions occurring between the same dyad within 15 minutes. Because female dominance rank is inherited through the matriline and female vervet dominance hierarchies are generally stable (Bramblett *et al.*, 1982), we chose to be conservative and to include females in the dominance calculations as of their first intragroup female-female agonistic interaction, regardless of their age.

To calculate female dominance rank, we assigned each female an initial Elo score of 1,000 and estimated a single optimized k value across all three groups (Neumann *et al.*, 2011; Neumann & Kulik, 2014). Following Neumann and Kulik (2014), we calculated an optimized k for each group (function `optimizek`, package `EloRating`; Neumann & Kulik, 2014) by testing a range of k values from 4-200 at a resolution of 491 and calculating log likelihoods for each value. The resolution determines how many k values are tested, where a resolution of 491 evenly divides our range of k values into 0.4-unit increments (i.e., we tested $k = 4, 4.4, \dots, 199.6, 200$). Because agonistic bouts in each group presumably contribute equally to their respective dominance hierarchies, we standardized the optimized k across the three groups ($M = 69.2$, $HC = 69.2$, $KS = 72.4$) by calculating the difference between the log-likelihood of each tested k value and the optimized k for the associated group. We

selected the integer k value with the lowest standard deviation as the optimized k across the three study groups ($k = 70$).

To examine the role of female dominance rank on IBI, we used all female-female agonistic interactions leading up to a female's estimated date of conception and then extracted her Elo score on that date. We chose the conception date to extract Elo scores, because factors related to dominance (e.g., access to resources) leading up to that date may influence a female's IBI whereas gestation length is relatively fixed (Andelman, 1987; Bramblett *et al.*, 1975; Kavanagh *et al.*, 2011). To examine which dominance rank metric was best suited to our analyses (Levy *et al.*, 2020), we used these Elo scores and the hierarchy size (i.e., number of females in a given group) on the date of conception to calculate the corresponding ordinal rank (i.e., a female's ordered position in the hierarchy), proportional rank (calculated as $[\text{hierarchy size} - \text{ordinal rank}] / [\text{hierarchy size} - 1]$), and Jenks Natural Breaks (calculated using the `plotJenks` function in package `GmAMisc` (Alberti, 2019) to classify each female as high-, mid-, or low-ranking). Our results indicated that proportional rank was best suited to our analysis and thus was used throughout (see below). We excluded ten females who engaged in five or fewer female-female agonistic interactions from the dominance analyses (Neumann *et al.*, 2011).

To test if higher-ranking females have priority of access to resources, we calculated the proportion of scans per month in which a female was feeding relative to the total number of scans in which she was observed. In using a proportion rather than a count, we standardized our values to account for the change in sampling methods (i.e., sampling every 15 vs. 30 minutes) and the observability of each individual. We further determined the proportion of monthly feeding scans in which a female was observed eating an anthropogenic food, operationally defined as a species known to be cultivated for human consumption, stolen from kitchens, provided by a tourist, or food refuse (Online Resource Table S1). We determined each female's dominance rank on the last day of the month to represent her position in the hierarchy during that month. For females who disappeared before the end of the month, we calculated their rank the day before their disappearance.

Data Analyses

We used circular statistics to analyze birth and conception seasonality. We computed: 1) circular mean angle, indicating the average day on which births/conceptions occurred in the year; 2) vector length, r , representing the degree of dispersion of the dataset where 0 indicates uniformly distributed throughout the year and 1 indicates all events occurred in the same month; and 3) the variance, standard deviation, standard error, and confidence intervals (Kovach, 2011). We conducted a Rayleigh Uniformity test to identify deviations from a uniform distribution and a Watson-Williams F-test to examine whether birth seasonality differed between the groups (Kovach, 2011). The Rayleigh Uniformity test does not produce high rates of type I errors even when the data being analyzed are binned (Landler *et al.*, 2020), as

done in the current study. We also used a chi-square test to assess infant survival to one year relative to whether they were born within or outside the birth peak.

We further relied on circular statistics for mating seasonality and for phenological analyses of food availability. We inputted the data as vector pairs, where the month was the angle (i.e., direction), while the length (i.e., magnitude) of the vector was the monthly proportion of copulations and the average monthly fruiting score, respectively. We calculated weighted statistics where the weighted mean vector (WMV) represents the mean angle, and the length of the weighted mean vector (r) is analogous to vector length. To determine whether the monthly proportion of copulations and fruit availability differed from a uniform distribution, we performed a Moore's Modified Rayleigh test—a nonparametric version of the Rayleigh test (Kovach, 2011). We conducted all circular statistics in Oriana 4.02 (Kovach, 2011).

To assess crop foraging, we used a Kruskal-Wallis rank-sum test to examine monthly differences in the proportion of crop foraging scans. We then conducted a Welch's ANOVA with Games-Howell *post-hoc* test to examine differences in crop foraging between groups. To assess reproductive timing relative to environmental factors, we fit linear models with cumulative rainfall, mean maximum daily temperature, mean humidity, and ripe and unripe fruit scores as predictors, and one of three measures of reproduction as response variables. For each response variable, we calculated a proportion of births/conceptions (i.e., frequency) that occurred each month relative to the total number in that year. Our three measures of reproduction (all binned into months) were peak-lactation date (DOB + 60 days), weaning date (DOB + 180 days), and frequency of conceptions. For peak-lactation and weaning date, we fit a rolling mean (function `rollapply`, package `zoo`; Zeileis & Grothendieck, 2005) of the weather variables and fruit scores over two months to capture the average conditions from 60 to 120 days and 180 to 240 days, respectively. We shifted the weather data back one month for the frequency of conceptions, because we expected that weather conditions would act as a cue for the subsequent month (Perret & Aujard, 2001; Schoof *et al.*, 2016). Our binned data reflected the number of months in which we had weather, phenology, and birth/conception data (conceptions: $N = 89$; peak-lactation and weaning: $N = 87$). We also conducted a correlation matrix among all reproductive measures, weather variables, and fruit scores.

We compared the mean IBI of females among groups when infants i_n survived to six months with a one-way Welch's ANOVA (function `oneway.test`) assuming unequal variances. We also compared population-wide IBIs when infants i_n did and did not survive to six months using a one-tailed, two-sample t-test assuming unequal variances. To test for an effect of rank on IBI, we fit linear mixed models (function `lmer`, package `lmerTest`; Kuznetsova *et al.*, 2020) with rank, group identity, and sex of the previous infant as predictors, and maternal identity as a random effect. We expressed group identity as a fixed effect because we had fewer than the five recommended levels for a random effect to properly estimate variation (Gelman & Hill, 2007), group identity was consistently included as a fixed effect among our most parsimonious models, and we also wanted to test for differences in reproductive parameters between groups.

We investigated the influence of rank on the proportion of scans dedicated to feeding in general and to feeding on anthropogenic foods using generalized

linear mixed models with a quasibinomial distribution to account for overdispersion (glmmPQL in the MASS package; Ripley *et al.*, 2020). We fit models with rank and month as fixed effects, and year and maternal identity as random effects. We omitted group identity as a factor because of a singularity issue when running the models. For all our models, we conducted an automated model selection process (function dredge, package MuMIn; Bartoń, 2020) and selected the best model using the corrected Akaike Information Criterion (AICc; Wagenmakers & Farrell, 2004) and the highest variance explained. For each best model, we used Wald chi-square tests (function Anova, package car; Fox *et al.*, 2020) to determine whether the effects of our predictors differed from zero. We acknowledge that hypothesis testing following automated model selection may produce Type I errors since we did not adjust the alpha value. All models were also checked for co-linearity between variables and normality when assumptions included a normal distribution. We conducted all analyses in R version 3.6.2 (R Core Team, 2019), and code is available from: <https://mschweg.github.io/VervetBreeding2020/>.

Ethical Note

This research was approved by the McGill University Animal Care Committee (2011-2015) to CAC and York University Animal Care Committee (2015-present) to VAMS, as well as the Uganda Wildlife Authority and Uganda National Committee for Science and Technology to CAC and VAMS. The authors declare they have no conflicts of interest.

Data Availability The datasets analysed during the current study are available on Figshare (reproduction data: <https://doi.org/10.6084/m9.figshare.14866146>, <https://doi.org/10.6084/m9.figshare.19312373>; weather data: <https://doi.org/10.6084/m9.figshare.14847750>; food availability data: <https://doi.org/10.6084/m9.figshare.14847726>; dominance data: <https://doi.org/10.6084/m9.figshare.14866233>). Code is available on Figshare (https://figshare.com/articles/software/Schwegel_et_al_R_scripts/19665339) and on GitHub (<https://mschweg.github.io/VervetBreeding2020/>).

Results

Reproductive and Food Seasonality

We recorded 126 births from 44 mothers between July 2012 and June 2020 (HC = 13, KS = 42, M = 71 infants from HC = 5, KS = 21, and M = 18 mothers). Although we recorded births in all months and calculated conceptions in all but October, neither had a uniform distribution (Fig. 1a, b; Table II). Mean birth date in each group was in, or on the cusp of, November, whereas mean conception date was at the cusp of May and June (Table II). Among all births, 61.1% occurred in October to December, but the three groups differed in the proportion of births occurring within a three-month period (Table III). Mean birth dates differed between M and

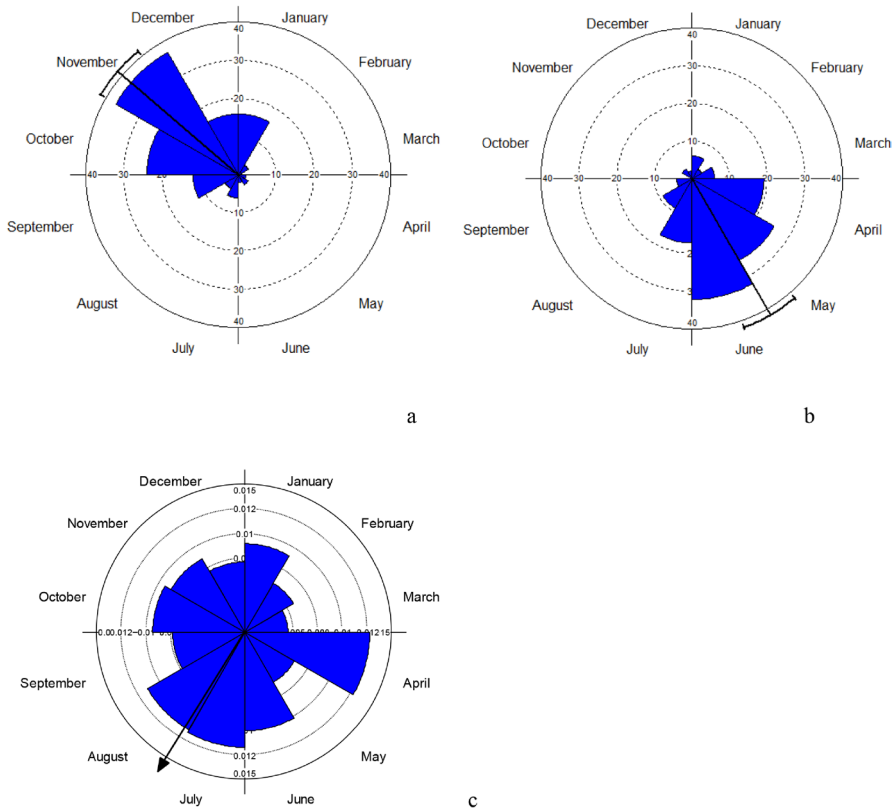


Fig. 1 Rose diagrams indicating the distribution of **a** births and **b** conceptions corresponding to births between July 2012 and June 2020, and **c** mean proportion of copulations from January 2012 to June 2020, for all three vervet monkey (*Chlorocebus pygerythrus*) groups (M, HC, KS) at Lake Nabugabo, Uganda. The black radius indicates the mean vector for a) births, $\mu = 310.598^\circ$, b) conceptions, $\mu = 150.216^\circ$, and c) copulations, $\mu = 211.854^\circ$; the black arc represents the 95% confidence interval for non-uniform distributions only (i.e., births and conceptions).

both HC and KS groups but not between HC and KS (Watson-Williams multisample F-test: $F = 3.597$, $df = 2$, $P = 0.03$; Table IV). We recorded 1351 copulations/mounts across all months (Fig. 1c), and their distribution did not differ from uniform (Moore’s modified Rayleigh test: $R^* = 0.389$, $P > 0.5$).

Of 101 infants born before June 2019, 59 were born in the October–December birth peak, but they were not more likely to survive to one year than infants born outside this peak ($\chi^2 = 3.60 \times 10^{-31}$, $df = 1$, $P = 1$). Overall, the infant mortality rate in the first year was 30.7% ($N = 31$).

The monthly availability of ripe and unripe fruit and that of the top five most commonly consumed fruit species did not differ from uniform (Fig. 2, Online Resource Table S2). The average proportion of feeding scans per month in which the monkeys were crop-foraging was relatively low (HC: 11.0%, KS: 18.7%, and M: 14.9%) and

Table II Results of circular statistics, run in Oriana v 4.02, for birth and conception data from the three groups of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda (column 2)

	Birth vs. conception	All groups	M	KS	HC
Observations (N)	Both	126	71	42	13
Mean Vector (μ) ^a	Birth	310.568° (~Nov 11)	299.456° (~Oct 31)	320.595° (~Nov 21)	330° (~Dec 1)
Mean group	Conception	150.216° (~June 1)	136.709° (~May 19)	160.413° (~June 12)	176.408° (~June 28)
Length of mean vector (r)	Birth	0.609	0.569	0.732	0.561
	Conception	0.590	0.542	0.713	0.643
Circular variance	Birth	0.391	0.431	0.268	0.439
	Conception	0.410	0.458	0.287	0.357
Circular standard deviation	Birth	57.03°	60.879°	45.236°	61.606°
	Conception	58.844°	63.428°	47.174°	53.865°
Standard error of mean	Birth	5.256°	7.656°	6.929°	19.007 ^{ob}
	Conception	5.481°	8.128°	7.251°	15.637°
95% Confidence interval(±) for μ	Birth	300.264°/320.872°	284.448°/314.464°	307.012°/334.178°	292.739 ^{ob} /7.261 ^{ob}
	Conception	139.471°/160.962°	120.775°/152.642°	146.197°/174.629°	145.753°/207.062°
Rayleigh test: Z (P)	Birth	46.785(< 0.001)	22.959(< 0.001)	22.518(< 0.001)	4.091(0.014)
	Conception	43.883(< 0.001)	20.846(< 0.001)	21.323(< 0.001)	5.372(0.003)

Birth dates ranged from July 2012 (M group) or July 2016 (HC and KS) to June 2020 and conceptions ranged from January 2012 (M group; July 2012 - 163 gestation days) or January 2016 (HC and KS) to January 2020. Births and conceptions were binned according to the month in which they occurred. Mean vector reflects the mean date on which births or conceptions occurred. Length of mean vector ranges from 0 to 1 where 0 is a uniform distribution and 1 indicates that all births/conceptions occurred in the same month. Results of Rayleigh Uniformity test presented ($P < 0.05$ indicates non-uniform distribution)

^a Approximate date of year calculated from mean vector by $\mu \times 365 \text{ days}/360^\circ$. This formula assumes that it is not a leap year

^b Values may not be accurate as the distribution is not clustered enough (i.e., approaching a uniform distribution) due to small sample size

Table III Percentage of births of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda from July 2012 (M group) and July 2016 (HC and KS) until June 2020 that occurred within a 3-month period

	Birth peak		Degree of seasonality
	October - December	November - January	
All Births (N = 126)	61% (N = 77)	55% (N = 69)	Moderate (Oct-Dec)
HC (N = 13)	62% (N = 8)	54% (N = 7)	Moderate (Oct-Dec)
KS (N = 42)	69% (N = 29)	71% (N = 30)	High (Nov-Jan)
M (N = 71)	56% (N = 40)	45% (N = 32)	Moderate (Oct-Dec)

All births are considered together and then separated according to the group in which they occurred (HC, KS, M). The corresponding degree of seasonality is based on van Schaik *et al.* (1999) where low seasonality indicates 33% or fewer births occurring in a 3-month period, moderate seasonality involves 33-67%, and high seasonality indicates >67% of births occurred in a 3-month birth peak

Table IV Results of Watson-Williams pairwise F-test, computed in Oriana v 4.02, comparing the distribution of births and mean birth dates between groups (HC, KS, M) of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda

Groups	F	df	P
M vs HC	4.478	1	0.037
M vs KS	4.162	1	0.044
HC vs KS	1.071	1	0.305

Births span from either July 2012 (M group) or July 2016 (HC and KS) until June 2020 and were binned according to the month in which they occurred

there was no difference across months (Kruskal-Wallis rank-sum test: $\chi^2 = 15.4$, $df = 11$, $P = 0.164$). However, there were differences between groups (Welch's ANOVA: $F(2, 53.1) = 8.20$, $P < 0.001$), with crop foraging being lower in HC group than in both KS (Games Howell *post-hoc*: mean difference = 0.077 (95% confidence interval [CI]: 0.017-0.137), adjusted- $P = 0.009$) and M (mean difference = 0.039 (95% CI: 0.011-0.066), adjusted- $P = 0.004$), whereas there was no difference between KS and M (mean difference = -0.038 (95% CI: -0.097-0.020), adjusted- $P = 0.260$).

Breeding Seasonality Relative to Weather and Phenology

Between 2011 and 2020, average daily maximum temperature was 24.1 ± 1.4 °C SD and average monthly rainfall was 138.2 ± 103.1 mm; however, 2019 and

Fig. 2 Distribution of mean fruiting scores for various plant species at Lake Nabugabo, Uganda from monthly phenological data collected from June 2011 to January 2020. The fruiting score is a sum of the ripe and unripe fruit scores where each varies from 0 to 4 (0 = 0% of the tree crown contains fruit, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%).

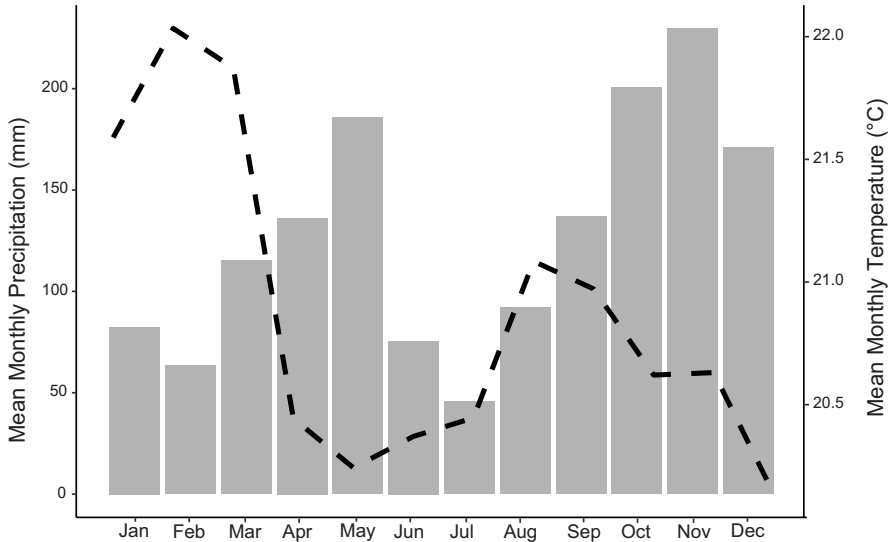
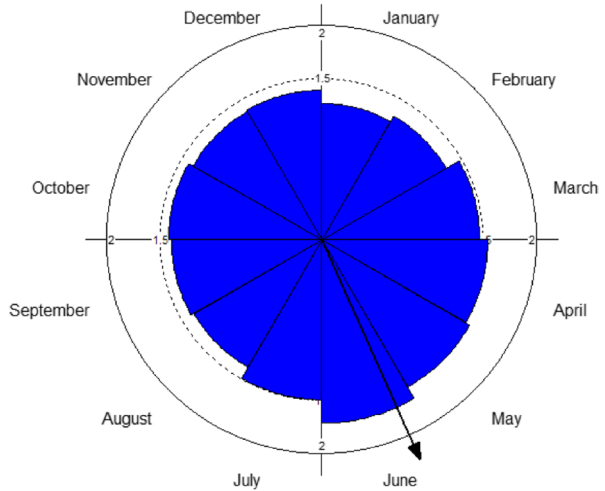


Fig. 3 Mean monthly cumulative rainfall (mm), represented with blue bars, and mean maximum daily temperature, represented with the orange line – June 2011 to June 2020 at Lake Nabugabo, Uganda. We interpolated the data using the inverse distance weighting method and climate data from the two nearest weather stations to Lake Nabugabo: Entebbe International Airport and Mbarara.

2020 were noticeably rainier than previous years, while maintaining wet and drier seasons (Fig. 3). Neither weather variables nor fruit scores predicted peak-lactation or weaning date (Table V). In addition, weather and fruit availability in one month did not predict conceptions in the following month (Table V). The results were consistent when we only considered the fruiting scores for the top five most consumed food species: the correlation coefficients (r) between the

Table V Results of generalized linear models (GLMs) regarding the association of the frequency of births (January 2012 to June 2020) and/or conceptions (relative to total per year) to weather variables and tree fruiting scores (June 2011 to January 2020) for vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda

Response variable	Model type	Fixed effect	Coefficient \pm SE	χ^2	<i>P</i>	Deviance (DF)	AIC (Δ)	R ²
Weaning date	Weather	Max temp*	-0.236 \pm 0.317	0.590	0.442	14.6 (79)	25.4 (8.2)	0.008
		Rainfall*	0.001 \pm 0.004	0.026	0.873			
	Phenology	UF score*	-0.216 \pm 3.000	0.005	0.943	11.3 (59)	21.2 (3.9)	<0.001
		RF score*	0.010 \pm 1.106	<0.001	0.993			
Peak-lactation	Weather	Max temp*	0.188 \pm 0.287	0.416	0.519	15.4 (83)	27.0 (4.0)	0.006
		Rainfall*	0.001 \pm 0.004	0.033	0.855			
	Phenology	UF score*	-1.07 \pm 2.68	0.157	0.692	12.8 (63)	23.0 (0.0)	0.002
		RF score*	-0.340 \pm 1.006	0.115	0.735			
Relative conceptions	Weather and Phenology	UF score	1.97 \pm 2.70	0.562	0.454	10.1 (73)	26.8 (8.0)	0.024
		RF score	0.413 \pm 1.048	0.158	0.691			
		Max temp	-0.191 \pm 0.505	0.145	0.704			
		Humidity	0.006 \pm 0.098	0.004	0.950			
		Rainfall	-0.003 \pm 0.007	0.294	0.588			

Max temp = maximum temperature; *UF* = unripe fruit; *RF* = ripe fruit. *Deviance* = residual deviance and degrees of freedom. *AIC* = Akaike Information Criterion of the alternative model (difference in AIC between the alternative and the null model). We did not reject the null hypothesis for any of our models

*Represents the rolling mean of that variable

relative number of conceptions and all the fruiting scores and weather variables were weak ($-0.24 \leq r \leq 0.25$). Results were qualitatively similar when examining the probability of a conception occurring in a month (analysis not presented).

Interbirth Interval

The IBI for females whose infants survived six months was 370.9 ± 146.8 days (mean \pm SD, $N = 64$) for all groups considered together. There was no significant difference in IBI among groups (Table VI, Welch's ANOVAs). IBI was significantly longer when a female's preceding infant (i_n) survived to six months than when it did not (Table VI, t -test). These relationships were maintained when the two upper outliers from M group were excluded (Table VI): overall mean IBI became 348.8 ± 47.3 days ($N = 62$).

Given the mean IBI is approximately 1 year, we also checked how many females gave birth in successive birth seasons. Only one birth was recorded in March, so we defined a reproductive year as spanning from April to March, inclusive. Using this definition, among 30 multiparous mothers and 83 births, 93.3% ($N = 28$) of adult females gave birth consistently without missing a reproductive year, and occasionally gave birth twice within 1 year.

The best model for explaining IBI ($AICc = 615.4$, $\Delta AICc = 2.76$, $R^2 = 0.197$) involved proportional rank (coefficient \pm SE: -40.3 ± 27.7 , $F = 4.018$, $P = 0.05$), sex of the previous infant (female coded as 0 and male as 1: 14.6 ± 12.1 , $F = 1.459$, $P = 0.232$), and group identity (relative to HC: $KS = 16.3 \pm 24.3$, $M = -8.67 \pm 23.0$, $F = 1.459$, $P = 0.249$) as fixed effects along with maternal identity as the

Table VI Mean interbirth interval (IBI) values of vervet monkeys (*Chlorocebus pygerythrus*) at Lake Nabugabo, Uganda born between January 2012 (M group) and July 2016 (HC and KS) and June 2020 following infants which did and did not survive to six months

Survivorship	Survived to 6 months				Did not survive to 6 months	
	N	Mean	N (no outliers*)	Mean (no outliers*)	N	Mean
All	64	370.9 ± 146.8	62	348.8 ± 47.3	19	310.1 ± 53.9
HC	5	352.6 ± 37.4	N/A		3	299.3 ± 11.7
KS	17	361.4 ± 35.7	N/A		4	342.0 ± 49.6
M	42	376.9 ± 179.9	40	343.0 ± 52.3	12	302.1 ± 59.9
Welch's ANOVA	Range: 230-1412 $F(2, 14.3) = 0.278$ $P = 0.76$		Range: 230-491 $F(2, 11.9) = 1.109$ $P = 0.36$		Range: 220-417 $F(2, 7) = 1.256$ $P = 0.34$	
t -Test	$t(77.4) = 2.75$, $P = 0.004$ no outliers: $t(27.1) = 2.82$, $P = 0.004$					

N = number of infants. Mean \pm standard deviation in days. All = combined dataset from each group. Welch's ANOVA: one-way, assuming unequal variances comparing HC, KS, and M IBIs for a given survivorship; t -test: one-tailed, two sample assuming unequal variances comparing IBIs following infants who and did not survive

*We removed IBI outliers with values of 698 and 1,412 days

random effect (Online Resource Table S3). Only proportional rank was a significant predictor of IBI.

Dominance Rank vs Feeding Models

From June 2011 to November 2019, among the reproductive females observed in a month (i.e., those females who conceived during and/or any time before that month), we recorded between 1 and 219 scans per female per month (mean: 45.4 scans, median: 40 scans). Based on model selection, we did not reject the null models: female rank and month did not predict the proportion of feeding scans, nor of anthropogenic feeding scans (all models: $R^2 \sim 0$).

Discussion

The Nabugabo vervets are moderately seasonal breeders. Conceptions, peak-lactation, and weaning were not predicted by temperature, rainfall, humidity, or fruit availability. To our knowledge, the mean interbirth interval (IBI) for these groups is the shortest reported for any population of wild vervet monkeys (Table 1). Higher-ranking females had shorter IBIs; however, dominance rank did not predict feeding behaviour.

As is characteristic of income breeders, who use external cues to time reproduction (Brockman & van Schaik, 2005; Clauss *et al.*, 2021), the Nabugabo vervets exhibited a birth peak despite their year-round copulations. We observed moderate breeding seasonality consistent with the availability of anthropogenic foods, but we also expected some seasonal variation in natural foods to explain the clustering of births; we found no such variation. Therefore, despite our reliance on estimates for peak-lactation, weaning, and conception dates, it is unsurprising that fruit availability did not predict peak-lactation or weaning (as predicted for income breeders) nor conceptions (as predicted for capital breeders). The lack of a relationship between fruit availability and reproductive parameters could indicate that the Nabugabo vervets use external cues, not related to fruit availability, to time reproduction. However, none of the weather variables we tested were associated with any reproductive parameters. Notably, there was no difference in the survivorship of infants born within and outside the birth peak, suggesting the timing of the peak is not conferring a survival advantage.

The lack of relationship between fruit availability and reproduction may have resulted from our fruit availability scores not adequately reflecting changes in resource availability. For instance, we did not distinguish preferred from less desirable foods (Chapman *et al.*, 2012), trees of different sizes (Chapman *et al.*, 1992), nor did we consider the diversity of foods available.

Ecotypic differences among vervet populations may explain the variation in reproductive seasonality. Recent analyses indicated that across primates, latitudinal range had a weak association with reproductive seasonality, whereby species whose habitat was closer to the equator had longer birth peaks (Heldstab *et al.*, 2021). Similarly, within the genus *Macaca*, there was a negative relationship between distance

to the equator and degree of reproductive seasonality with species furthest from the equator having the highest degree of seasonality (Trébouet *et al.*, 2021). These results are consistent with our comparison of published data on reproductive seasonality in vervets (Table I), and a report that vervet populations farthest from the equator have the highest degree of reproductive seasonality (Rowell & Richards, 1979).

At Nabugabo, most females gave birth in consecutive years and in about half of the successive births (43 of 83 infants born to a multiparous female), the mother simultaneously invested in two offspring at once via gestation and lactation (i.e., direct stacked investment; Vayro *et al.*, 2021). This high maternal investment may be possible because of consistent year-round food availability either from natural sources or access to anthropogenic foods. Nabugabo vervets also experience different predators (i.e., dogs, snakes Teichroeb *et al.*, 2015), and birds (unpublished data) compared with other wild populations that are subject to snakes, birds, baboons, and leopards (Isbell & Jaffe, 2013). Thus, a comparison of predation risk, alongside habitat type and food availability, may be a useful future study, given that infant mortality is much lower at Nabugabo (30.7%) than for the latitudinally similar Amboseli population (57%; Hauser, 1993).

While regional differences in latitude, habitat-type, weather, food availability, photoperiod, and predation risk may explain some of the interpopulation differences in vervet breeding seasonality, of these ecological factors, only food availability is likely to influence intrapopulation differences. Differences in home range quality, seasonal variation in fruit availability, and access to crops within each group's home range could potentially explain why two of our study groups (M, HC) are categorized as moderately seasonal breeders and one group (KS) as highly seasonal breeders. There were between-group differences in the proportion of scans in which vervets were crop foraging, but these differences do not appear to explain differences in reproductive seasonality. Differences in social factors could also play a role in intrapopulation variation in reproductive parameters. For example, instability of the male dominance hierarchy is a social stressor and is associated with increased female glucocorticoid levels (Carnegie, Fedigan, & Ziegler, 2011b), male-mediated prenatal loss (Zipple *et al.*, 2019), and infanticide (Palombit, 2015). If male dispersal is associated with infanticide, then this social factor may contribute to some of the observed birth seasonality (Tinsley Johnson *et al.*, 2018). At Nabugabo, male dispersal is timed with conception seasonality (L'Allier *et al.*, *in press*), but we lack sufficient data to assess to what degree such events are associated with infanticide.

As predicted, Lake Nabugabo vervets have shorter IBIs than those reported elsewhere for wild vervets. This finding is consistent with the low seasonal variation in natural foods, and their ability to supplement their diet with anthropogenic foods. Given the limiting role of energy constraints on female reproduction (Emery Thompson, 2013), it is not surprising that females whose infants did not survive to 6 months had significantly shorter IBIs than females whose infants did survive. While there was no significant effect of sex of the previous infant, we found that higher-ranking females had shorter IBIs. In contrast, Cheney *et al.* (1988) reported no correlation between dominance rank and IBIs in the Amboseli population; however, it is not clear which dominance rank metric was used in the Amboseli study. Despite having shorter IBIs, we did not find that high-ranking females spent a greater

proportion of scans feeding in general nor feeding on anthropogenic foods. Nonetheless, differences in food quality or feeding rate by females of different dominance ranks could contribute to the observed rank-dependent variation in IBIs.

Overall, our results are consistent with vervet monkeys exhibiting the reproductive flexibility associated with using external cues to time reproduction and internal cues to moderate this timing. However, the mechanisms leading to the lessened degree of breeding seasonality and shortened IBIs remain unclear. Reproductive seasonality in the Nabugabo vervets does not confer any obvious advantages: we found no evidence of 1) peak-lactation coinciding with high fruit availability and thus possibly improving maternal survival, nor of 2) improved infant survival for those born within a birth peak. Instead, the reproductive seasonality observed in this population may be the result of phylogenetic constraints (as proposed for other species; Heldstab *et al.*, 2021): an ancestral *Chlorocebus* evolved in a seasonal environment (Turner *et al.*, 2019) with high food variability, at which point a birth season was likely advantageous for their survival and reproduction. Such phylogenetic constraints may prove to be neutral or maladaptive, where species that can breed year-round may have the advantage when facing changing conditions that influence the seasonality of natural foods.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10764-022-00313-y>.

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