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Seasonality of Conceptions Under Varying Conditions in a Rhesus Macaque Breeding Colony

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SEASONALITY OF CONCEPTIONS UNDER VARYING CONDITIONS IN A

RHESUS MACAQUE BREEDING COLONY

by

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ABSTRACT
SEASONALITY OF CONCEPTIONS UNDER VARYING CONDITIONS IN A
RHESUS MACAQUE BREEDING COLONY

by

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Under the Supervision of Andrew J. Petto, Ph.D

Rhesus macaques (*Macaca mulatta*) are well documented as seasonal breeders. Despite

this, little is known about what factors influence seasonal reproduction in rhesus. It has

been proposed that rhesus are "relaxed income breeders" (Brockman and van Schaik,

2005), which means they respond to changes in photoperiod but endogenous cues can

allow deviations from photoperiod-timed seasonality. This study presents the results of a

natural experiment on the influence of different housing conditions (featuring different

levels of environmental exposure) on the seasonal pattern of reproduction in rhesus.

Once the number of attempts was controlled for, rhesus did not exhibit a seasonal

distribution in their conceptions regardless of their level of exposure to environmental

cues. This indicates that no conceptual model as of yet has adequately assessed the

variation in seasonal reproduction in rhesus macaques.

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Dedicated to

Kelly, Fuzzy, Gaazhegains,

and my parents

Introduction

While human reproduction in developed nations generally occurs year-round, this is not common throughout the animal kingdom. Instead, we find that many species of animals, particularly those residing in temperate regions, show a distinctly seasonal pattern of conceptions and births. In fact, this is precisely what evolutionary theory predicts: where seasonal variation in availability of resources necessary for survival and reproduction exists, selection should act in a way to minimize resource use in lean times and schedule costly reproductive demands in such a way that they coincide with times of relative abundance.

There are three primary ways in which this reproductive resource optimization is thought to be accomplished, and these comprise what is called the "income-capital continuum model" (Brockman and van Schaik, 2005). The first is income breeding, whereby females use current available resources to invest in reproduction (Stearns, 1989). The opposite of this is capital breeding, in which females store energy for future reproductive effort (Stearns, 1989). Intermediate between strict income breeding (income breeding as described above) and capital breeding is relaxed income breeding (Brockman and van Schaik, 2005).

Strict income breeders, then, have a selective pressure to time their most energetically demanding reproductive efforts such that they coincide with the time of highest resource availability. In smaller organisms where infant survival is more advantageous than maternal survival, this time corresponds to immediately after weaning. In larger and longer-lived organisms, however, maternal survival is more advantageous, and the time of greatest resource stress for her is mid-to-late lactation (Janson and

Verdolin, 2005). Because rhesus macaques are long-lived, large-bodied, iteroparous organisms, the case of maternal survival will be primarily considered here, following Brockman and van Schaik (2005). We would thus expect income breeders to respond primarily to exogenous cues that predict with regularity the oncoming period of resource abundance so as to time their reproductive efforts in a way that infants are nursing during times of relatively abundant resources.

Capital breeders, on the other hand, are able to store resources during the times of relative resource abundance, begin reproduction at that time, and use stored reserves for energy while nurturing offspring. We should thus expect capital breeders to respond to endogenous cues such as fat amount or another measure of body condition. These two extremes form a continuum of responses between them, the approximate midpoint of which may be thought of as relaxed income breeding: a condition where exogenous cues are used as a primary method of timing reproductive output, but endogenous cues can either fine-tune or override the general time set by the exogenous cues. That is, females in superior condition can reproduce even in times outside of the conception window set for them as income breeders (Brockman and van Schaik, 2005).

It is worth noting here that Brockman and van Schaik's model was developed with primates in mind; in many other mammals, gestation periods are much shorter, and mating occurring at the beginning of a resource flush may produce young well before the resources are gone. Such an opportunistic breeding style would look similar to capital breeding. Further, with the short life spans that accompany this shortened gestation time, it may be advantageous to reproduce if possible regardless of conditions, as death may otherwise occur before reproduction.

When comparing *Peromyscus* (deer mice), lagomorphs (rabbits and hares), and *Odocoileus* (deer), Bronson and Heideman (1994) found that in all groups seasonality of reproduction decreased as latitude decreased, which is consistent with a decrease in the seasonality of available food. However, they further found that each time body size increased (from mice to lagomorphs and again from lagomorphs to deer), seasonality persisted at relatively lower latitudes. They ascribed this to a change in breeding opportunism: the smaller species were quicker to begin year-round breeding even when considerable seasonal changes in food availability still existed, as they have a much smaller window of opportunity (total, not seasonally) for breeding time. For larger-bodied organisms such as the deer, however, seasonal breeding persisted for a much larger range of latitude; *Odocoileus* exhibited year-round breeding only under 10 degrees north. Thus, for deer, the advantage of delaying reproduction such that the most energetically costly parts of reproduction occur during the time of greatest resources is greater than the advantage of such a pattern in mice.

For income breeders, both strict and relaxed, there must exist a cue that sets in motion physiological changes leading to the reactivation of reproductive behaviors. Variability between years in most environmental variables could lead to erroneous cueing. It is assumed that this is the reason that photoperiod is generally regarded as the proximate variable responsible for seasonal reproduction. Photoperiod varies predictably throughout the year and has extremely little variation between years. This circannual variation in photoperiod is absent on the equator, small in the tropics, but is considered to be of sufficient magnitude to provide a reliable cue in subtropical and, especially, temperate latitudes. Photoperiod is responsible for reproductive cueing in birds (Dawson

et al., 2001), the Syrian hamster (*Mesocircetus auratus*), the white-footed mouse (*Peromysucs leucopus*), the brown hare (*Lepus europaeus*), the domestic sheep, and many more (Bronson and Heideman, 1994).

In tropical regions, where photoperiod varies little throughout the year, seasonality is less well studied. While it is perhaps rarer, seasonal breeding does occur in the tropics. Many regions in the tropics have a very seasonal pattern of rainfall that creates seasonal variation in food quality and availability (Bronson and Heideman, 1994). It is unclear, however, whether rainfall serves as a *zeitgeber*, controlling the pattern of reproduction by serving as a cue, or if individuals tend to respond to seasonal fluctuations in resources directly.

It is well recognized that seasonal reproduction is the norm rather than the exception in primates (Lancaster and Lee, 1965; Lindburg, 1987; Janson and Verdolin, 2005); seasonality in primate reproduction has been found in nearly all species studied outside the tropics, and many within (Lindburg, 1987). Lancaster and Lee (1965) were the first to show convincingly that primates were seasonal; they also introduced the concept of varying amounts of seasonality. In their work, they consider a birth season as a pattern wherein births are concentrated in a discrete period with no births occurring in other months. A birth peak, on the other hand, is a period with a higher proportion of births, but births can and do occur year-round. These terms will be adopted in this thesis, but the overarching term seasonality has been and will continue to be used to mean a general condition that may include either a birth season or a birth peak, in agreement with Lindburg (1987).

To help determine the factors leading to reproductive seasonality among primates, Janson and Verdolin (2005) conducted an ANCOVA and multiple regression analyses. They found seasonality in births to be significantly and distinctly explained by latitude squared (which they used instead of latitude to account for an insignificant variation in seasonality in latitudes below 15°), the natural log of body mass, diet, continent, and the seasonality of the main item in the diet while holding other variables constant. They also found a significant correlation between mean birth date and mean date of peak food availability. Thus, their findings support the model of seasonality responding to both proximate and ultimate causal variables for primates.

Of all the non-human primates, none has been as extensively studied as the rhesus macaque (*Macaca mulatta*). Lindburg (1987) described rhesus as the species most prominently featured in discussions on seasonality in primates; however, while much is known about rhesus behavior, reproductive biology, and endocrinology, seasonality in rhesus reproduction is poorly understood. This is not, however, due to a lack of research effort. Rather, the many studies on the subject seem to reach little consensus on how seasonal rhesus are, and what drives that seasonality.

Rhesus macaques (*Macaca mulatta*) have a seasonal pattern of reproduction in their natural range (Heape, 1897; Hingston, 1920; Carpenter, 1942; Prakash, 1958, 1962; Southwick *et al.*, 1961; Ghosh and Sengupta, 1992; Wang *et al.*, 1996; Tian *et al.*, 2013), in free-ranging research colonies located in Puerto Rico (Altmann, 1962; Conaway and Koford, 1964; Drickamer, 1974; González-Martínez, 2004; Hoffman and Maestripieri, 2012; Koford, 1965, 1966; Lindburg, 1971; Rawlins and Kessler, 1985; Vandenbergh

and Vessey, 1968), the Florida Keys (Lehman *et al.*, 1994; Johnson and Kapsalis, 1995), and Brazil (Coimbra-Filho and Maia, 1977), in outdoor enclosures in Cambridge, England (Rowell, 1963) and the states of Georgia (Vandenbergh, 1973; Herndon, 1983; Ruiz de Elvira *et al.*, 1983; Bernstein, 1993) and Kentucky and Nebraska (Vandenbergh, 1973), in indoor enclosures exposed to natural light (Birkner, 1970), and in zoos in both hemispheres (Heape, 1897; Hartman, 1931; Zuckerman, 1931; Jarvis and Morris, 1962; Brand, 1963; Bielert and Vandenbergh, 1981; Gomes and Bicca-Marques, 2003). While variable among sites, the pattern is generally characterized by a period of conceptions in the fall and winter months, with a subsequent distribution of births occurring in the spring and summer. In laboratory breeding populations with controlled temperature and (usually) 12:12 hour light:dark patterns the occurrence of seasonality is more variable; some researchers found no evidence for seasonality (Ponce de Lugo, 1964; Eckstein and Kelly, 1966), but most did (Hartman, 1931; Valerio *et al.*, 1969a, 1969b; Riesen *et al.*, 1971; Vandenbergh, 1973; Hutz *et al.*, 1985), albeit with a lesser intensity compared to outdoor colonies.

Researchers have proposed several variables that might serve as the proximate causation of seasonality in rhesus. Daylight was the first *zeitgeber* proposed to be controlling the seasonal reproductive pattern in rhesus macaques; a six month difference in annual patterns (corresponding to the same season) between northern and southern hemisphere rhesus colonies (Hartman, 1931; Brand, 1963; Bielert and Vandenbergh, 1981) certainly lends some credence to this explanation. However, daylight alone cannot sufficiently explain the seasonal pattern seen.

As previously mentioned, laboratory animals raised in a year-round 12-hour daylight environment still showed some seasonality of reproduction; further, experimental manipulation of light intervals to long-day (20 hr light) and short-day (4 hr light) patterns did not significantly change ovulatory patterns when compared to individuals in a 12-hr light pattern (Wehrenberg and Dyrenfurth, 1983), although others have argued it is not the absolute period of light but rather the shortening of daylength that rhesus respond to. Furthermore, multiple colonies at similar latitudes in Puerto Rico differ significantly in their annual reproductive fluctuations (Altmann, 1962; Conaway and Koford, 1964; Koford, 1965, 1966; Vandenbergh and Vessey, 1968; Drickamer, 1974; Rawlins and Kessler, 1985; González-Martínez, 2004).

These results led Vandenbergh and Vessey (1968), and later Rawlins and Kessler (1985), to propose a model of rhesus reproductive seasonality that cites the onset of the rainy season as the proximate environmental cue responsible for reproductive seasonality, with daylight playing a more relaxed role, merely setting the general time that the breeding season may occur. Rawlins and Kessler (1985) found a strong and highly significant correlation between the median birth or conception date and the onset of the rainy season when tested at Cayo Santiago, Puerto Rico and noted that their correlation matched published information on reproductive seasonality at the La Parguera, Puerto Rico colony as well (which is where Vandenbergh and Vessey (1968) had collected data).

However, Lehman *et al.* (1994) found no correlation between the onset of the rainy season and the seasonality of reproduction for two rhesus colonies in the Florida Keys, despite similarities in latitude between the Puerto Rican colonies and the Keys (although Johnson and Kapsalis (1995) dispute Lehman *et al.*'s (1994) data as being

based on incomplete records). Thus, while specific environmental variables are difficult to ascertain, the general consensus is that daylight sets a wide range of potential times for a reproductive season, and other environmental conditions play a more proximal role in the timing of rhesus reproduction. This would make rhesus relaxed income breeders, and indeed that is precisely how Brockman and van Schaik (2005) classified them.

Despite the large quantity of data collected on rhesus reproduction, few data exist that specifically compare reproductive seasonality in differing environments directly. Herndon and colleagues (1985) did test for and find a change in breeding seasonality in individuals moved from an indoor to an outdoor enclosure. Unfortunately, their study had a treatment group of only five females and did not compare individuals pre- and post-transfer. Herndon *et al.*'s (1985) findings suggest that a study with a large sample size and varying levels of environmental exposure would be useful in assessing the level of disruption of seasonal breeding patterns in indoor-housed rhesus. Such a study could also offer useful insights into the environmental mechanisms that help regulate such a pattern and look for potential seasonal variations in attempt-corrected conceptions across treatments. It is the aim of this study to do just that.

Materials and Methods

Rhesus monkeys at the New England Regional Primate Research Center (NERPRC: at the time of data collection, this facility was named as above; in 2002, the name was changed to the New England National Primate Research Center) used in this study were housed in three different environments in the course of normal breeding and husbandry conditions. Two groups were involved in timed mating programs with limited access to males: the first was housed indoors in individual cages with a 12h:12h light/dark cycle and with controlled temperature and humidity (hereafter referred to as the "indoor" treatment).

The second group in the timed mating program was housed in group enclosures containing 4 or 5 females per group and consisted primarily of individuals moved from the indoor treatment. Each enclosure had one wire window, except for corner cages which had two. These windows allowed in sunlight, fresh air (during the non-winter months), and other environmental influences as well. During cold or inclement weather, these windows were covered by a translucent plastic shutter. Group enclosures were heated during winter months, but humidity was not controlled during any season. This treatment will be called the "exposed" treatment.

The third environmental condition consisted of multifemale rhesus groups living with one male in an outdoor/indoor facility. The outdoor part of these facilities was covered by a roof, but featured chain-link fencing on three sides of the enclosure (the other side was the wall of the indoor portion) and was thus exposed to open air except in winter, when translucent plastic panels were used for shelter. This condition will be referred to as the "outdoor" treatment. These three treatments exhibit a range of exposure

to both mate access and environmental conditions that form a natural experiment on the importance of environmental variables on the seasonality of rhesus reproduction.

Data exist on the indoor treatment from two different time periods. The first is census data of births from January 1970 through December 1983, which includes, among other things, information on the sire and date of parturition. The second data set for the indoor treatment contains detailed records beginning in the breeding season from July 1983 through June 1984 (the "84" breeding season) and extending for four years through June 1987. These data include details on sire, date of parturition, date of conception, and the date and potential sire of breeding attempts that did not result in a conception. The detailed and the census data sets, as defined above, do not overlap. Detailed records as described above, including mating attempts not resulting in a conception, exist for the exposed treatment for only one breeding season, from June 1989 through May 1990. Data for the outdoor treatment exist as census data (as described above) from January 1979 through December 1990.

For the two census data sets, conceptions were estimated by subtracting 168 days from date of birth. This number was chosen because it was the middle value in a range of average pregnancy duration given by Johnson *et al.* (1989) for NERPRC, was the same value used by Van Horn (1980), and agrees with the average found by van Wagenen et al. (1965), though Silk et al. (1993) found an average of 166.5 days in a more recent study with a larger sample size. Thus, four data sets exist comprising three different treatments: indoor detailed, indoor census, exposed detailed, and outdoor census. A summary of the treatments and their differing methodologies is given in **Table 1**.

Table 1. Summary of treatments.

	Exposure to Natural Light	Exposure to Fresh Air and Ambient Temperature	Exposure to Conspecifics	Conception Date	Records
Indoor Detailed	None	None	Single caged, Timed mating	Known within 1-5 days	July 1983 to June 1987
Indoor Census	None	None	Single caged, Timed mating	Estimated from births	January 1970 to December 1983
Exposed Detailed	Total	Sheltered during winter	Groups of 4-5 females, Timed mating	Known within 1-5 days	June 1989 to May 1990
Outdoor Census	Total	Sheltered during winter	One male with 4-5 females	Estimated from births	January 1979 to December 1990

All monkeys were served Monkey Chow or a similar bulk food product 2 cups per animal, twice daily (groups were fed in a common hopper and thus individual consumption may have differed from the 2 cup allotment). Fruit, cracked corn, and sunflower seeds were added a few times weekly as supplement. In the indoor and exposed treatments, females underwent a daily vaginal swab to detect onset of menses and were placed in isolation with a compatible male from roughly the 11th through the 15th day of their cycles. Females who became pregnant usually delivered through Caesarian section, though live births did occur, as well as stillbirths. Infants were cared for in a nursery to prevent lactational amenorrhea in their mothers. All infants born were assigned a unique identification number, and birth date and sire were recorded. Additional details about animal husbandry for the NERPRC can be found in Johnson *et al.* (1986, 1989) and Toloczko McIntyre and Petto (1993).

Statistical Tests

Conceptions

A preliminary analysis of the conception data revealed that while conceptions occurred throughout the year, they were concentrated in the fall and winter. This presented a problem of statistical analysis because a standard calendar year runs from January through December. A good portion of the winter season's conceptions occurred in January, and using a standard January-December year would split one season's conceptions into two years' data. Standard linear statistical analyses (such as an ANOVA) of the data would thus be flawed because the data would form a bimodal distribution, with the average being pulled toward summer because of the January

conceptions. Thus, two different methods, linear and circular, for dealing with this problem were adopted, and for all tests regarding conceptions, the data was subjected to both linear and circular analysis.

For linear analysis, instead of a break point of December 31– January 1, a break point of June 30– July 1 was adopted. This coincided with the general time of fewest conceptions, and also represented the exact middle of the year, both in conventional 12-month form and in day of year ($365/2 = 182.5$, rounded to 183, which is July 1). The resulting distributions appeared normal or semi-normal, and thus linear statistics were carried out on the conceptions with day-of-year days ranging from 183 to 548.

While linear statistical tests are more familiar, more comparable, conceptually simpler, and have a greater amount of mathematical research behind them, conception data occur in a cyclical pattern throughout the year. Rather than split the year at all, circular statistics is a branch of statistics that allows data occurring in a continuous circular fashion (time of day, compass orientation, or day of year as examples) to be analyzed without the need for any arbitrary break point. To conduct circular statistics, conception dates were converted to angular measurements using the following formula: $a = (360° * X) / k$, where X is the unmodified day of year and k is 365 days. In this thesis, linear tests will serve as the primary method of statistical analysis and circular analogs will serve as secondary support of the findings. Unless otherwise stated, all linear statistical tests were carried out in Systat, and all circular statistical tests were carried out manually, using Excel for computational efficiency and using Systat to assess the significance of the test statistics.

The first hypotheses of interest were whether conceptions in the four treatment groups were seasonally distributed throughout the year. This was tested linearly using a one-sample Kolmogorov-Smirnov test against a uniform (183,548) distribution. Note the minimum and maximum dates correspond to the linearly modified days-of-year described above. The circular analog chosen was the Rayleigh test for uniformity (Fisher, 1993; Zar, 1999), which tests whether the mean vector ρ is significantly different from zero. The mean vector ρ (and its sample statistic r) is a measure of dispersion around the circle which ranges from 0 (data are uniformly distributed around the circle or oppositely bimodal) to 1 (data all occur on the same point).

Next, the main hypothesis of interest regarding conceptions was tested: whether the treatments differed from one another in the timing of their mean conceptions (*i.e.*, their breeding peaks). For the standard linear test (a one-way ANOVA), *a priori* tests were conducted to determine if a significant difference existed between: a) the treatments exposed to any environmental condition and those exposed to none (exposed detailed and outdoor census *vs.* indoor detailed and indoor census; note this also divides the individuals exposed to group living from the individuals caged singly), b) the two indoor treatments (indoor census *vs.* indoor detailed), which would indicate if the methodology of estimating conception dates from census birth dates is flawed, and c) the exposed detailed and outdoor group treatment, which differed both in amount of environmental exposure and access to males. *Post-hoc* pairwise tests between all treatments were conducted using Tukey's honestly significant difference method.

For the circular analog of the one-way ANOVA, the Watson-Williams test was used (Zar, 1999); it is also referred to as an approximate ANOVA (Jammalamadaka and

SenGupta, 2001). *Post-hoc* pairwise tests were conducted via the Watson-Williams test as well; however, when multiple tests are applied to the same family of data, it increases the chance of a type I error (incorrect rejection of null hypothesis) occurring. In the linear tests, Tukey's HSD method controls this; in the circular analog, p-values for the multiple pairwise tests were adjusted using the Holm-Šidàk correction (Abdi, 2010) as it is computationally simpler and at least as stringent (likely more so) than Tukey's method.

The final tests on the conception data were conducted to determine if the treatments differed in the spread of conceptions throughout the year. For the linear data, Levene's test for homogeneity of variances (Sokal and Rohlf, 2005) was used. The closest circular analog available is the test of homogeneity of circular distribution factor κ. While κ is not strictly analogous to variance, it does give a measure of the spread of the data, and is the best test available for circular data to approximate a test of heteroscedasticity besides that already inherent in ρ.

Paired conceptions

In addition to the above tests which included all individuals, a subset of the data was examined that included individuals who had recorded detailed conceptions both indoors and exposed (n=52). Differences in seasonality were measured linearly by a repeated-measures ANOVA of the mean indoor conception date *versus* the mean exposed conception date. Instances in which only one conception occurred under a treatment (which was especially common for the exposed treatment) had that singular value used as the mean. These values were also converted to angular measurements and tested circularly using the Hotelling test for paired samples of angles (Zar, 1999).

Attempt-corrected conceptions

For two treatments, the indoor detailed and exposed detailed, detailed records (hence the name) exist not only for the successful pregnancies, but also for both recognizable conceptions terminated before birth and mate-pairing attempts that did not result in a recognized conception. This allows for the conception data considered previously to be corrected for number of mating attempts. This is useful, because although attempts were conducted with the same protocol throughout the year, differences exist in the number of attempts, and conceptions were highly correlated with the number of attempts. These data were used as an extension of the conception data to determine whether the probability of conceiving changed seasonally in the same manner as the actual conceptions; it can be seen that this then verifies if seasonal changes in conceptions are actually due to biologic changes or merely an artifact of sampling intensity (*i.e.*, mating attempts), and is similar in theory to fecundability, a measure used in demography (Bongaarts, 1975; Biggers, 1988). The test for homogeneity of slopes, a necessary prerequisite to ANCOVA, had to be conducted in SPSS, as Systat treated the months×exposure interaction term and the months×exposure×attempts three-way interaction terms as using 11 degrees of freedom, which led to a loss of degrees of freedom and a failure to execute the model properly. SPSS treated the above interaction terms with 1 degree of freedom and processed the test for homogeneity of slopes without issue. None of the interaction terms was significant; thus, the standard ANCOVA model was able to be applied. An ANCOVA of conceptions was completed with month of the year and treatment (indoor detailed or exposed detailed) as factors and attempts as a covariate.

Heritability

Heritability, in the narrow sense, measures the proportion of a trait's phenotypic variance that is due to additive genetic effects. It is most frequently measured by regressing the mean value of a trait in a pair of parents on the mean value in their offspring (Futuyma, 2013). While the overall census data contain many offspring from colony parents (in fact a majority of the individuals are colony born), only the detailed data sets suffice for evaluating the heritability of attempt-corrected conceptions. Further, only individuals in the indoor detailed treatment were analyzed in order to eliminate any influences of environmental variation between treatments. With these limits placed on the data, there were not enough mother-daughter pairs to reliably estimate heritability via parent-offspring regression. However, an alternate heritability analysis was possible, using half-sibs and testing for sire effects (Falconer and Mackay, 1996; Lynch and Walsh, 1998). There are few males used for maintenance of the breeding colony (relative to the number of females), so the data lend themselves well to this type of analysis. Overall, 40 females (as attempt-corrected conceptions are a female-only trait) were found that shared 11 sires amongst them. Nine of the 40 females formed four groups of full siblings; the analysis requires half siblings, so for each group of full siblings the number of conceptions and failed attempts were averaged and entered as one data point, bringing the total number of offspring in the analysis to 35. An ANCOVA was performed with conceptions as the dependent variable, sire as the factor, and attempts as the covariate. Heritability was then calculated by taking the proportion of the within-sire variance to the total variance and multiplying by four (Falconer and Mackay, 1996; Lynch and Walsh, 1998).

Summary of statistical methods

To recapitulate, the main research question of this study is: *In provisioned, captive rhesus macaques, what effect does season have on reproduction?* This question was analyzed first by looking for a birth season or birth peak in the four data sets described in detail above; it was then determined if differences exist in the timing of birth peaks between treatments. Paired data were used to verify differences between the indoor and exposed treatments, and heritability in the likelihood of conceiving was tested to eliminate the possibility of variation between treatments being due to relatedness of individuals. Finally, in the two timed mating treatments, number of conceptions were corrected by the number of attempts. These attempt-corrected conceptions (an estimate of likelihood of conception) were tested for seasonal fluctuation throughout the year and for a significant difference between treatments. **Table 2** gives a summary of the statistical methods used in this thesis.

Table 2. Summary of statistical methods.

Hypothesis or Data to be tested	Linear Test	Circular Test
Seasonality of conceptions	Kolmogorov-Smirnov test against Uniform (183,548) distribution	Rayleigh test of uniformity of mean vector ρ
Differences in breeding peak between treatments	ANOVA with *a priori* tests and *a posteriori* pairwise comparisons	Watson-Williams test of overall significance and pairwise comparisons
Differences in spread of conceptions	Levene's test for homogeneity of variances	Test for homogeneity of circular distribution factor κ
Paired conceptions (indoors *vs.* exposed)	Repeated-measures ANOVA	Hotelling test for paired samples of angles
Heritability of attempt-corrected conceptions	ANCOVA with sire as factor and attempts as covariate	None necessary
Attempt-corrected conceptions	ANCOVA with month and treatment as factors, attempts as covariate	None necessary

Results

Conceptions

In all four treatments (indoor detailed, indoor census, exposed detailed, and outdoor group census) conceptions occurred throughout the year, with a discernible peak that ranges among the four treatments from September and October to as late as May. This pattern is shown in **Figure 1** for the linear data and **Figure 2** for the circular data. As is evident from both of these figures, conceptions occurred year-round in all treatments, but all treatments also displayed a distinct breeding peak (but not a breeding season, as per Lancaster and Lee [1965]). Therefore, the removal of photoperiod does not eliminate seasonal variation in number of conceptions; this suggests other variables affect seasonality. The other striking feature of the graph is the paucity of data in the exposed detailed treatment relative to that in the other three treatments. Unfortunately, the data available for this analysis terminated shortly after the colony was moved to this condition, but there are 78 conceptions recorded for that treatment, which is sufficient for statistical analyses.

Summary statistics are provided in **Table 3**. Oriana was used to calculate the circular median and 95% confidence intervals of the circular mean. It can be seen that while linear measures of median and mean provide estimates similar to the more accurate circular ones, they are in no case exactly the same, and in some, fairly different. For example, while three of the linear means fall within the 95% confidence intervals of the circular mean (the outdoor census does not), the opposite (circular mean falling within 95% confidence interval of linear mean) is only true in two cases, indoor detailed and exposed detailed.
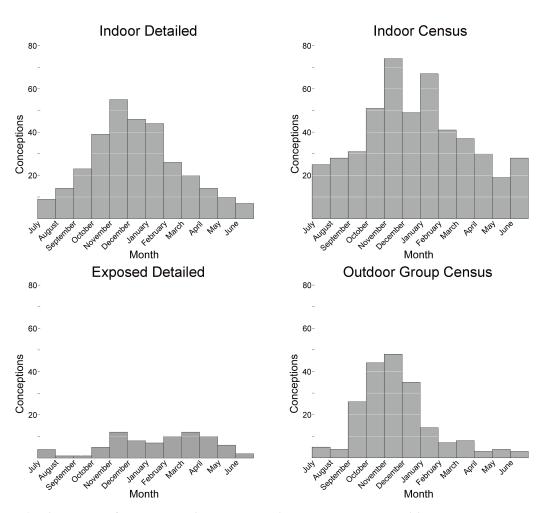
Figure 1. Histograms of total conceptions by month in each treatment condition.
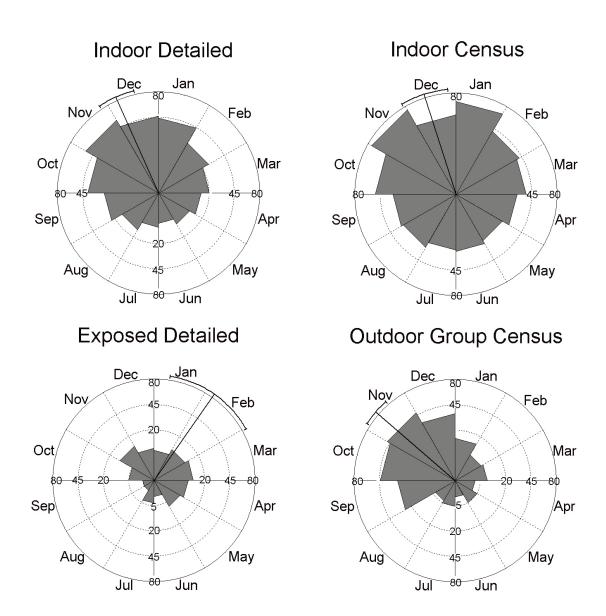
Figure 2. Equal-area rose diagrams of total conceptions by month in each treatment condition. Black Ts represent the mean with 95% confidence interval.

Table 3. Summary statistics of conceptions for both linear and circular data.

	Indoor Detailed	Indoor Census	Exposed Detailed	Outdoor Census
# Cases (N)	307	480	78	201
Linear Median	339 (Dec. 4)	351 (Dec. 16)	397.5 (Feb. 1/2)	318 (Nov. 13)
Circular Median	336 (Dec. 1)	339 (Dec. 4)	43 (Feb. 12)	317 (Nov. 12)
Linear Mean	350 (Dec. 15)	358 (Dec. 23)	386 (Jan. 21)	327 (Nov. 22)
95% CI of Linear Mean	341-358 (Dec. 6-23)	350-366 (Dec. 15- Jan. 1)	367-404 (Jan. 2- Feb. 8)	318-335 (Nov. 13-30)
Circular Mean	341 (Dec. 6)	347 (Dec. 12)	35 (Feb. 4)	315 (Nov. 10)
95% CI of Circular Mean	330-351 (Nov. 25- Dec. 16)	334-360 (Nov. 29- Dec. 25)	9-62 (Jan. 9- Mar. 2)	307-323 (Nov. 2-18)
Linear SD	75.892	88.333	81.781	62.855
r (circular dispersion)	0.4216	0.2696	0.3348	0.6235

The timing of conceptions was found, with high statistical significance, to be seasonally distributed throughout the year (**Table 4**).

An overall ANOVA conducted on the uncorrected linear conception data found overall significance (F=12.478, p=5.053×10^{-8}), as did the Watson-Williams test on the circular data (F=19.423, p=2.903×10^{-12}). The *a priori* test of significant differences between the indoor treatments combined against the exposed detailed and outdoor group census combined was found to be not significant (F=0.144, p=0.704), as was the test of significance between the indoor detailed and indoor census data (F=2.282, p=0.131). The *a priori* test for significant differences between the exposed detailed and outdoor group census treatments was highly significant (F=30.743, p=3.716×10^{-8}; **Table 5**). P-values for pairwise comparisons for both the linear data and the circular data are given in **Table 6**.

As both the *a priori* test on the linear data and the *a posteriori* tests on both the circular and linear data show, the indoor census and indoor detailed data sets did not differ in their mean breeding peak, which is expected given their identical treatment methods. This finding lends support to the method of estimation of conception dates used in this study, which is identical to that used in other studies (*e.g.*, [Van Horn, 1980]).

Although the *a priori* test for significant differences between the indoor treatments combined *versus* the treatments with some environmental exposure combined was found to be insignificant, this is likely due to the fact that the exposed detailed and outdoor group treatments shift the breeding peak in opposite directions; thus, when combined, they have a cancelling effect; the pairwise differences between all indoor and exposed or outdoor treatments were significant.

Table 4. Results of statistical tests of uniformity.

Treatments	Kolmogorov-Smirnov D	Linear p-value (Kolmogorov-Smirnov[1])	Rayleigh's z	Circular p-value (Rayleigh[1])
Indoor Detailed	0.177	8.949×10^{-9}	54.575	1.529×10^{-25}
Indoor Census	0.114	6.844×10^{-6}	34.876	3.842×10^{-16}
Exposed Detailed	0.193	5.911×10^{-3}	8.743	1.308×10^{-4}
Outdoor Census	0.335	1.192×10^{-7}	78.134	1.079×10^{-38}

[1]As described in the text, uniformity was tested both linearly using the Kolmogorov-Smirnov test and circularly using the Rayleigh test.

Table 5. ANOVA table for conception tests.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Treatment	239879	3	79959.6	12.478	5.1×10^{-8}
Indoor detailed and indoor census *vs.* exposed detailed and outdoor census	922.797	1	922.797	0.14401	0.704
Indoor detailed *vs.* indoor census	14625.7	1	1.4625.7	2.2825	0.131
Exposed detailed *vs.* outdoor census	196996	1	196996	30.743	3.7×10^{-8}
Error	6805120	1062	6407.83		

Table 6. P-values for pairwise comparisons of both linear and circular data sets.

Tukey's HSD (linear):				
	Indoor detailed	Indoor census	Exposed detailed	Outdoor census
Indoor detailed	1			
Indoor census	0.431	1		
Exposed detailed	0.002	0.025	1	
Outdoor census	0.009	1.532×10^{-5}	1.490×10^{-6}	1
Watson-Williams with Holm-Šidàk correction (circular):				
	Indoor detailed	Indoor census	Exposed detailed	Outdoor census
Indoor detailed	1			
Indoor census	0.352	1		
Exposed detailed	2.983×10^{-6}	2.908×10^{-5}	1	
Outdoor census	1.375×10^{-4}	1.274×10^{-5}	2.433×10^{-12}	1

Both Levene's test of homogeneity of variances (F=16.003, p=7.025×10^{-10}) and the test of homogeneity of circular distribution factor κ (F=11.082, p=7.272×10^{-7}) found significant differences among treatments in the spread of the data. However, the distribution of conceptions across all treatments seem to approach normality; it is possible, then, that the difference is based largely on an inflation of significance due to large sample sizes and only to a lesser extent due to important underlying differences among treatments.

Paired

The 52 individuals who had recorded conceptions both in the indoor detailed and exposed detailed treatments differed significantly between the two treatments in mean conception date, as shown linearly by a repeated-measures ANOVA (F=10.144, p=0.002) and circularly by the Hotelling test for paired samples of angles (F=6.639, p=0.003). **Figure 3** depicts the mean conception date in both treatments for these individuals. For most individuals, then, movement to the exposed treatment resulted in a later date of conception, in line with the changes seen in the breeding population as a whole.

Heritability

The half-sib ANCOVA found sires to be an insignificant source of variation in number of conceptions once number of attempts was accounted for (F=1.162 and p=0.364 for sires). Regardless, an estimate of heritability was calculated; it was found to be small (h^2=0.018). R.A. Fisher argued that the more closely a trait is tied to fitness, the more natural selection should have already acted on it and selected out the available
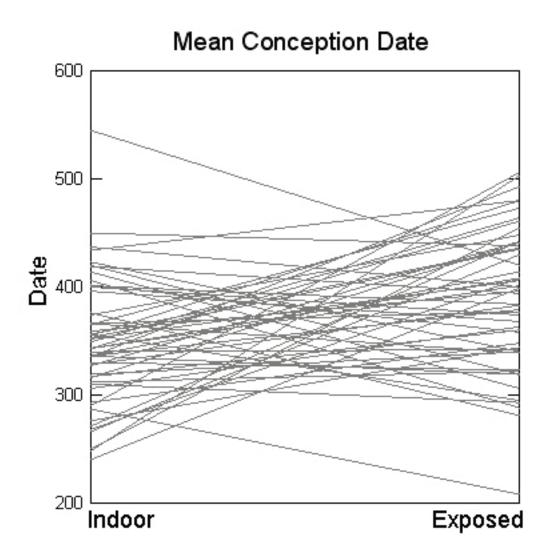
Figure 3. Mean conception date for individuals in the indoor detailed *vs.* exposed detailed treatments.
Note that the dates cannot exceed 548 (600 shown on Y-axis is for scale).

variance due to genetic components (*e.g.*, Mosseau and Roff (1987), but see Price and Schluter (1991)). Thus, a lack of heritability for attempt-corrected conceptions is not surprising, but was not a foregone conclusion. The finding of no heritable differences in attempt-corrected conceptions allowed for an analysis of the full data sets of attempt-corrected conceptions without the possibility of familial relationships obscuring the variations in the data set.

Attempt-corrected conceptions

The ANCOVA table is shown in **Table 7**. In the ANCOVA, neither month nor treatment (indoor detailed *vs.* exposed detailed) had a significant effect on number of conceptions once variation in the number of attempts was accounted for, though treatment approached significance. Also, the interaction of month and treatment was not significant. Number of attempts was highly significantly correlated with conceptions and the only part of the model that showed a significant effect on conceptions; this shows that, at least for the indoor detailed and exposed detailed conditions, there was no significant variation in conceptions between treatments or throughout the year beyond that due to variation in the number of attempts.

Table 7. ANCOVA table for attempt-corrected conceptions.

Source of variance	Type III SS	df	Mean Squares	F-Ratio	p-Value
Treatment (Indoor v. Exposed)	28.78002	1	28.78002	3.72122	0.05880
Month	118.33602	11	10.75782	1.39097	0.20291
Treatment×Month Interaction	41.74009	11	3.79455	0.49063	0.90129
Attempts	531.01856	1	531.01856	68.66007	2.36453×10^{-11}
Error	433.10526	56	7.73402		

Discussion

Conceptions

Conceptions were found to occur year-round in all treatments; however, the distribution of conceptions in all treatments was found to be significantly seasonal. The finding of seasonality in the outdoor group is not surprising and agrees with comparable findings in wild and free-ranging populations (Heape, 1897; Carpenter, 1942; Prakash, 1958, 1962; Southwick *et al.*, 1961; Altmann, 1962; Conaway and Koford, 1964; Koford, 1966; Vandenbergh and Vessey, 1968; Lindburg, 1971; Drickamer, 1974; Coimbra-Filho and Maia, 1977; Wang *et al.*, 1996; Tian *et al.*, 2013), although as the outdoor group is in enclosures which restrict long-distance movement and rely solely on human provisioning for food, this treatment is more comparable to individuals in other outdoor colonies (Vandenbergh, 1973) and those found in zoos (Brand, 1963). In fact, in wild and free-ranging populations rhesus have a distinct breeding season, but the outdoor group data conform more to outdoor colonies and zoos in showing a breeding peak.

The exposed treatment was also found to be seasonal. Unlike the outdoor or indoor treatments, this is a much more novel finding. Birkner (1970) had a treatment in which individuals were housed indoors, but had exposure to daylight through a window. The exposed treatment, however, has exposure to sunlight, temperature, and humidity throughout most of the year. Thus, there are no treatments in the literature I am aware of to make direct comparisons to, but Birkner's (1970) treatment did find seasonality.

The seasonality exhibited in the indoor, isolated treatment confirms that reported by several researchers (Hartman, 1931; Valerio *et al.*, 1969a, 1969b; Riesen *et al.*, 1971; Vandenbergh, 1973; Hutz *et al.*, 1985), but contradicts others (Ponce de Lugo, 1964;

Eckstein and Kelly, 1966). This shows that seasonal cues such as photoperiod, temperature, or seasonal fluctuations of food availability are not required for rhesus to conceive in a seasonal pattern.

When the mean of the most "natural" group, the outdoor census, is compared to Van Horn's (1980) regression for rhesus macaques in natural conditions, it is found to fall very far short of where his line predicts it. A group with a mean birth date of 327 (such as that of the outdoor group treatment) corresponds to a latitude of about 32 degrees north on his line, while the NERPRC is located at roughly 42° 20' N, a latitude well outside the range of the data used to generate the regression. If the line were extrapolated to the latitude of the NERPRC, the expected mean birth date would be around 367, which would actually be day 2 of the following year, January 2. January 2 is included in the 95% confidence interval of the mean only for the exposed treatment (although the indoor census mean is closer), but it is at the very beginning of it. While Van Horn's (1980) data did not include individuals in a treatment similar to any in this study, it is still interesting to note the lack of fit to his model.

It is also interesting to note that when comparing the circular dispersion statistic r of all groups, the largest is for the outdoor group, which most closely resembles a natural condition out of the four treatments. When comparing this number (r=0.6235) to those of similar species in Janson and Verdolin (2005), it most closely resembles that found for *Macaca fascicularis* (r=0.6094) and *Macaca sinica* (r=0.6140). However, Brockman and van Schaik (2005) describe both *Macaca mulatta* (rhesus) and *M. sinica* as relaxed income breeders, while *M. fascicularis* is described as a capital breeder, despite a nearly equivalent seasonality. Other capital breeders designated by Brockman and van Schaik

include *Macaca nemestrina* and *Macaca silenus*, and their r values are much lower

(0.2479 and 0.2546 for the former, 0.3286 for the latter [Janson and Verdolin, 2005]),

while relaxed income breeders *Macaca sylvanus* and *Macaca radiata* have r values of

0.8943 and 0.9404 (highest of all macaques) for *M. sylvanus* and 0.8647 for *M. radiata*

(Janson and Verdolin, 2005), much larger values than that found for rhesus. *Macaca*

fuscata (referred to initially by Brockman and van Schaik [2005] as a strict income

breeder but later in the same chapter as a relaxed income breeder) had the second highest

r of all macaques, 0.9227 (Janson and Verdolin, 2005), which is quite seasonal. This

variation between different species in circular dispersion of breeding times clearly shows

that Brockman and van Schaik's categories of capital and relaxed income breeding are

ill-defined and constitute a wide range of seasonal distributions (at least in the macaques).

Attempt-corrected conceptions

It is important to note that while the ANOVA and subsequent pairwise

comparisons of uncorrected conceptions between the indoor detailed and exposed

detailed treatments found highly significant differences between them and a highly

seasonal distribution in each, when corrected for attempts, conceptions were not found to

differ significantly between months and treatments. This indicates that, at least for these

two treatments, most of the variation found in conceptions was due to differences in

number of mating attempts, a variable for which a protocol was set in place to try to keep

it fairly constant throughout the study. As the protocol for setting up mating attempts

involved vaginal swabs to check for ovulation, a possible reason for variation in attempts

is that during certain parts of the year (*i.e.*, summer), ovulation and possibly menses

occur less frequently (as found by Hutz *et al.* [1985] and Riesen *et al.* [1971]), thus mate-pairs are formed less frequently; those that are formed, however, have an equal chance of conception. Attempts were not found, however, to vary significantly by months.

If photoperiod, temperature, or humidity was the main proximate cue that these timed-mating rhesus used to time conceptions, we would expect to find that, when controlled for attempts, there would be a significant interaction between months and treatment for conceptions. That is, in months that the cue should be increasing reproduction (fall and winter), conceptions in the exposed treatment should exceed those in the indoor treatment, while in months that the cue should decrease reproduction (spring and summer), conceptions in the exposed treatment should be less frequent than those in the indoor treatment. The interaction term was insignificant, and thus it can be concluded that proximate environmental cues have no bearing on the timing of reproduction in the timed-mating groups.

If endogenous cues were responsible for seasonality in these two groups, we may expect to find a significant effect of months; it is not significant, and thus it must be concluded that endogenous cues do not maintain seasonality between these two treatments. What the results instead show is that none of the proposed proximate environmental or endogenous cues maintains seasonality in these two groups; all seasonality of conceptions in the indoor and exposed timed mating treatments was due to variation in the number of attempts.

If rhesus seasonality is dictated by photoperiod, as the traditional model suggests, we should expect that rhesus maintained indoors on a constant light cycle would not

show seasonal variation in the number of conceptions, while those exposed to a natural photoperiod would. In this thesis, it has been shown that rhesus do not have a seasonal variation in conceptions once corrected for number of attempts, regardless of their exposure to light.

Brockman and van Schaik's (2005) income-capital continuum model suggests that rhesus are relaxed income breeders. As such, rhesus should show a response to photoperiod even when maintained in captivity, although the response may be damped and females may continue reproductive cycling for a greater portion of the year. However, timed-mating rhesus macaques did not vary in their conceptions as a result of exposure to photoperiod; the only variable shown to affect distribution of conceptions was number of attempts. This indicates that their model is not very useful in differentiating subtle variations in reproductive patterns in captive macaques, and that these captive populations provide a unique opportunity to explore the complex relationships between season and reproductive biology.

Conclusion

In all four treatments, the distribution of conceptions throughout the year was seasonal. If photoperiod or other environmental cues were the only proximate cues maintaining seasonality, we would expect seasonality to exist only in individuals exposed to those variables; however, individuals maintained in constant photoperiod and temperature still showed a seasonal peak of conceptions.

Once number of attempts was controlled for, it was found that the likelihood of conception did not vary throughout the year, did not vary between treatments, and did not vary in an interaction of treatment by month, which would be expected if environmental cues were serving as the main source of seasonal variation. Instead, it was found that for rhesus with limited access to males, number of attempts was the only significant predictor of number of conceptions.

These data indicate that while photoperiod, rainfall, food availability, and/or other environmental variables are important in the maintenance of seasonal reproduction in wild and free-ranging rhesus, in timed mating colonies with little variation in food or shelter, their effect is less powerful. This suggests that in wild and free-ranging populations, there is a complex interaction of social interaction, resource availability and limitation, and proximate environmental cues that serves to maintain rhesus reproductive seasonality.

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