# Life history correlates of inbreeding depression in mandrills (*Mandrillus sphinx*)

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## Abstract

**Inbreeding depression reflects the negative consequences of increased homozygosity at
genes that affect fitness. We investigate inbreeding depression in a semi-free-ranging
colony of mandrills (*Mandrillus sphinx*), using high-quality pedigree data, comprising five
maternal generations and 20 years of morphological and demographic data. We examine
the relationship between inbreeding coefficients and four fitness correlates: two growth
parameters (mass and height for age) and longevity in both sexes, and age at first conception
in females. Inbreeding was correlated with both growth parameters, but only in females,
with inbred females being smaller than noninbred females. Inbreeding was also correlated
significantly with age at first conception, with inbred females giving birth earlier in life
than noninbred females. We suggest that sex-biased maternal investment may explain
this sex-differential response to inbreeding, although the lack of a significant association
between inbreeding and growth in males may also be due to the provisioned nature of the
colony. The surprising relationship between age at first conception and inbreeding may be
related to smaller adult size in inbred females, or to their being less able to escape from
male sexual coercion.**

*Keywords*: age at first conception, growth parameter, inbreeding depression, *Mandrillus sphinx*,
maternal investment, sex-differential response

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## Introduction

Inbreeding depression, which may occur in offspring
born to closely related parents, reflects the deleterious
consequences of increased homozygosity at loci that affect
fitness (Charlesworth & Charlesworth 1999). In animal
populations, inbreeding has been shown to reduce survival
(Coulson *et al.* 1998; Gharrett *et al.* 1999; Mandal *et al.* 2004),
and to negatively affect both growth (Coltman *et al.* 1998;
Coulson *et al.* 1998; Hildner *et al.* 2003; Pujolar *et al.* 2005)
and reproductive parameters (Cassinello & Alados 1996;
Laikre *et al.* 1997; Keller 1998; Slate *et al.* 2000; Amos *et al.*
2001; Gallardo *et al.* 2004; Mackintosh & Briskie 2005).
Inbreeding depression can be substantial in wild populations

(see for review: Crnokrak & Roff 1999; Keller & Waller 2002)
and can contribute to driving populations to extinction
(Frankham 1998). Inbreeding depression has also been
shown to be environment dependent (Jimenez *et al.* 1994;
Keller *et al.* 1994; Henry *et al.* 2003; but see Armbruster *et al.*
2000), and sex dependent (Coulson *et al.* 1999; Prugnolle
*et al.* 2004) in some cases.

The most straightforward approach to estimating inbreed-
ing in natural populations is through the use of well-resolved
pedigrees. Such studies are relatively rare (Pemberton 2004)
as the generations of deep and dense pedigrees represent
a great deal of effort, particularly for long-lived organisms.
It is thus tempting to use estimators of heterozygosity based
on genetic markers as a surrogate for inbreeding. However,
the quality of such estimates has recently been seriously
questioned (Coltman & Slate 2003; Balloux *et al.* 2004;
Pemberton 2004; Slate *et al.* 2004).

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Studies examining effects of inbreeding using genetic data are still rare in the primate literature. Several field studies of savannah baboons (*Papio cynocephalus*) have examined the effect of inbreeding on infant mortality or early abortion, comparing conceptions involving non-natal vs. natal males. In 1979, Packer found that inbreeding led to 40% reduction in infant viability in olive baboons (*Papio cynocephalus anubis*). However, these results were disputed (Moore & Ali 1984) and the question of how costly inbreeding was among these baboons has not been resolved. Bulger & Hamilton (1988) reported no effect of inbreeding on infant mortality in chacma baboons (*Papio cynocephalus ursinus*), whereas Alberts & Altmann (1995) found that conceptions assigned to natal male savannah baboons resulted in perinatal death of fetuses. However, the latter study was based on only two potentially inbred conceptions. All studies of baboons to date relied on observations of mating behaviour to estimate paternity.

In captive golden lion tamarins (*Leontopithecus rosalia*), close inbreeding, based on behavioural observations, resulted in the death of all inbred infants compared to 20% mortality for noninbred ones (Dietz & Baker 1993). Using electrophoretic techniques to determine paternity, Smith (1986) examined inbreeding depression in captive rhesus monkeys (*Macaca mulatta*), and found that more homozygous individuals showed significantly lower (estimated) birthweight. However, this study has been criticized and the results found to be inconclusive (Moore 1993). Finally, using microsatellite paternity determination, Charpentier *et al.* (2005a) found that captive *Cercopithecus solatus* females showed significantly increased interbirth intervals following the birth of an inbred infant, indicating possible increased maternal costs of rearing inbred infants.

The existing studies of inbreeding depression in primates do not yield conclusive results, mainly due to small sample sizes, the methods employed or the unnatural conditions of captivity. However, there is clearly potential for inbreeding depression in primates (see for review on infant mortality rates in captive primates: Ralls & Ballou 1982). This prompted us to examine fitness correlates of inbreeding in a semi-free-ranging colony of mandrills (*Mandrillus sphinx*, Cercopithecinae), at the CIRMF (Centre International de Recherches Médicales de Franceville), Gabon. This colony was established in 1983, from unrelated founder animals originating from the wild (Wickings 1995). Charpentier *et al.* (2005b) recently showed that reproductive success in the colony is extremely skewed towards dominant males, but that incest avoidance occurs (incest is defined here as reproductive events between related individuals which give birth to inbred offspring), particularly between first-order relatives (full-sibs for example). The CIRMF mandrill colony offers an excellent opportunity to study inbreeding depression on various fitness correlates, as data on morphology, survival, birth and death dates have been recorded since the creation of the colony.

We were able to analyse an entire, well-resolved pedigree representing five maternal generations. It was thus possible to obtain the exact inbreeding coefficient for the vast majority of individuals, i.e. more than 200 individuals, using the identity-by-descent method. We examine potential effects of inbreeding depression on: (i) growth parameters, which represent a potential source of variance in fitness (Lochmiller *et al.* 2000; Dobson & Oli 2001; Johnson 2003); (ii) age at first conception in females, as an estimate of reproductive success (Willner & Martin 1985); and (iii) longevity in both sexes. Age at first reproduction could not be analysed for males, since high variance in male reproductive success, and the small number of sires, resulted in too few individuals being available for statistical analysis (Charpentier *et al.* 2005b).

## Methods

### Study species and husbandry

Mandrills are primarily terrestrial primates found in the tropical forests of western Central Africa, from southern Cameroon to southwestern Republic of Congo (Harrison 1988). Mandrill social organization has been variously described as single-male harems (Hoshino *et al.* 1984), aggregations of these harems into larger groups, or multimale–multifemale hordes consisting of hundreds of individuals (Rogers *et al.* 1996; Abernethy *et al.* 2002). The breeding colony of mandrills at the CIRMF was established in 1983–1984 when 15 unrelated animals, originating from the wild (eight females aged from 1 to 11 years and seven males aged from 1 to 3 years), were released into a 6-ha rainforest enclosure (Wickings 1995). Any further increase in the group has been due to natural reproduction of these founder animals, countered by deaths and some removals for experimental purposes. Removal of those individuals should not bias our results, as removal was independent of inbreeding, and only permanent members of the semi-free-ranging colony were considered in the present study. The mandrills are provisioned twice a day with locally available fruits and monkey chow. Water is available *ad libitum*.

Between June 1983 and June 2002, 231 infants were born into the colony. Since the establishment of the colony, the majority of animals have been captured annually for veterinary controls. During those controls, various morphological measures are made, including body mass and crown-rump length. Blood samples for genetic analyses were also collected from 1990 onwards. In 2002, DNA samples were available for 205 of the 231 offspring born in the colony, as well as for all 14 potentially reproductively active founders (one female never reproduced successfully). Twenty-six mandrills born in the colony could not be sampled (2 stillborns, 16 that died before 1 year of age, and 8 that were never captured).

*Genetic analyses*

DNA was extracted from blood samples obtained during annual captures. Six to 10 microsatellite loci were genotyped for the majority of the 205 offspring except for four individuals which were genotyped at fewer than four loci [mean loci typed per individual ± standard error (SE): 7.42 ± 0.07, $n = 219$ individuals]. Paternities were assigned using CERVUS 2.0 (Marshall *et al*. 1998) and PARENTE (Cercueil *et al*. 2002) computer software. We obtained an accurate assignment of paternity for 193 (94%) of the 205 offspring for which blood samples were available (for details of methods and paternity assignment criteria, see Charpentier *et al*. 2005b).

Inbreeding coefficients (*f*) were calculated directly from the five generation pedigree using the identity-by-descent method (IBD, e.g. Blouin 2003). None of the founder individuals were related as evidenced by band-sharing scores from DNA fingerprints (Wickings 1995), and all dams and potential sires were genotyped. Thus, offspring born from father–daughter (or mother–son or full-sibs) conceptions are expected to be inbred at $f = 0.25$. All 193 individuals analysed fell into one of the six following classes: $f = 0$ ($n = 135$), 0.063 ($n = 17$), 0.125 ($n = 28$), 0.156 ($n = 1$), 0.187 ($n = 1$), and 0.25 ($n = 11$).

*Inbreeding depression and fitness-related parameters*

*Growth parameters.* We obtained measures of body mass-for-age and crown-rump length-for-age for each individual as follows. Body mass (to the nearest 100 g) and crown-rump length (CRL, to the nearest 0.5 cm) measurements were extracted from colony records for all individuals born into the enclosure. Five hundred and sixty-five mass data points were available for 127 females (1–24 points per female, excluding females > 2 months pregnant) and 295 CRL data points were available for 117 females (1–8 per female; age 0.0–20.1 years). Six hundred and sixty-eight mass data points were available for 106 males (1–32 points per male) and 362 CRL data points were available for 96 males (1–13 per male; age 0.0–16.4 year). Data were treated as a mixed longitudinal and cross-sectional sample and locally weighted least squares regression (lowess, f = 0.3, 10 iterations) was used to fit curves to the data for each sex following Moses *et al*. (1992). This method is useful in that it produces an estimated average value for each age without assuming any underlying form for the curve. 'Residuals' were computed for each data point contributing to the curves of body mass and stature (CRL) for each sex as the natural logarithm of the ratio of the observed value to the average value given by the lowess curve for that age (Moses *et al*. 1992). Residuals were plotted against age for each individual to examine whether individual patterns showed persistence over time (i.e. whether animals that were above or below the average

for size or length at one capture also showed a deviation in the same direction at other ages). The mean of an individual's residuals was then used as a measure of its relative size-for-age. Females were treated separately from males in all analyses. When examining growth parameters, we included maternal age, parity (primiparous vs. multiparous females), and social rank (high-ranking, mid-ranking and low-ranking classes) at the birth of each offspring as covariables, because these variables are known to influence offspring size-for-age in mandrills (Setchell *et al*. 2001). Rank relations between females were determined using *ad libitum* records of avoidance behaviour made during daily observation periods. Female-dominance ranks are stable and maternally inherited in mandrills (Setchell 1999).

*Survival.* We used Kaplan–Meier survival analyses to examine the age at disappearance (presumed mortality) in both sexes to account for the bias introduced by animals that were still alive at the end of the data collection period. Log-rank test statistics (*L*) were used to test for equality of survival distributions. We compared survival in inbred individuals vs. noninbred individuals, and also survival of individuals with $f < 0.25$ and $f = 0.25$ (only three individuals with $f = 0.25$ died during the study period). As males die earlier than females (Setchell *et al*. 2005), we analysed female and male survival separately. Several confounding variables, which could not be taken into account in survival analyses, may have biased our results, including maternal age, parity and rank at the birth of each offspring. We therefore also compared individuals that died with those that survived (regardless of age) using logistic regression, and included the explanatory variables inbreeding coefficient and sex, as well as the maternal variables described above.

*Age at first conception in females.* We used Kaplan–Meier survival analyses to compare age at first conception in inbred vs. noninbred females. We stratified our analysis by female rank because age at first conception is significantly correlated with dominance rank, high-ranking females giving birth earlier than lower-ranking females do (Setchell *et al*. 2002). Founder females were excluded from examination of age at first conception, as their age was estimated at their arrival at CIRMF. We also analysed the potential effect of body mass or CRL on age at first conception. Too few inbred females ($n = 2$) gave birth to more than one offspring to permit analysis of correlation between inbreeding and interbirth intervals, or between inbreeding and number of offspring produced.

*Statistical analyses*

We used generalized linear models (SAS version 9, GLM procedure) to model the relationship between growth

**Table 1** Association between inbreeding and growth parameters in both sexes (GLM procedure)

| Tested variables | Sex | Sample size | F | P |
|---|---|---|---|---|
| Mass | F | 94 | $F_{1,92} = 11.99$ | 0.001 |
| | M | 95 | $F_{1,93} = 0.08$ | 0.781 |
| CRL | F | 84 | $F_{1,82} = 4.85$ | 0.030 |
| | M | 89 | $F_{1,87} = 0.35$ | 0.557 |

parameters (body mass and CRL-for-age) and inbreeding, with a Gaussian error structure, as residuals were always normally distributed. When an association between inbreeding, maternal age, rank or parity and the given fitness correlate was detected, we tested a posteriori for homoscedasticity between samples, using Levene's tests (SAS, version 9). Equalities of variance were always verified. When a correlation between mass or CRL and maternal rank was detected, we used the Lsmeans procedure followed by a Tukey test to ordinate the three classes of social rank. We used the descending model selection procedure (Burnham & Anderson 1998) to select a set of explanatory variables, with a *P* value cut-off of 10%.

Survival analyses were performed with SPSS for Windows release 11.0.0 (SPSS Inc.). GLM was then used to model the relationship between age at first conception and body mass or CRL, as residuals were normally distributed. In this analysis, female rank was taken into account as a covariable. Finally, logistic regression was used to model the relationship between survival (individual dead at a given sample time = 1; individual still alive = 0) and the explanatory variables defined above (SAS version 9, GENMOD procedure). For these two last analyses the descending procedure was used until all *P* values were below the cut-off of 10%.

## Results

### Growth parameters

Inbreeding was significantly, negatively correlated with both mass and CRL-for-age, but only in females, with inbred individuals being smaller than noninbred individuals (Table 1; Fig. 1a, b). Body mass and CRL values were highly correlated (Pearson correlation: $r = 0.736$, $P < 0.001$).

Maternal rank was significantly associated with offspring mass and CRL in males (mass: $F_{2,92} = 2.88$, $P = 0.061$; CRL: $F_{2,86} = 3.43$, $P = 0.037$), with high-ranking females raising heavier (Lsmeans$_{mass} = 0.038 \pm 0.022$) and longer (Lsmeans$_{CRL} = 0.023 \pm 0.008$) sons than low-ranking females (Lsmeans$_{mass} = -0.047 \pm 0.038$, $P = 0.048$; Lsmeans$_{CRL} = -0.007 \pm 0.010$, $P = 0.045$). No other factor considered significantly influenced growth parameters in either males or females.
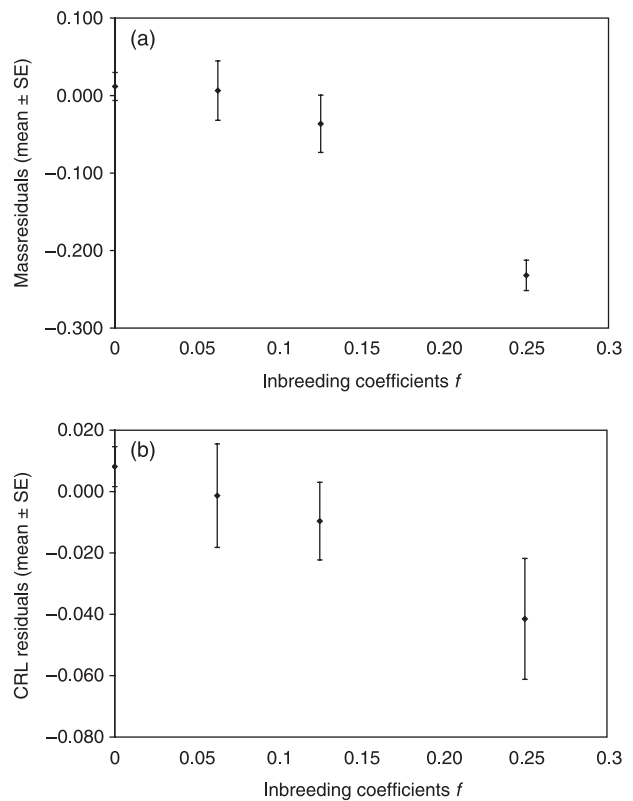


**Fig. 1** Relationship between inbreeding coefficients and growth in females. Figures show mean ± SE for each inbreeding value. (a) Mass-for-age; (b) CRL-for-age.

### Survival

We found no difference between age at death in inbred vs. noninbred individuals (males: $n = 93$, $L = 1.08$, $P = 0.299$; females: $n = 100$, $L = 0.27$, $P = 0.606$). Nor did individuals at $f = 0.25$ differ in survival from those at $f < 0.25$ (males: $L = 1.48$, $P = 0.224$; females: $L = 1.07$, $P = 0.301$). Finally, logistic regression analysis modelling the probability of dying (regardless of age) showed no correlation between this parameter and inbreeding ($n = 193$, $\chi^2 = 0.62$, $P = 0.430$). Of the variables tested, maternal parity and sex significantly influenced the probability of dying (parity: $\chi^2 = 4.47$, $P = 0.035$; sex: $\chi^2 = 4.75$, $P = 0.029$), with offspring born to primiparous females being more likely to die (9/38 dead offspring) than those born to multiparous dams (15/155 dead offspring); and males being less likely to survive (17/93 dead males by the end of the 20-year period) than females (7/100 dead females).

### Age at first conception

Inbreeding significantly influenced age at first conception in females, when female rank was controlled for ($n = 69$; $L = 6.45$, $P = 0.011$). Inbred females gave birth earlier (median
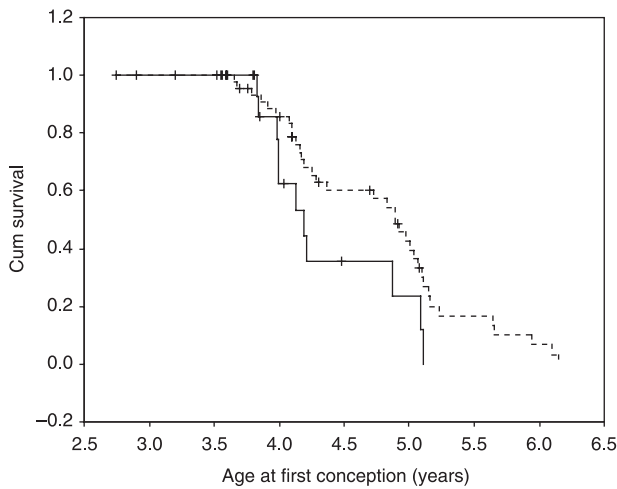
**Fig. 2** Cumulative survival curve showing age at first reproduction in inbred (solid line) and noninbred (dashed line) female mandrills. Crosses indicate censored cases.

**Table 2** Association between inbreeding and age at first conception (year) in females (median ± SE) according to female rank (Kaplan–Meier survival analysis)

| | Inbred females | Noninbred females |
|---|---|---|
| High-ranking females | 3.83 ± 0 | 4.13 ± 0.12 |
| Mid-ranking females | 4.87 ± 0.53 | 4.89 ± 0.42 |
| Low-ranking females | 3.99 ± 0.01 | 5.23 ± 0.38 |

± SE: 4.19 ± 0.16) than noninbred females (4.89 ± 0.13) (Fig. 2). This result persists when the association between inbreeding and age at first conception is considered separately for each female rank (Table 2). This effect does not appear to be due to the smaller size of inbred females, as neither body mass nor CRL were significantly correlated with the age at first conception (GLM controlling for the influence of female rank; mass: $F_{1,44} = 0.16$, $P = 0.69$; CRL: $F_{1,42} = 0.59$, $P = 0.45$).

## Discussion

Access to a deep and well-resolved pedigree for five generations of mandrills allowed us to assign inbreeding coefficients confidently in this study, as the founder animals of the colony were unrelated (Wickings 1995). We found evidence of inbreeding depression for two correlated growth parameters, but, surprisingly, this was only true in females, with female body mass and CRL decreasing with inbreeding. Growth rate has been used previously as a surrogate for fitness in studies relating genetic variability and fitness (Britten 1996) and correlations between growth rates and fitness have been documented (Lampert & Trubetskova

1996; Lochmiller *et al*. 2000; Dobson & Oli 2001; Johnson 2003). Moreover, negative associations between growth rate and heterozygosity have been reported in a variety of taxa (Allendorf & Leary 1986; Mitton 1993; Britten 1996; Coltman *et al*. 1998; Coulson *et al*. 1998; Hildner *et al*. 2003; Pujolar *et al*. 2005).

### Sex-differential response to inbreeding

One potential explanation for our finding that inbreeding depression only influences body size in females is that mothers invest more in sons. Sex-dependent maternal investment has been associated with sex-specific payoffs, with greater investment in the sex of offspring with the highest variance in reproductive success (Trivers & Willard 1973). Setchell *et al*. (2002) found no evidence that female mandrills bias their expenditure toward either sex, in terms of gestation length (prenatal investment) or interbirth interval (postnatal expenditure). However, a potential explanation for our finding is that mothers invest more in sons in terms of social apprenticeship during raising (postnatal investment). Furthermore, some cryptic effects may occur. For example, in macaques, fetal testes produce testosterone from 40 to 50 days (Bercovitch *et al*. 2000), and it has been argued that fetal androgens could enter the maternal circulation and augment maternal adiposity, via aromatization to oestrogen (Norman & Litwack 1997). Other studies have also shown that differential investment in relation to hormones and immune function components can occur in birds and may affect offspring survival (Soler *et al*. 2003). Thus, if female mandrills do invest more heavily in sons, this may compensate for costs associated with inbreeding. Under such a scenario, inbreeding depression may therefore be detectable in females only.

Alternatively, the provisioned nature of the mandrill colony may result in a sex-differential association between inbreeding and growth. Inbreeding depression can be environment dependent (Henry *et al*. 2003 and references therein) and can be undetectable in captivity (Joron & Brakefield 2003). The negative consequences of inbreeding depression may be compensated by the positive influence of provisioning. If males were better than females at compensating for inbreeding depression through increased food acquisition — which might be possible in a nonlimiting environment — this may disguise any inbreeding depression in males. This hypothesis is supported by behavioural observations of feeding in the mandrill colony where males tend to monopolize food while females are more peripheral (E.J. Wickings, unpublished data). Some long-lasting effects of maternal investment, such as an increased access to food of infant and juvenile males with high-ranking mothers, may therefore have occurred.

While the differences in inbreeding sensitivity between males and females are suggestive of a sex-specific response

to inbreeding, this result may also be due to a lack of power of our test to detect inbreeding depression in males. To test for the power of our analysis, we simulated new data sets following an alternative hypothesis, $H_1$, under which an effect of inbreeding on fitness occurs in males. Simulated data sets had the same sample size for each $f$ and the same error structure as in the observed male data set. Residuals were generated in relationship to the average mass-for-age estimated for each $f$. On the whole male data set, residuals followed a normal distribution with a mean equal to zero and a standard deviation equal to 0.121. One thousand data sets were simulated under $H_1$, according to the following equation: mass-for-age = $-0.736\,f + 0.020$. This equation is the one obtained with the female data set where we detected a significant association between inbreeding and growth in mass. The significance of the relationship was tested for each new, randomly generated data set. After 1000 simulations (s-PLUS 2000, MathSoft Inc., 1999), the proportion of $P$ values ≤ 0.05 was 98.9%. We did the same analysis for CRL in males, with CRL-for-age = $-0.175\,f + 0.009$, which is the equation of the relationship between CRL and inbreeding in females. We also considered an error structure with a mean equal to zero and a standard deviation equal to 0.043. After 1000 simulations, we found 75.8% of $P$ values ≤ 0.05. These simulations suggest that our statistical analyses had adequate power for detecting inbreeding depression in males, and suggest therefore the absence of inbreeding depression in males to be a genuine feature.

### Age at first conception

We found an association between inbreeding and age at first conception in female mandrills, with inbred females giving birth earlier than noninbred ones. Female reproductive success has been repeatedly shown to be negatively correlated with inbreeding (Cassinelo & Alados 1996; Laikre *et al*. 1997; Keller 1998; Amos *et al*. 2001; Mackintosh & Briskie 2005), the inverse of our finding in female mandrills. Decreased age at first reproduction may increase reproductive success, despite the costs of growing and reproducing at the same time (Willner & Martin 1985). However, Smucny *et al*. (2004) recently showed that female marmosets (*Callithrix jacchus*) that begin to reproduce later survived longer than those that began reproduction at an earlier age. Early reproduction in female rhesus macaques (*Macaca mulatta*) also significantly delays the next birth (Bercovitch & Berard 1993). It thus appears that early reproduction does not necessarily confer a fitness advantage to females and could even have detrimental effects on their general health, thereby decreasing their lifespan, particularly in low-ranking females. However, this does not appear to be the case in mandrills (Setchell *et al*. 2002). The association between inbreeding and age at first conception remained consistent across female ranks,

suggesting that inbreeding depression affects all females, regardless of social rank.

The results concerning inbreeding and age at first conception may be an indirect consequence of the effect of inbreeding on body mass and size. Inbred females may reach the ratio of body mass for size required for breeding earlier than larger-framed females (Frisch & McArthur 1974). However, this hypothesis is unlikely, as we detected no relationship between body size-for-age and age at first conception. Finally, female mandrills exert active choice upon which males they mate with, and when (Setchell 2005). Thus, an alternative possibility is that lighter and smaller inbred females may be less able to refuse mating and escape from male coercion.

An exceptionally well-resolved pedigree from a semi-free-ranging primate population allowed us to test for fine patterns of inbreeding depression. We documented a sex-specific effect with females being affected but males seemingly immune to inbreeding. Even more surprisingly, age at first reproduction in females was decreased rather than increased in inbred females. This study suggests that inbreeding depression can be far more complex than often recognized and opens several perspectives for future investigations.

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