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Reproductive efficiency of captive Chinese- and Indian-origin rhesus macaque (*Macaca mulatta*) females

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Abstract

Reproductive and survival records (n = 2,913) from 313 Chinese-origin and 365 Indian-derived rhesus macaques at the Tulane National Primate Research Center spanning 3 generations were studied. Least-squares analysis of variance procedures were used to compare reproductive and infant survival traits while proportional hazards regression procedures were used to study female age at death, number of infants born per female and time from last birth to death. Chinese females were older at first parturition than Indian-females because they were older when placed with males, but the two subspecies had similar first and lifetime post-partum birth intervals. Females that gave birth to stillborn infants had shorter first post-partum birth intervals than females giving birth to live infants. Post-partum birth intervals decreased in females from 3 to 12 years of age but then increased again with advancing age. Chinese infants had a greater survival rate than Indian infants at 30 d, 6 mo and 1yr of age. Five hundred and forty-three females (80.01 %) had uncensored, or true records for age at death, number of infants born per female, and time from the birth until death whereas 135 females (19.91 %) had censored records for these traits. Low and high uncensored observations for age at death were 3 and 26 years of age for Chinese and 3 and 23 years of age for Indian females. Uncensored number of infants born per female ranged from 1 to 15 for Chinese females and 1 to 18 for Indian females. Each of these traits was significantly influenced by the origin × generation interaction in the proportional hazards regression analyses, indicating that probabilities associated with age at death, number of infants born per female and time from last birth to death for Chinese and Indian females did not rank the same across generations.

Keywords

Rhesus macaque; Reproduction; Chinese-origin; Indian-origin; Survival

INTRODUCTION

Rhesus macaques (*Macaca mulatta*) are an important species in biomedical research and are used to model human diseases, in studies of infectious agents or use of therapeutic stem cells or in vaccine development [Kuai et al., 2009, Pahar et al., 2009, Veazey et al., 2010; Ren et al., 2010; Yuan et al., 2010, Gagliardi and Bunnell, 2011; Sina et al., 2011, Lin et al., 2011].

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India was the primary source of rhesus macaque monkeys being imported into the US until an export ban was imposed in 1978. Since then rhesus macaques have been imported primarily from China.

There are a number of studies that have described phenotypic as well as genetic differences between the two subpopulations and in some cases these have been shown to influence research outcomes. For example, Clarke & O'Neil [1999] reported significant morphological differences including variations in size and weight, while others have suggested possible differences in ocular development [Qiao-Grider et al., 2007], and there are reports of behavioral differences [Champoux et al., 1997]. There is also evidence that geographical origin accounts for much of the variation in mitochondrial DNA sequences found among Chinese and Indian macaques with the Indian population moreover showing much less internal variation than their Chinese counterparts [Kanthaswamy & Smith, 2004; Smith & McDonough, 2005]. Similar differences exist in MHC class II alleles where distinct DQA, DQB1 and DRB haplotypes have been identified and whose distribution appear to be determined by geographical origin [Viray et al., 2001; Doxiadis et al., 2001, 2003]. A number of nuclear microsatellites have been identified whose allelic distribution facilitates not only assignment of kinship but also discrimination between subpopulations [Smith, 2005; Smith et al., 2006]. Similarly, discovery of a relatively large number of single nucleotide polymorphisms (SNPs) has led to development of assays for verification of geographic background [Ferguson et al. 2007].

In contrast, relatively little is known about differences between subpopulations in reproductive performance either in wild or among captive breeding colonies. While rhesus reproduction has been under study for many decades, there is a dearth of information on specific differences between Indian and Chinese rhesus macaques. We previously reported heritability coefficients for a number of female reproductive parameters such as birth intervals, infant survival and lifetime productivity and concluded that there was, indeed, a genetic component in these traits in Indian rhesus monkeys [Gagliardi et al., 2010]. This again raises the possibility that given the duration of geographic separation between various subpopulations there may be measurable differences in reproductive traits.

The objective of this research, therefore, was to compare the reproductive characteristics and longevity traits in three generations of captive Chinese and Indian rhesus macaque females maintained in breeding groups at the Tulane National Primate Research Center (TNPRC).

METHODS

Animals and Housing

Subjects of this study were members of rhesus breeding colonies maintained at TNPRC. The Indian animals were part of the long-established breeding colony at TNPRC. Over the years, additional animals were purchased from various temperate zone breeding colonies in the southern United States and England which were descendants of Indian animals imported from India or Cayo Santiago Island in Puerto Rico. During an expansion of the breeding colony in the mid-1980's, Chinese rhesus males and females were imported directly from China (Coulston Corp., White Sands NM) arriving in four shipments over an 18-month period from 1986 to 1988. Shipment records indicate the Chinese rhesus were colony-born in northern China primate breeding facilities in 1983 and 1984 (Clarke and O'Neil, 1999). Birth dates were not provided with all shipments however import documents gave an approximate age of the animals when shipped. This information was used to assign an approximate birth date and age to all females as they arrived. Indian females born in 1983 and 1984 at the TNPRC and the imported Chinese females were used to establish a breeding colony to provide animals for simian autoimmune deficiency research at the TNPRC.

Breeding groups were formed within each subpopulation. Sires were selected based on pedigree data based on their least likelihood of being related to any females in the group they were to join. Sire-to-female ratios were kept similar across all breeding groups. Females were removed from breeding groups in response to requests from researchers and the Chinese and Indian populations remained purebred while at TNPRC. Housing and management procedures precluded any possibility of mating between Chinese and Indian animals. Breeding groups were maintained in outdoor corrals, field cages, and corncribs, ranging in size from 8 to 40 animals depending upon the size of the enclosure and were identical for each subspecies. Each enclosure had perching and various other structures. Since enclosures were adjacent to each other, climatic conditions were identical for all groups. All feeding and handling procedures, veterinary care, and behavioral management were the same as per IACUC-approved breeding colony management protocols. Over the years, juvenile animals were removed to supply research needs while adequate numbers of juvenile females from each birth cohort were maintained in the breeding colonies as replacement breeders. Only females that remained in the breeding colony until their death or the end of the study were included in these data.

All research reported in this manuscript adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-human Primates. All research protocols reported in this manuscript were reviewed and approved by the Tulane National Primate Research Center's (TNPRC) Institutional Animal Care and Use Committee. All research reported in this manuscript complied with the protocol approved by the TNPRC Institutional Animal Care and Use Committee.

Records

Reproductive records maintained included origin and birth date of the female, female age at the birth of each offspring, the birth date of each offspring, the order of birth of each offspring, and the date and age at death of each female. Sex of offspring and survival at various intervals to a year of age was recorded for each infant. Permanent identification was maintained on all animals. None of the females that provided reproductive data were involved in any research projects and were solely maintained to produce offspring.

Female reproductive traits of interest in this report include age at first parturition, first post-partum birth interval, and lifetime post-partum birth intervals. Age of dam at death, number of infants born per female, and time from birth of the last infant to death were also evaluated. In addition, survival status of infants at birth, 30 days, 6 months, and again at 1 year was studied.

The data were edited to remove observations that were considered out of range. For age at first parturition, observations were limited to those from 2.6 through 7.5 years of age. This removed two females in each subgroup with ages at first parturition above 9 years of age. Post-partum birth intervals were limited to those from 0.45 to 6.0 years. This editing allowed removal of records with recording errors as well as those outside the mean $\pm$ 3 standard deviations.

Imported Chinese rhesus females were not mated until all had arrived at the TNPRC and had gone through a quarantine period. Males were placed with Chinese females in mid 1988 slightly before the start of the seasonal breeding period so that first offspring would be born in the spring and early summer of 1989 when females were 4 to 6 years old or older. The Indian females born in 1983 and 1984 and assigned to this study were already at TNPRC and were placed with males as juveniles following normal management. Their first progeny were born in 1986 and 1987.

Statistical analyses

The data included 2,913 records from 313 Chinese and 365 Indian females which spanned 3 generations. Generations 1, 2, and 3 included 347, 258, and 73 females, respectively. Procedures in the Statistical Analysis System (SAS) programs (SAS Institute Inc., Cary, NC, USA) were used for all analyses. Least-squares statistical procedures were used to analyze reproductive traits and infant survival. Statistical models included origin of female, generation, origin $\times$ generation, and female birth year within generation. Infant sex, female age, or infant survival status was included in statistical models for certain traits. Predicted differences among preselected levels of main effects were determined.

Proportional hazards regression procedures in SAS were used to evaluate female age at death, number of infants born per female, and the time from the last birth to death. Age at death, number of infants born per female, and time from the last birth to death for females that had died were considered true or uncensored records whereas age of females alive at the end of the study, number of infants born at that time from the live females, and time from the last birth to the end of the study were considered censored data or incomplete. Censored records for age at death contained the ages of females alive at the end of 2008 and censored records for time to death from the last parturition entailed the time period ending in 2008. Censored records for number of progeny born per female consisted of the number of progeny born up to the end of 2008. Explanatory variables included in the proportional hazards regression models included origin, generation, and origin $\times$ generation.

RESULTS

The numbers of Chinese and Indian females that produced at least one infant in generations 1, 2, and 3 and the numbers of Chinese and Indian infants born in generations 1, 2, and 3 are given in Table 1. More Indian than Chinese foundation females were available to initiate generation 1 and more total Indian females were represented in the data set than Chinese females. Due to management decisions in generation 3, fewer Indian females were available than Chinese females.

Monthly birth frequencies by origin of female and generation are given in Figures 1 and 2. Distributions in generations 1 and 2 generally were similar for Chinese and Indian females. A total of 2,913 infants were born in the study. Among Chinese infants, males represented 48.27 %, females represented 47.38 % and those of undetermined sex represented 4.34 %. For Indian infants, males represented 51.80 %, females represented 46.35 %, and those with unknown sex represented 1.86 %.

Age at first parturition

Variation in age at first parturition was significantly influenced by origin ($F_{1, 631} = 45.30$, $P < 0.0001$), generation ($F_{2, 631} = 54.51$, $P < 0.0001$), dam birth year within generation ($F_{26, 631} = 1.79$, $P = 0.0100$), and the origin $\times$ generation interaction ($F_{2, 631} = 34.09$, $P < 0.0001$). Least squares means $\pm$ standard errors for the primary sources of variation are given in Table 2. Chinese females were older at first parturition (5.00 ± 0.06 years) than Indian females (4.31 ± 0.08) over the three generations. Because of the significant origin $\times$ generation interaction, the statistical analysis included predicted differences for preselected levels within each main effect. Age at first parturition in generation 1 Chinese females was greater than that of generation 1 Indian females as well as in generation 2, but not generation 3. Foundation Chinese females were older than foundation Indian females when first placed with males because of time restraints in getting the Chinese females shipped to the U.S. Females in both subpopulations were of similar ages when placed with males in generation 2 and 3.

First post-partum birth interval

Least squares means and standard errors for first post-partum birth interval due to origin, generation and origin $\times$ generation are shown in Table 2. None of the primary sources of variation were significant for variation in first post-partum birth interval (origin: $F_{1, 475} = 0.04$, $P = 0.8322$; generation: $F_{2, 475} = 0.43$, $P = 0.6537$; origin $\times$ generation: $F_{2, 475} = 0.63$, $P = 0.5325$), however, females that gave birth to a stillborn infant had a shorter post-partum birth interval than females that had a live born infant (1.10 ± 0.15 years vs 1.39 ± 0.06 years; $F_{1, 475} = 4.42$, $P < 0.0360$).

Lifetime post-partum birth intervals

Factors in the statistical model that significantly influenced variation in lifetime post-partum birth intervals were generation ($F_{2, 2155} = 4.16$, $P = 0.0158$), origin $\times$ generation ($F_{2, 2155} = 3.05$, $P = 0.0477$), infant survival at 6 mo ($F_{1, 2155} = 10.29$, $P = 0.0014$), and the linear ($F_{1, 2155} = 31.73$, $P < 0.0001$) and quadratic ($F_{1, 2155} = 23.02$, $P < 0.0001$) effects of post-partum birth interval on female age at the time of birth. The linear and quadratic effects of lifetime post-partum birth interval on age of female are plotted in Figure 3. The equation used to plot the curve in Figure 3 was $LPPBI = 1.6171 - 0.09937(\text{age}) + 0.004131(\text{age}^2)$. Birth interval decreased as the age of females increased from 3 to 12 years of age and then increased slightly as the females aged.

Least squares means and standard errors for lifetime post-partum birth interval due to origin, generation and origin $\times$ generation for lifetime post-partum birth intervals are given in Table 2. Chinese and Indian females had similar lifetime birth intervals (1.21 ± 0.04 vs 1.14 ± 0.07 years; $F_{1, 2155} = 0.61$, $P = 0.4365$). Lifetime post-partum birth interval decreased as generations advanced.

Generation 1 Indian females had a lower lifetime birth interval than generation 1 Chinese females (1.21 ± 0.03 vs 1.35 ± 0.03 years) and generation 2 Indian females had a lower lifetime birth interval than generation 2 Chinese females (1.00 ± 0.06 vs 1.26 ± 0.07 years) but not in generation 3.

Females whose infant failed to survive to six months of age gave birth earlier during the next year than females whose infants had survived to 6 months resulting in a shorter interval to the birth of the next offspring (1.09 ± 0.06 vs 1.24 ± 0.05 years).

Survival of females

A total of 678 females were represented in this study. The survival analysis included 543 females (80.09 %) that had died and 135 (19.91 %) that were still alive at the end of the study. Descriptive statistics of the uncensored and censored data for length of life are shown in Table 3. The maximum censored age for age at death was 25 years whereas the maximum uncensored age at death was 26 years. Origin ($\chi^2 = 9.2322$, $df = 1$, $P = 0.0024$), generation ($\chi^2 = 11.8067$, $df = 2$, $P = 0.0027$), and origin $\times$ generation ($\chi^2 = 7.4944$, $df = 2$, $P = 0.0236$) influenced variation in length of life. The survival functions for Chinese and Indian females by generations are plotted in Figure 3. Probability levels for female survival to 10, 15, and 20 years of age are given in Table 4. The origin $\times$ generation source of variation indicated that the probability for survival for Chinese and Indian females tended to rank differently across generations. Chinese had similar but slightly higher probabilities of survival in generations 1 and 2 than Indian females and higher survival probabilities in generation 3. The lifetime survival functions in Figure 3 indicate clearly that generation 3 Indian females had a much lower survival age than generations 1 and 2 whereas Chinese females had similar survival functions across generations.

Number of infants born per female

Minimum, maximum, and average numbers of offspring produced per female for censored and uncensored data are given in Table 3. Variation in uncensored and censored data for number of infants born per female was significantly influenced by origin ($\chi^2 = 9.3599$, $df = 1$, $P = 0.0022$), generation ($\chi^2 = 10.5002$, $df = 2$, $P = 0.0052$) and origin $\times$ generation ($\chi^2 = 12.1942$, $df = 2$, $P = 0.0022$). The probability for 5, 10, or 15 infants born per female is given in Table 4. Indian females had a slightly higher probability of producing 5, 10 or 15 infants in generation 1 than Chinese females whereas probabilities were similar for number of progeny born in generation 2. Chinese females had a higher probability of producing more infants in generation 3 because a high proportion of the generation 3 Chinese females survived to an older age. Mean number of infants born per female from the proportional hazards regression analysis are given in Table 4.

Time from the last parturition to death

Minimum, maximum, and average censored and uncensored records for time from the last parturition to death are given in Table 3. Although the average values were relatively small, one censored record was 8.58 yr and one uncensored record was 11.16 yr. Origin ($\chi^2 = 10.1626$, $df = 1$, $P = 0.0014$), generation ($\chi^2 = 7.7270$, $df = 2$, $P = 0.0210$) and origin $\times$ generation ($\chi^2 = 15.8235$, $df = 2$, $P = 0.0004$) influenced variation in time from the last parturition to death. Probability levels for time to death of less than 1 yr, 1 to 2 yr, and more than 2 yr are given in Table 3 for the origin $\times$ generation interaction. Indian females had a higher probability for living longer after the last birth than Chinese females in generations 1 and 2 for all three survival intervals. Generation 3 Chinese females had higher probabilities for living longer after the last infant than generation 3 Indian females.

Infant survival

Information on birth status (stillborn or alive) and age at death for infants that died before a year of age was used to analyze survival at birth, 30 days, 6 months and 1 year of age (Table 5). Infants that were alive at a given age were assigned a score of 1 whereas those that were not alive at that age were assigned a score of 0.

Models to analyze infant survival included origin, generation, sex of infant, origin $\times$ generation and dam birth year within generation. Origin approached significance ($F_{1, 2795} = 3.30$, $P = 0.069$) and the origin $\times$ generation interaction significantly influenced variation in survival status at birth ($F_{2, 2795} = 5.04$, $P = 0.0065$). Chinese infants had a birth survival rate of 95.9 ± 1.0 % compared to 92.4 ± 2.0 % for Indian infants. Generation 1 live birth rate for Chinese infants was 93.0 ± 0.8 % compared to 95.8 ± 0.7 % for Indian infants. No differences in live birth rate between Chinese and Indian infants were found in generation 2.

Origin ($F_{1, 2795} = 4.19$, $P = 0.0407$) and the origin $\times$ generation interaction ($F_{2, 2795} = 5.79$, $P = 0.0031$) were significant sources of variation for infant survival at 30 days of age. Chinese infants had a higher survival rate to 30 days of age than Indian infants (93.0 ± 1.3 % vs 88.0 ± 2.0 %). However, generation 1 Chinese infants had a lower 30 day survival rate than generation 1 Indian infants (88.3 ± 1.1 vs 92.1 ± 0.9 %). In generation 3, Chinese infants had a higher 30 day survival rate than Indian infants (98.0 ± 3.1 vs 79.5 ± 5.7 %). These origin reversals for 30 day survival contributed to the significant origin $\times$ generation interaction.

Origin was the only significant source of variation for infants' 6 month survival ($F_{1, 2795} = 8.02$, $P = 0.0047$). Chinese infants had a 91.0 ± 1.6 % survival rate compared to an Indian infant 6 month survival rate of 82.7 ± 2.4 %.

Origin ($F_{1, 2795} = 6.46$, $P = 0.0111$) and sex of infant ($F_{1, 2795} = 4.33$, $P = 0.0375$) significantly influenced variation in 1 year survival. Chinese infants had a greater survival rate to 1 year of age than Indian infants (86.2 ± 1.8 vs 77.5 ± 2.8 %). Female infants had an 83.4 ± 1.8 % survival rate to 1 year of age compared to 80.3 ± 1.8 % for male infants. Generation 1 and 2 Chinese infants had greater survival rates at 1 year than generation 1 and 2 Indian infants (83.7 ± 1.5 and 88.8 ± 2.8 % vs 77.2 ± 1.2 and 78.1 ± 2.6 %, respectively).

DISCUSSION

Fossil records suggest that rhesus monkeys migrated into Asia at least 2 mya ultimately colonizing an area ranging from present-day Afghanistan to China [Abegg and Thierry 2002]. A number of rhesus subspecies are recognized although there is no consensus on their precise number with suggestions ranging from 6 to as many as 13 [Fooden 2001; Groves 2001]. Based on mitochondrial DNA sequence analysis Smith and McDonough [2005] have confirmed significant genetic differences between Indian and Chinese populations, but have also reported considerable variation within the Chinese population which appears to coincide with the extent of their geographical range. This phenomenon is also seen among Indian animals, albeit to a lesser degree. Given the length of time since not only the migration of rhesus into Asia, but also the geographic separation of Indian and Chinese populations, it seems reasonable to expect that evolutionary adaptations may have resulted in genetic differences between various subpopulations and that some of these differences would still be detectable in captive breeding colonies.

Here we report the results of an analysis of reproductive parameters among three generations of females with either Indian or Chinese background. Our study expands on observations that have shown not only DNA sequence variations but also differences in a number of anatomical and behavioral traits [Clarke & O'Neill, 1999; Qiao-Grider et al. 2007; Champoux et al, 1997; Kanthaswamy & Smith, 2004; Smith and McDonough, 2005; Viray et al, 2001; Doxiadis et al 2001, 2003]. Rhesus macaques are seasonal breeders with a menstrual cycle lasting 28 days and a gestation length of around 166 days [Hutz et al., 1985; Silk et al. 1993]. Overall the annual distribution of births was similar in both populations with the number of births peaking in April and May reflecting the fact that ovulation in outdoor housed rhesus females occurs primarily in the fall and winter months [Wilson & Gordon 1989, Wilson et al. 1983].

The significant influence of origin on age at first parturition seen here was likely due to the greater age of Chinese females when they were first introduced to males in the late summer of 1988. Chinese females were born in China in 1983 and 1984 and arrived at TNPRC in four shipments over an 18 month period from 1986 to 1988. Because not all females arrived with accurate documentation of birth dates it is possible that their actual ages at the start of the breeding season in 1988 were greater than for the Indian females already in the breeding colony at the TNPRC. Consequently, the greater age of generation 1 Chinese females at the time of their first parturition is likely to some degree the result of older females at the start of the breeding season in 1988.

However, a similar delay in first parturition of Chinese females persisted into the 2nd generation with a similar (albeit statistically not significant) trend in the third generation. It is noteworthy that a recent study by Kanthaswamy et al. [2011] of hybrid rhesus monkeys at the California National Primate Research Center has shown that maturation among females is delayed with increasing Chinese contribution. It is interesting that age at first parturition also decreased significantly between the first two generations. This decrease was more pronounced in Chinese animals which may be a reflection of the fact that animals were imported directly from China whereas Indian animals were obtained from various North

American sources and the differences in the decline between first and second generation may merely reflect differences in their ability to adapt to new environments. There is evidence that captive rhesus monkeys may reach sexual maturity earlier than their wild counterparts, an observation that may primarily reflect a better nutritional status among captives [Catchpole & van Wageningen 1975]. However, it is not known whether the triggering mechanism for this phenomenon is simply the attainment of greater body weight or an overall positive energy balance [Frisch et al. 1970; Wilen et al 1977].

The differences in age at first parturition did not affect the length of the first post-partum birth interval which is consistent with our previous study [Gagliardi et al. 2007]. The average lifetime postpartum differences were similarly not influenced by geographic origin, but there was a significant reduction in length from females of the first to those in the third generation. Similarly, post-partum birth intervals decreased as age of female increased from 3 to 12 years and then increased as the female aged further, which is consistent with studies which have shown that postpartum intervals increase with the age of the mother [Wilson et al. 1983; Gagliardi et al. 2007]. Presumably this is a reflection of increasingly irregular ovulation patterns among older animals [Nozaki et al. 1995]. The interval between births has also been shown to be affected by the sex of the infant with daughters resulting in longer intervals [Simpson & Simpson 1982; Maestripietri 2001]. Interestingly, estimates of heritability of birth intervals have generally been modest [Blomquist 2009; Gagliardi et al 2010] and it is worth noting that, as rhesus monkeys are seasonal breeders, a fetal loss late in the season may prevent a female to become pregnant until the next season, thereby lengthening the birth interval by as much as nearly a year.

The overall percentage of infants born alive did not differ significantly between the two populations, however there were differences within each generation, although these did not appear to be consistent. Origin was, however, a significant factor in infant survival with Chinese infants having a greater likelihood of surviving and this was the case regardless of the time point at which the survival was determined. Infant survival is determined by a number of factors some of which are a consequence of the social status of the female [reviewed by Bercovitch 1997], her age [Gagliardi et al 2007] and the sex of the infant [Drickamer 1974; Maestripietri 2001, Gagliardi et al. 2007], while there appears to be only a modest genetic component [Gagliardi et al 2010]. Because Indian and Chinese females were housed separately, and consequently had their own respective social hierarchies, the confounding effects that social structures could have had on any analysis of reproductive outcomes are likely to be negligible.

The proportional hazards regression procedure facilitated inclusion of records of all females that had died as well as those still alive. These analyses revealed that the average age at death for censored as well as uncensored animals was similar. Probabilities for survival to ages 10, 15, and 20 were likewise similar although the analysis showed that generation 3 Chinese females had a higher probability of surviving to 20 years than generation 3 Indian females. It is noteworthy that Smucny et al [2004] found that age at first parturition was reliable predictor of age at death in captive common marmoset females and while we did not include age at first parturition in our proportional hazards regression analysis for age at death, we did find a correlation between age at first parturition and age at death in both Chinese and Indian females.

Probabilities reported by Smith [1982] for female survival to 10 years of age in captive rhesus monkeys in California and free ranging rhesus monkeys on the island of Cayo Santiago were slightly smaller than the probabilities of living to 10 years or older in our data while Tigges et al [1988] reported longer life spans in female rhesus monkeys maintained at the Yerkes Regional Primate Research Center. However, life tables of female *Macaca*

mulatta survivorship reported by Gage and Dyke [1988] show probabilities for survival to 10 years of age that are similar to those reported in the present study.

There appeared to be differences in the length of time a female lived from birth of her last infant to death, although this was not consistent across generations or subspecies. It is likely that there are numerous factors determining productivity and lifespan. Estimates for heritability for longevity and productivity among rhesus macaques have been found to be slightly higher than for most other reproductive traits [Blomquist 2009; Gagliardi et al. 2010], and are similar to those reported in other primate species such as the baboon [Martin et al. 2002] or humans [Herskind et al. 1996; Ljungquist et al. 1998]. It is also known that social rank among rhesus monkeys is inversely related to stress level [Kaplan et al. 1984; Saltzman et al. 1991; Shively et al. 1997a, b] and that such stress can influence the incidence or the progression of diseases ranging from atherosclerosis, respiratory infections and even depression [Williams et al. 1991; Shively & Clarkson 1994; Shively et al. 2000; Kaplan et al. 1996, 2002; Cohen et al. 1997; Cohen 1999; Skantze et al. 1998].

Overall our study shows that some reproductive parameters appear to differ between Chinese and Indian populations which may provide valuable insights into either evolutionary differences or abilities to adapt to captive life. It is at present unclear to what extent such insights can determine or aid management strategies of captive populations. Such strategies will ultimately be guided by demand for research animals as well as by population genetics that will be aimed at maintaining genetically viable populations. The fact that we found that survival of Chinese infants is greater than that of Indian infants would suggest that management measures could be taken to enhance survival among Indian offspring.

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Figure 1.
Distribution of Chinese births by generation and month.

Figure 2.
Distribution of Indian births by generation and month.

Figure 3.
Linear and quadratic regression of post-partum birth interval on dam age.

Figure 4.
Probability of survival for Chinese and Indian females by generations.

Figure 5.
Probability of number of infants born per Indian and Chinese female by generation.

Figure 6.
Probability of time to death after birth of last infant for Chinese and Indian females.

Table 1

Number of females with at least one infant and number of infants by origin and generation.

Category	Number of Females	Percent Females	Number of Births	Percent Offspring
Overall	678	100	2,913	100
Chinese	313	46.2	1,243	42.67
Gen 1 ^I	155	22.9	732	25.13
Gen 2	101	14.9	374	12.84
Gen 3	57	8.4	137	4.70
Indian	365	53.8	1,670	57.33
Gen 1	192	28.3	1,062	36.46
Gen 2	157	23.2	572	19.64
Gen 3	16	2.4	36	1.24

^INumber and percent of females and infants by generation within origin.

Table 2

Least-squares means (LSM) $\pm$ standard errors (SE) for age at first reproduction (AFR), first post-partum birth interval (1st PPBI), and lifetime post-partum birth intervals (LPPBI) due to origin, generation, and origin $\times$ generation sources of variation.

Source of variation	AFR			1 st PPBI			LPPBI		
	No of records	LSM $\pm$ SE	P	No of records	LSM $\pm$ SE	P	No of records	LSM $\pm$ SE	P
Origin (O)			P < 0.01 ^a			P > 0.05			P > 0.05
Chinese	303	5.00 $\pm$ 0.06		223	1.26 $\pm$ 0.09		899	1.21 $\pm$ 0.04	
Indian	360	4.31 $\pm$ 0.08		284	1.23 $\pm$ 0.13		1290	1.14 $\pm$ 0.07	
Generation			P < 0.01			P > 0.05			P < 0.05
1	339	5.17 $\pm$ 0.04		285	1.29 $\pm$ 0.07		1418	1.28 $\pm$ 0.02	
2	251	4.44 $\pm$ 0.07		187	1.22 $\pm$ 0.10		674	1.13 $\pm$ 0.06	
3	73	4.35 $\pm$ 0.12		35	1.22 $\pm$ 0.17		97	1.11 $\pm$ 0.10	
O $\times$ G			P < 0.01			P > 0.05			P < 0.05
C-G1	149	5.85 $\pm$ 0.06		124	1.31 $\pm$ 0.08		556	1.35 $\pm$ 0.03	
C-G2	97	4.58 $\pm$ 0.09		71	1.30 $\pm$ 0.11		266	1.26 $\pm$ 0.06	
C-G3	57	4.56 $\pm$ 0.14		28	1.16 $\pm$ 0.18		77	1.01 $\pm$ 0.10	
I-G1	190	4.49 $\pm$ 0.06		161	1.27 $\pm$ 0.08		862	1.21 $\pm$ 0.03	
I-G2	154	4.31 $\pm$ 0.08		116	1.14 $\pm$ 0.11		408	1.00 $\pm$ 0.06	
I-G3	16	4.13 $\pm$ 0.22		7	1.27 $\pm$ 0.32		20	1.22 $\pm$ 0.19	

^aProbability levels for origin, generation and origin $\times$ generation from general linear model ANOVA.

Table 3

Descriptive statistics of uncensored and censored data for female age at death, number of offspring born per female, and time after the last birth to death.

	Age at death, yr	Number of infants born	Time from last birth to death, yr
Right censored records, %	19.91	19.91	19.91
Minimum censored record	4.0	1	0.17
Maximum censored record	25.0	17	8.58
Average censored record	10.77	4.7	1.93
Uncensored records, %	80.09	80.09	80.09
Minimum uncensored record	2.9	1	0.0
Maximum uncensored record	26.0	18	11.16
Average uncensored record	10.35	4.23	1.30

Table 4

Adjusted mean female age at death, number of infants born, and time from the last birth to death from the origin $\times$ generation source of variation in the proportional hazards regression analyses.

	Age at death, yr	Number of infants born per female	Time from last birth to death, yr
Chinese – Gen 1	11.68	3.83	0.50
Chinese – Gen 2	10.12	4.09	1.11
Chinese – Gen 3	10.94	7.15	2.75
Indian – Gen 1	10.62	4.83	0.86
Indian – Gen 2	9.87	4.07	1.49
Indian – Gen 3	6.52	2.37	0.67

Table 5

Probability of female survival to different ages, number of infants born, and time from the last infant to death from the origin $\times$ generation interaction source of variation.

Probability for survival to 10, 15, or 20 years of age at death						
Years	India Gen1	India Gen2	India Gen3	China Gen1	China Gen2	China Gen3
10	54.7 %	49.0 %	15.6 %	58.7 %	50.9 %	57.0 %
15	26.0 %	20.2 %	1.6 %	30.4 %	22.1 %	28.5 %
20	6.6 %	4.0 %	0.02 %	9.0 %	4.8 %	7.9 %

Probability for 5, 10, or 15 infants born in a female's lifetime						
No Born	India Gen1	India Gen2	India Gen3	China Gen1	China Gen2	China Gen3
5	46.6%	41.3%	19.3%	39.2%	41.2%	61.1%
10	15.7%	11.6%	1.8%	10.2%	11.6%	30.2%
15	5.3%	3.3%	0.2%	2.7%	3.3%	15.0%

Probability of females living less than 1 year, from 1 to 2 years or more than 2 years after the birth of the last infant.						
Years to death	India Gen1	India Gen2	India Gen3	China Gen1	China Gen2	China Gen3
0 to 1 yr	45.2%	63.9%	37.0%	26.0%	53.4%	75.3%
1 to 2 yr	21.4%	41.9%	14.5%	7.3%	29.5%	57.7%
2+ yr	12.8%	31.3%	7.6%	3.0%	19.6%	48.0%

Table 6

Least-squares means (LSM) $\pm$ stand errors (SE) for percent infants alive at birth, 30 days, 6 months and 1 year due to origin, generation, origin $\times$ generation, and infant sex.

Source of variation	Number of records	Percent alive at birth	Percent alive at 30 d	Percent alive at 6 mo	Percent alive at 1 yr
Origin (O)		$P > 0.05^a$	$P < 0.05$	$P < 0.01$	$P < 0.05$
Chinese (C)	1,189	95.9 $\pm$ 1.0	93.0 $\pm$ 1.3	91.0 $\pm$ 1.5	86.2 $\pm$ 1.8
Indian (I)	1,639	92.4 $\pm$ 2.0	88.0 $\pm$ 2.0	82.7 $\pm$ 2.4	77.5 $\pm$ 2.8
Generation (G)		$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
1	1,744	94.4 $\pm$ 0.5	90.2 $\pm$ 0.7	85.4 $\pm$ 0.8	80.4 $\pm$ 1.0
2	918	95.1 $\pm$ 1.3	92.5 $\pm$ 1.6	89.1 $\pm$ 2.0	83.4 $\pm$ 2.3
3	166	93.0 $\pm$ 2.4	88.7 $\pm$ 3.0	86.0 $\pm$ 3.7	81.7 $\pm$ 4.3
O $\times$ G		$P < 0.01$	$P < 0.01$	$P > 0.05$	$P > 0.05$
C – G1	700	93.0 $\pm$ 0.8	88.4 $\pm$ 1.1	86.7 $\pm$ 1.3	83.7 $\pm$ 1.5
C – G2	358	94.5 $\pm$ 1.5	92.6 $\pm$ 2.0	91.3 $\pm$ 2.4	88.8 $\pm$ 2.8
C – G3	131	100.0 $\pm$ 2.5	98.0 $\pm$ 3.1	94.9 $\pm$ 3.8	86.1 $\pm$ 4.4
I – G1	1,044	95.8 $\pm$ 0.7	92.1 $\pm$ 0.9	84.1 $\pm$ 1.1	77.2 $\pm$ 1.2
I – G2	560	95.7 $\pm$ 1.5	92.5 $\pm$ 1.9	86.8 $\pm$ 2.3	78.1 $\pm$ 2.6
I – G3	35	85.8 $\pm$ 4.5	79.5 $\pm$ 5.7	77.0 $\pm$ 6.9	77.3 $\pm$ 8.0
Infant sex		$P > 0.05$	$P > 0.05$	$P > 0.05$	$P < 0.05$
Male	1,465	93.8 $\pm$ 1.0	90.0 $\pm$ 1.3	86.0 $\pm$ 1.5	80.3 $\pm$ 1.8
Female	1,363	94.5 $\pm$ 1.0	91.0 $\pm$ 1.3	87.6 $\pm$ 1.6	83.4 $\pm$ 1.8

^aProbability levels from general linear model ANOVA.