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# Estimates of heritability for reproductive traits in captive rhesus macaque females

**Christine Gagliardi**[1], **Kathrine P. Falkenstein**[2], **Donald E. Franke**[3], and **H. Michael Kubisch**[2,4]

[1] Division of Gene Therapy, Tulane National Primate Research Center, Covington LA 70433 USA

[2] Division of Veterinary Medicine, Tulane National Primate Research Center, Covington LA 70433 USA

[3] School of Animal Sciences, Louisiana State University AgCenter, Baton Rouge, LA 70803

## Abstract

Records from a colony of captive Indian rhesus macaques (*Macaca mulatta*) were used to estimate heritability for a number of reproductive traits. Records were based on a total of 7,816 births by 1,901 females from 1979 to 2007. Heritability was estimated with a linear animal model using a multiple trait derivative free REML set of programs. Because no male parents were identified, the numerator relationship matrix contained female kinships established over six generations. Reproductive traits included female age at the birth of the first, second and last infant, age at death, inter-birth intervals, number of infants born per female and infant survival. Heritability for each trait was estimated as the ratio of the additive genetic variance to phenotypic variance adjusted for significant fixed effects. Estimates of heritability for early reproduction ranged from 0.000 ± 0.072 for birth interval following the first reproduction to 0.171 ± 0.062 for age of female at the first infant. Higher estimates of heritability were found for female longevity [0.325 ± 0.143] and for productivity of deceased females born before 1991 [0.221 ± 0.138]. Heritability for infant survival ranged from 0.061 ± 0.018 for survival from 30d to 1yr to 0.290 ± 0.050 for survival from birth to 30d when adjusted to an underlying normal distribution. Eight of the 13 estimates of heritability for reproductive traits in this study were different from zero [$P < 0.05$]. Generally, heritability estimates reported here for reproductive traits of captive rhesus macaque females are similar to those reported in the literature for free ranging rhesus macaque females and for similar reproductive traits of other species. These estimates of heritability for reproductive traits appear to be among the first for a relatively large colony of captive rhesus macaque females.

### Keywords

rhesus macaque; heritability; reproductive and survival traits; animal model estimates

## INTRODUCTION

Estimates of heritability for reproductive traits among non-human primates have been determined only for a small number of species. In part, this is a reflection of the fact that data collection in wild populations is often difficult and that many captive species exist only in relatively small populations and have often very limited pedigree information. Moreover, because of the utility of several non-human primate species as models for human diseases,

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[4] To whom correspondence should be addressed at: Tulane National Primate Research Center, 18703 Three Rivers Road, Covington LA 70433, Phone 985-871-6493, mkubisch@tulane.edu.

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estimates of heritability have often focused on those traits that affect general health status or disease susceptibility in humans rather than on reproduction. For example, Kammerer et al. [2001] reported a genetic component on hypertension among baboons, while Rainwater et al. [2002] found substantial heritability coefficients for HDL cholesterol in the same species. Heritability has also been calculated for anatomical traits such as organ weights. Mahaney et al. [1993] showed modest but statistically significant heritability coefficients for the weights of heart, kidney and liver in the baboon. Weight and volume of the brain and various regions therein have similarly been shown to have significant heritability coefficients in squirrel monkeys, baboons and rhesus macaques [Cheverud et al., 1990; Lyons et al., 2001; Rogers et al., 2007]. Blomquist [2009] reported heritability estimates for life history traits in free ranging rhesus macaques, but to date such estimates have not been reported for reproductive traits in captive rhesus macaques.

It is surprising that little is known about the heritability of reproductive traits among females in non-human primates because such studies may ultimately not only provide valuable information on the possibility of using selection strategies in captive animals, but also reveal important insights into evolutionary processes among primate species. Evolutionary change is linked to the degree of additive genetic variance present in a population for various traits and natural selection pressures favoring certain phenotypes can result in changes in allele frequency. Direct traits such as body form [Cheverud and Dittus, 1992] or maternal traits such as growth rate [Wolf et al., 1998; Wilson et al., 2005] that have adequate heritability are likely to respond to such selection pressures. Indeed, models have suggested that maternal genetic effects can significantly influence the rate of evolutionary change [Lande & Kirkpatrick, 1990], although very few studies have actually been reported in which the response of maternal effects to selection pressures has been demonstrated in wild populations [e.g. McAdam & Boutin, 2004]. Nevertheless, an understanding of inheritance of fitness traits such as fecundity is essential for a better understanding of forces that drive evolution.

The objective of this study was to estimate direct additive genetic and phenotypic variance associated with various female reproductive responses in a captive breeding colony of rhesus macaque monkeys and to calculate estimates of heritability using data collected over several decades. We are not aware of any published heritability estimates for reproductive traits in captive populations of rhesus macaque.

# METHODS

## Animals

Reproductive records from a colony of Indian rhesus macaques maintained at the Tulane National Primate Research Center (TNPRC) in Covington, LA were available from the years 1979 to 2007. Information on housing and management of the colony was described previously [Gagliardi et al., 2007]. Briefly, rhesus females were housed in large outside half-acre corrals that offered activity and housing components with accessibility to food and water. Generally, 40–45 adult females were housed in a corral along with 4–5 adult males. Random samples of male and female progeny were routinely removed at 1.5–2 years of age for transfer to other research organizations or to be assigned to research within the TNPRC. Female progeny not transferred remained with their natal groups throughout their lives, although some females were moved among corrals to balance numbers. Male progeny were removed from their natal groups at puberty (~3.0–3.5 yrs), kept in peer groups for at least two years, and then were introduced to unrelated females. Adult males were removed from a social group when known or possible daughters reached breeding age and new unrelated males were then introduced.

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Most females were experimentally naïve. A few females were exposed to research projects at various times in their lives, but these were removed from our study because of the possibility that experimental treatments may have influenced their subsequent reproductive potential. Similarly, females that had no parental identification or had no daughters that produced progeny in the colony were omitted from the analysis. Several females had been used in observational behavioral studies, and as these would not be expected to have any bearing on their fertility, they were retained in the records. The remaining 1,901 females produced 7,816 progeny over the study period for average of 4.1 offspring per female.

Foundation females were defined as those that had no parental information, but produced at least one daughter with progeny. A total of 592 foundation females were identified with an average of 3.2 female members per foundation family. The number of female members in foundation families ranged from 2–20. Up to six generations of female kinship were identified in the female pedigrees. The average number of generations of female relatives per foundation female was 2.7 and ranged from 2.0–4.4. Kinships consisted of maternal half-sib, dam-daughter, dam-granddaughter, dam great-granddaughter, aunt-niece, cousin and other less related females. Thus, the pedigree structure of rhesus females in this study involves a relatively large number of families with a limited number of females per family. We assume that paternal ties within and across female families within a corral is random, however, we have no way to document this.

Animals were cared for and monitored daily by staff trained to provide food and water, observe for sickness or other abnormalities and to record reproductive and survival data. No information was available on female social rank with matrilines or corrals. All animals were housed in conditions approved by the TNPRC Institutional Animal Care and Use Committee and adhered to the requirements described in the Animal Welfare Act [USDA, 1991].

## Records

Females included in the data set had given birth to at least one infant. Although some infants were born in all months of the year, about 80% of the births occurred in April, May and June, with the largest number occurring in May. The distribution of infant birth dates in this study is similar to that reported by Rawlings & Kessler [1985] for births of rhesus monkeys in a free ranging colony near La Parguera, Puerto Rico, but the peak birth dates in our colony occur slightly later in the year.

A reproductive record included identification of the female and the infant, their birthdates, age of female at the time of birth of the infant, subsequent birth intervals, birth order of each infant, infant sex, number of infants produced by the female up to that time in her life, survival of the infant, age of the female at her death or transfer and whether the female was alive, deceased or had been transferred out of the colony.

Female age at first, second and last infant and age at death were recorded in years as real numbers with one decimal, while birth interval was recorded in years as a real number with two decimals. Available information on age at puberty and gestation length in rhesus macaque females was used to determine outliers, i.e. for the analysis of female age at first birth a record was omitted if the value was less than 2.6 years and postpartum birth intervals were deleted if they were less than 0.45 years (164 days), regardless of the survival of the previous infant. For other traits, records exceeding a trait mean ± 3 standard deviations (representing 99% of a normal distribution) were removed as were records with an infant sex code of ‘unknown’.

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## Reproductive traits

The reproductive records analyzed were divided into early reproductive traits, birth interval traits, female longevity and productive traits and infant survival. Early reproductive traits included age of female at the birth of the first and second infant and the birth interval after the first and second births. Age of female at birth of the first infant is most likely associated with age at puberty while the two subsequent birth intervals are determined by the timing of the return of postpartum menstrual cycles. Both traits provide information about the early reproductive success of the female.

In contrast postpartum birth intervals between all progeny and mean postpartum birth interval of individual females are measures of reproductive success throughout a lifetime and may suggest a measure of adaptability in a particular environment. For deceased females, age at the birth of their last infant and age at death are measures of longevity while the number of infants born during their lifetime has been referred to as a measure of fitness [Kruuk et al., 2000]. Because more recently born deceased females will have younger death ages than their live older contemporaries, they would introduce bias into records relating to age at death. To avoid this, females born after 1990 were not included in the analysis for age at death, number of infants born at death or age at the birth of the last infant. Over 95% of the females born before 1991 contributed to these records.

Birth status of infants (alive or dead), survival of live infants at birth to 30 days of age and survival of live infants at 30 days to 1 year of age are generally considered to be maternal traits, although survival of infants from 30 days to 1 year may be due to factors not related to maternal care. Such traits are usually described as threshold traits [Lush et al., 1948; Robertson and Lerner, 1949] and were recorded as “1” for survival and “0” for failure to survive. The assumption for survival or threshold traits is that there are many loci and environmental effects that create a normal underlying distribution. A threshold point P on this underlying normal distribution separates those that survive from those that failed to survive [Gianola 1982; Falconer & McKay 1996; Lynch & Walsh 1996].

## Statistical analyses

The multiple trait derivative free REML (**MTDFREML**) programs of Boldman et al. [1995] were used to estimate heritability for reproductive traits. The MTDFREML program is an animal model procedure in which all sources of additive genetic relationships among animals (i.e. the females in this study) are used to estimate additive genetic variances. The pedigree file used to calculate the additive genetic covariance (A) matrix included female identification, a ‘0’ for sire of female since sires were unknown and dam of the female. The MIXED procedure of the Statistical Analysis System (SAS) set of programs [Littell et al., 1996] was used to obtain additive genetic and residual variance priors for MTDFREML and to identify the various fixed sources of variation significantly ($P < 0.10$) influencing each response trait. Significant sources of variation found with proc MIXED were included in the animal model procedure to account for those sources of influence for a particular trait. Fixed sources of variation found to significantly influence the respective reproductive traits were:

Age at first reproduction: female birth year,

Birth interval after first reproduction: infant birth year, infant birth month, and birth status (alive or dead),

Age at second reproduction: female birth year,

Birth interval after second reproduction: infant birth year,

All birth intervals: infant birth year, infant birth month and birth order,

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Mean birth interval: female birth year,

Time from last baby to death: number of infants born,

Number of infants born: female birth year,

Female age at death: female birth year,

Female age at last infant: female birth year,

Birth status (dead or alive): infant sex, infant birth year, infant birth month and female age,

Survival birth to 30d: infant birth year, infant birth month and female age,

Survival 30d to 1yr: infant sex, infant birth year, and infant birth month.

General linear model procedures in SAS were used to determine model fit for each of the reproductive traits given above. All models had R-square values between 73% and 79% except the models for infant survival traits and the model for all birth intervals, which ranged from 25% to 30%.

The assumption underlying a quantitative genetically influenced trait is that a response of an individual can be partitioned into fixed contemporary group effects, random (animal) additive genetic effects and random residual effects [Henderson, 1984; Lynch & Walsh, 1996]. These effects can be represented in matrix notation as

$$\mathbf{y}=\mathbf{Xb}+\mathbf{Zu}+\mathbf{e},$$

where known matrices **X** and **Z** relate the unknown fixed contemporary group (**b**), the random direct genetic effects (**u**), and random environmental effects (**e**), respectively, to observations in **y**. Expectations for the random vectors are $E(\mathbf{u}) = E(\mathbf{e}) = 0$, which leads to $E(\mathbf{y}) = \mathbf{Xb}$. Residual effects are assumed independent from the direct additive genetic effects.

A total of 2,557 females contributed information to the **A-**matrix in the animal model program. Heritability for each trait was estimated with a single trait model and was calculated as Va/Vp where Vp is the residual phenotypic variance after adjusting for significant fixed sources of variation. Analyses were initially performed at a convergence of $1 \times 10^{-6}$ and then rerun to a convergence of the simplex of $1 \times 10^{-9}$. Cold restarts were made to insure a global maximum was reached. This was assumed when the −2(log likelihood) did not change in the second decimal place. Variances were assumed to be adjusted for fixed effects included in the various analyses of the reproductive traits. Animal model procedures using restricted maximum likelihood rely on maximum use of genetic relationships among relatives in the pedigree and allow unbalanced sets of related individuals.

Estimates of heritability from the analysis of threshold traits with the linear animal model were transformed to an underlying normal scale using the formula proposed by Robertson & Lerner [1949] and discussed by Van Vleck [1972] and others. The transformation is:

$$h^2{}_n=h^2{}_b\,[P(1-P)]/(Z^2),$$

where $h^2{}_n$ is an estimate of heritability on the underlying normal scale, $h^2{}_b$ is the estimate of heritability from the linear model using binomial observations, P is the proportion of infants

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with survival observations of 1, and Z is the height of the ordinate at the truncation point for an area of P under the normal curve.

Phenotypic variance unadjusted for fixed effects in each trait is presented. These estimates are slightly larger than adjusted or residual phenotypic variance used to estimate heritability in this study. Heritability estimates calculated from the animal model were tested for significance from zero by using likelihood ratio tests comparing the likelihood of the full animal model to the likelihood of a model without animal as a source of variation [Lynch & Walsh, 1996; Shaw, 1987].

## RESULTS

### Reproductive traits

Simple statistics for the various reproductive traits are given in Table 1. Average age at first parturition was 4.44 (± 0.93) years with a subsequent first postpartum birth interval of 1.38 (± 0.64) years. Average age at second parturition was 5.80 (± 1.09) years with a postpartum birth interval of 1.21 (± 0.53) years.

The average postpartum birth interval for all females was 1.30 (± 0.46) years, while for deceased females born before 1991, the average postpartum birth interval was 1.24 (± 0.56) years with a range of 0.42–6.80 years.

For deceased females born before 1991, average age at death was 10.4 (± 4.36) years, ranging from 2.8–27.8 years. Average age at last infant was 9.56 (± 4.31) years ranging from 2.80–23.9 years. Death among females occurred on average 1.01 (± 1.16) years after giving birth to their last infant although this, too, revealed a significant range from 0.0–8.74 years. Deceased females had from 1–18 infants with an average of 4.92 (± 3.46) births. Ninety-six percent of 7,617 births resulted in live infants of which 95% survived the subsequent 30 days and of those a further 81% survived to one year of age.

### Estimates of heritability

The estimates of heritability for most traits were low (0.00–0.20) or moderate (0.21–0.40) in magnitude and are shown in Table 2. These estimates of heritability may be referred to as residual estimates because the phenotypic variance used to estimate heritability was reduced by variation due to significant fixed effects in the animal models. Heritability estimates using total or unadjusted phenotypic variance in this study would be only slightly smaller than when using residual phenotypic variance.

Heritability estimates for age of female at first and second parturition were 0.171 ± 0.062 and 0.132 ± 0.077, respectively. Birth intervals following the first two parturitions, and over all intervals during a female’s lifetime had heritability estimates ranging from 0.00 ± 0.072 for the first postpartum interval to 0.134 ± 0.148 for the interval from birth of the last baby to death of the female.

Traits that were indicative of a female’s life span, such as age at death or age at her last parturition had heritability estimates of 0.325 ± 0.143 and 0.247 ± 0.141, respectively. The estimate of heritability for number of infants born in the lifetime of a female was 0.221 ± 0.138 while the heritability of infant survival ranged from 0.021 ± 0.008 for birth status to 0.064 ± 0.011 for survival of infants at birth to 30 days when estimates were based on using binomial data. When binomial estimates of heritability were transformed to a normally distributed underlying scale, the estimates increased to 0.108 ± 0.050, 0.290 ± 0.050 and 0.061 ± 0.018 for birth status, survival to 30 days and survival to 1 year, respectively. In

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total, 8 of the 13 heritability estimates presented in this study proved to be significantly different from zero (P < 0.05).

## DISCUSSION

This study was carried out to determine estimates of heritability for a number of reproductive traits among captive rhesus macaque females maintained in an outdoors facility. Because females were housed in groups containing several males and no records on paternity were available, the possible kinds of relatives identified among the females over six generations were limited mostly to maternal half-sib, dam-daughter, dam granddaughter, dam great granddaughter, aunt-niece and cousins. Because DNA-based techniques to assign paternity through the use of short tandem repeats (STR) or single-nucleotide polymorphisms (SNP) have only recently become available, they could not be used for a retroactive a study covering several decades. However, Henderson [1988] and Westell et al. [1988] have discussed methods to account for unknown paternal parents in multi-sire mating of livestock for quantitative genetic studies. Similarly, Charmantier & Reale [2005] reported that social and genetic pedigrees in the blue tit bird (*Parus caeruleus)* gave similar heritability estimates when heritability is low and there is a low percentage (5–10%) of mis-assigned sires. They concluded that when the rate of mis-assignment of sires exceeded 20% or when levels of heritability were increased, heritability was underestimated by up to 17%. Cheverud & Dittus [1992] and Konigsbert & Cheverud [1992] used offspring-dam regression as well as maximum likelihood methods to estimate heritability of body measurements in non-human primates when sire of female was unknown. They concluded that heritability estimates were generally similar to estimates calculated when the paternal parent was assigned.

Reale et al. [1999] used an animal model and pedigree file based totally on female relatives for estimation of heritability of body mass in wild bighorn sheep. He noted that one limitation of the use of an all female pedigree file is that maternal additive genetic variance could not be obtained in order to calculate an estimate of maternal heritability.

The estimates of heritability for the various reproductive traits in this study were variable. This was most evident where heritability estimates for longevity and productivity were moderate and generally significant from zero whereas estimates for birth intervals were generally very low and not different from zero. These findings are consistent with results from other non-human primate species. However, the estimate of heritability of age at first birth in the present study was much smaller than that reported for baboons by Williams-Blangero & Blangero [1995], but numerically higher than the estimate obtained by Blomquist [2009] for free ranging rhesus macaques.

The estimates of heritability for birth intervals, even when different approaches were used to calculate them, showed only a negligible genetic component. Blomquist [2009] also reported a low heritability of 0.07 ± 0.19 for average inter-birth interval in rhesus macaques. It is important to keep in mind that rhesus macaques are seasonal breeders and their reproductive behavior is therefore much more constrained. The failure to conceive or an embryonic or fetal loss, particularly towards the end of the breeding season, can extend the interval between births by a much larger period than would be the case in animals cycling throughout the year.

Estimates of heritability for longevity and productivity overall were slightly higher, particularly when defined as the age of a dam's death, age at her last parturition or the overall number of infants she had produced. Estimates of similar lifetime traits in other species have been shown to range from 0.05–0.25 [Durr et al., 1999; Miller et al., 1967;

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Rogers et al., 2004; Tanida et al., 1988]. Indeed, Martin et al. [2002] reported an analysis of a breeding population of over 600 baboons and calculated a heritability coefficient of 0.23 for age at death. Heritabilities of 0.21 ± 0.17 and 0.08 ± 0.17 were reported for lifespan and for number of offspring produced in a lifetime, respectively, by Blomquist [2009] in rhesus macaques. It is noteworthy that previous reports have shown that female rhesus macaques can live a substantial amount of time between the birth of their last infant and their own death suggesting the occurrence of menopause in this species [Gagliardi et al., 2007; Borries & Koenig, 2008].

Low estimates of heritability were found for live birth and survival of infants when estimated on the binomial scale; although they were slightly higher when transformed to an underlying normal distribution. Unfortunately, birth weights were not available for any of the infants, which would have facilitated estimates of its influence on survival to 30 days. This would have been of interest because Ha et al. [2002] estimated a very strong genetic component for birth weights of pigtailed macaques, although they did not include its relevance to infant survival in their analysis.

The fact that most heritability estimates for reproductive traits in captive rhesus macaque females appear low is consistent with predictions made by Fisher’s theorem of natural selection which has been interpreted to mean that alleles in a population that are linked to traits conferring increased fitness should eventually become fixed resulting in low additive genetic variation [Fisher 1930]. However, while fitness itself is often only vaguely defined, the interpretations of Fisher’s theorem have been challenged as requiring assumptions that are unlikely to be found in natural populations [e.g. Charlesworth, 1987]. Moreover it cannot be stated with any degree of certainty whether observations in this study population reflect what would be observed in wild populations because it is simply unclear to what degree several generations of captivity of this particular population may have contributed to this phenomenon, despite the fact that no deliberate selection strategy has ever been implemented in its management. Nevertheless, the low heritability estimates for most reproductive traits in this study confirm observation from other non-domesticated species. Mousseau & Roff [1987] reviewed heritability estimates from the literature covering a large number of animal populations and showed that fitness traits had significantly lower heritability traits than morphological or physiological traits which are less likely to be subjected to selection pressures. Similarly, Gustafsson [1986] reported that heritability of a trait was inversely correlated with its association with fitness in the collard flycatcher (*Ficedula albicollis*) while Kruuk et al. [2000] made similar observations in red deer (*Cervus elaphus*). The comparison of traits that do not contribute to fitness to those that do has been challenged on the basis that much of the variability in heritability estimates may be due to large discrepancies in the number of contributing loci [Merilä & Sheldon, 2000]. Moreover, when fitness traits are considered separately the trend is not always consistent; for example Kruuk et al. [2000] found that the decline in heritability in fitness among deer was accompanied by an increase in residual variance in longevity. Merilä & Sheldon [2000] concluded that low heritability was the result of an increase in residual variance while Price & Schluter [1991] have proposed that such higher residual variance might be the consequence of the fact that most fitness traits manifest themselves over long periods of time, which makes them more subject to environmental variation.

The assumption that heritability estimates calculated in captive populations are reliable indicators of heritability in wild populations has been challenged because those indicators tend to be larger due to a smaller phenotypic variance [Riska et al., 1989; Prout and Barker, 1989]. However, Weigensberg & Roff [1996] compared estimates of heritability measured in a large number of field studies to laboratory estimates on wild, outbred species and

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reported that most laboratory heritability estimates appear to provide reasonable estimates of the magnitude and significance of heritability in nature.

A limitation to the analysis of reproductive traits that could contribute to an over estimation of the heritability coefficients in many non-human primates is their complex social hierarchy. Rhesus monkey groups usually consist of matrilines with distinct dominance hierarchies and there is evidence that the social status of a female may not only influence her reproductive output but also that of her daughters. For example, onset of puberty, which is presumably the key factor in determining age at first birth, has been shown to be influenced by social status, with ovulation generally occurring earlier in juveniles from dominant matrilines. However, others have reported significant variation among females even within the same social rank [Schwartz et al., 1985; Wilson 1992; Zehr et al., 2004]. Similarly, females that are socially dominant and are heavier tend to have more ovulatory cycles, and there is a strong relationship between social rank, body weight and reproductive success [Drickamer 1974; Pope et al., 1986; Small 1981; Walker et al., 1983; Wilson et al., 1978]. Studies on small groups, where access to males is limited, have demonstrated that a dominant female can nearly monopolize a single male, even when in some cases the male’s preference is for females of lower social rank. In most instances, higher ranked females appear to initiate sexual activity to a significantly higher degree.

The dominant social structure in macaques reported by many authors suggest daughters of dominant females and of subordinate females tend to be more like their mother than like unrelated females. This could contribute to differences among maternal half-sib families and daughter-dam pairs but less among other kinds of relatives. If these effects cannot be partitioned from the additive genetic variance, they will be part of the estimate of additive genetic variance, and could bias heritability upward [Wilson et al., 2005]. The fact that the present study revealed relatively low heritability estimates does not mean that bias is not likely. Hopefully the growing awareness that maintenance of social structures are important for captive rhesus macaques will lead to gathering of information on social hierarchies which in turn may facilitate genetic studies that can incorporate social rankings in their models.

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## TABLE 1

Descriptive statistics for reproductive traits of female rhesus macaques.

| **Trait**[a] | **No. of records** | **Mean** | **sd** | **min value** | **max value** |
|---|---|---|---|---|---|
| **Early reproduction** | | | | | |
| Female age at 1st infant | 1,897 | 4.44 | 0.93 | 2.6 | 9.10 |
| BI after 1st infant | 1,429 | 1.38 | 0.64 | 0.55 | 6.16 |
| Female age at 2nd infant | 1,436 | 5.80 | 1.09 | 3.70 | 12.00 |
| BI after 2nd infant | 1,097 | 1.21 | 0.53 | 0.42 | 6.09 |
| **Birth intervals** | | | | | |
| All BI | 5,917 | 1.24 | 0.56 | 0.42 | 6.80 |
| Mean BI | 1,432 | 1.30 | 0.46 | 0.475 | 6.16 |
| Interval from last infant to female death | 863 | 1.01 | 1.16 | 0.00 | 8.74 |
| **Longevity; Production** | | | | | |
| Female age at death | 863 | 10.42 | 4.36 | 2.80 | 27.80 |
| Female age at last infant | 877 | 9.56 | 4.31 | 2.80 | 23.90 |
| No. of infants born at female’s death | 863 | 4.92 | 3.46 | 1.0 | 18.0 |
| **Infant survival** | | | | | |
| Birth status (alive/dead) | 7,617 | 0.96 | 0.20 | 0 | 1 |
| Survival; birth to 30 d | 7,297 | 0.95 | 0.21 | 0 | 1 |
| Survival; 30 d to 1 yr | 6,995 | 0.81 | 0.39 | 0 | 1 |

[a] All age or time related dam traits are in years. Baby survival traits are 1=alive or survived and 0=dead or failed to survive.

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## TABLE 2

Summary of heritability estimates for reproductive traits of captive female rhesus macaques (*Macaca mulatta*) estimated with an animal model.

| **Trait** | $V_R$ | $V_A$ | $V_{TP}$ | $V_{AP}$ | **$h^2$ (se)**[c] | **Prob** |
|---|---|---|---|---|---|---|
| **Early reproduction** | | | | | | |
| Age at 1st infant | 0.681 | 0.141 | 0.865 | 0.822 | 0.171 (0.062) | 0.001 |
| BI after 1st infant | 0.382 | 0.000 | 0.410 | 0.382 | 0.000 (0.072) | 0.106 |
| Age at 2nd infant | 0.966 | 0.147 | 1.188 | 1.114 | 0.132 (0.077) | 0.084 |
| BI after 2nd infant | 0.247 | 0.026 | 0.281 | 0.273 | 0.095 (0.098) | 0.336 |
| **Birth intervals** | | | | | | |
| All BI | 0.291 | 0.011 | 0.314 | 0.302 | 0.036 (0.010) | <.001 |
| Mean BI | 0.182 | 0.027 | 0.212 | 0.209 | 0.129 (0.087) | 0.177 |
| Interval from last infant to female death | 1.137 | 0.176 | 1.345 | 1.313 | 0.134 (0.148) | 0.461 |
| **Longevity** [a]**; Productivity** | | | | | | |
| Age at death | 11.455 | 5.513 | 19.009 | 16.969 | 0.325 (0.143) | 0.001 |
| Age at last infant | 12.823 | 4.202 | 18.576 | 17.025 | 0.247 (0.141) | 0.040 |
| No. of infants born at female's death | 8.724 | 2.472 | 11.972 | 11.197 | 0.221 (0.138) | 0.005 |
| **Infant survival** [b] | | | | | | |
| Birth status (alive, dead) | 0.03500 | 0.00076 | 0.0400 | 0.03576 | 0.021 (0.008) | 0.009 |
| Survival; birth to 30 d | 0.04190 | 0.00338 | 0.0455 | 0.04528 | 0.075 (0.011) | <.001 |
| Survival; 30 d to 1 yr | 0.14058 | 0.00385 | 0.1521 | 0.14443 | 0.027 (0.008) | <.001 |

[a] Based on females born before 1991.

[b] Heritability estimates based on analysis of binomial observations with a linear animal model. Variances shown are from the analysis of binomial observations.

[c] Heritability calculated with adjusted phenotypic variance ($V_{AP}$). Total unadjusted phenotypic variance is shown as $V_{TP}$.