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**Fred B. Bercovitch · Anja Widdig · Peter Nürnberg**

# Maternal investment in rhesus macaques (*Macaca mulatta*): reproductive costs and consequences of raising sons

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**Abstract** Maternal investment in offspring is expected to vary according to offspring sex when the reproductive success of the progeny is a function of differential levels of parental expenditure. We conducted a longitudinal investigation of rhesus macaques to determine whether variation in male progeny production, measured with both DNA fingerprinting and short tandem repeat marker typing, could be traced back to patterns of maternal investment. Males weigh significantly more than females at birth, despite an absence of sex differences in gestation length. Size dimorphism increases during infancy, with maternal rank associated with son's, but not daughter's, weight at the end of the period of maternal investment. Son's, but not daughter's, weight at 1 year of age is significantly correlated with adult weight, and male, but not female, weight accounts for a portion of the variance in reproductive success. Variance in annual offspring output was three- to fourfold higher in males than in females. We suggest that energetic costs of rearing sons could be buffered by fetal delivery of testosterone to the mother, which is aromatized to estrogen and fosters fat accumulation during gestation. We conclude that maternal investment is only slightly greater in sons than in daughters, with mothers endowing sons with extra resources because son, but not daughter, mass has ramifications for offspring sirehood. However, male reproductive tactics supersede maternal investment patterns as fundamental regulators of male fitness.

**Key words** *Macaca mulatta* · Maternal investment · Sex ratio · Paternity

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F.B. Bercovitch (✉)
Caribbean Primate Research Center, P.O. Box 1053,
Sabana Seca, PR 00952, USA
e-mail: 104263.1232@compuserve.com
Tel.: +1-787-7954045, Fax: +1-787-7956700

A. Widdig · P. Nürnberg
Institut für Medizinische Genetik, Universitätsklinkum Charité,
Humboldt Universität zu Berlin, 10098 Berlin, Germany

## Introduction

Natural selection is impotent at adjusting birth sex ratios or guiding sex-biased maternal investment in offspring unless such modifications entail fitness consequences. Adjustments in sex ratios are adaptive only if individuals with an inherited tendency to produce one sex in excess leave more descendants than conspecifics lacking that tendency (Darwin 1871), but whether sex ratio adjustment is an adaptive trait, a result of stochastic factors, or an outcome of physiological epiphenomena is unclear and difficult to ascertain (Williams 1979; Clutton-Brock and Iason 1986; van Schaik and Hrdy 1991; Krackow 1995, 1997). Numerous studies have examined sex-biased progeny production and maternal investment (e.g., Clutton-Brock and Iason 1986; Frank 1990; Hardy 1997; Dittus 1998), but few have tried to link investment patterns with reproductive success of offspring.

The premise of facultative sex-biased allocation of resources is that reproductive rewards to mothers are a direct consequence of differential levels of investment in sons and daughters (Fisher 1930; Trivers and Willard 1973; Maynard Smith 1980; Frank 1990; Clutton-Brock 1991). Levels of maternal expenditure during the period of infant dependency are driven by the reproductive value of offspring at the termination of the period of parental expenditure, and since each sex supplies half the ancestry to future generations, the total reproductive value of males in one generation must equal that of females of the same generation (Fisher 1930). As a consequence, a numerical excess of one sex over the other at the end of the period of parental expenditure is expected to be compensated for by reduced investment in that sex so that expenditure in both sexes is comparable. Biased expenditure in rearing offspring, rather than simple deviations in birth sex ratios, is predicted to characterize species with lengthy periods of infant dependency (Fisher 1930; Trivers and Willard 1973; Hrdy 1987; Hewison and Gaillard 1999).

The key adaptive models linking maternal investment to sex-biased allocation of resources are the male quality (see

Trivers and Willard 1973) and the local resource competition (LRC), or advantaged-daughter (see Hamilton 1967; Clark 1978; Silk 1983) models (see Hardy 1997 for discussion). Male quality assumes that the crucial mechanism mediating investment is maternal condition, with females in good condition expected to invest heavily in sons. Females are expected to siphon more resources into boosting the size of infant sons compared to daughters when adult male body size is both a function of infant size and impacts progeny production. LRC, in contrast, assumes that sociodemographic factors are the crucial mechanism mediating maternal investment. In female philopatric societies, where recruitment of daughters bolsters alliance formation and access to resources that augment reproductive success, high-ranking females are expected to invest more heavily in daughters. The two models are not necessarily mutually exclusive (Armitage 1987; van Schaik and Hrdy 1991; Hardy 1997; Dittus 1998), but differ in emphasizing whether external or internal forces have a greater effect on resource allocation to sons or daughters.

Sex differences in infant growth rates could also be due to sex differences in metabolic profiles that are independent of levels of maternal investment. According to the metabolic-efficiency model, males are capable of converting maternal resources into accelerated growth rates as a byproduct of sexual selection favoring a larger size among adult males residing in polygynous societies (see Clutton-Brock 1991, 1994; Ono and Boness 1996; Birgersson et al. 1998; Moses et al. 1998; Hewison and Gaillard 1999). Hence, augmented male size at the termination of the period of maternal investment is not necessarily evidence in favor of biased maternal investment in sons.

Measuring maternal investment is difficult because, by definition, it must involve costs that diminish either future fertility or survivorship (Trivers 1972; Ralls 1977; Knapton 1984; Clutton-Brock 1991; Reznick 1992; Hewison and Gaillard 1999). Although maternal investment has been expanded in scope to include maternal support of mature offspring, especially in the LRC model, such behavior is maternal care, rather than investment, unless it decreases prospects for future reproduction. The distinction is important for investigating the evolution of behavior because maternal investment is based upon life history strategies designed to promote progeny production and nurturance at the expense of future reproduction (Trivers 1972; Reznick 1985), while maternal care is aimed at promoting fitness without regard to energetic or fitness costs (Clutton-Brock 1991). As a consequence, age-related reproductive tactics (Pianka and Parker 1975) are more likely to reflect maternal investment than maternal care.

### Maternal investment and rhesus macaques

Rhesus macaques reside in multimale mating systems, characterized by male dispersal, female philopatry, and female nepotistic alliance formation (Melnick and Pearl 1987; Bercovitch and Huffman 1999). Female rhesus macaques usually mate with about three to four males per cycle (Bercovitch 1997), so paternity is invisible in the absence of genetic analysis. Genetic analysis of paternity in rhesus macaques (Smith and Smith 1988), as well as in Barbary macaques, *Macaca sylvanus* (Paul and Kuester 1996), has linked differences in maternal rank to variation in sons' reproductive output, but has not investigated how this outcome might depend on either maternal investment patterns or body condition.

The influence of maternal rank on secondary sex ratios among rhesus macaques has been examined in multiple localities, with conflicting results. Female dominance rank had no significant impact on secondary sex ratios at either Cayo Santiago (Rawlins and Kessler 1986c; Berman 1988), or at the California Regional Primate Research Center (Small and Hrdy 1986). On the other hand, high-ranking females living on the islands of La Cueva and Guyacan, Puerto Rico, tended to produce more sons than daughters, in conformity with the male quality model (see Meikle et al. 1984), while dominant females living in the diminutive social groups at Madingley, England, bore more daughters than sons, in accordance with the LRC model (see Simpson and Simpson 1982; Nevison et al. 1996). This report is not intended to delve into reasons for these discrepancies, but to shift the focus away from assessing rank-related secondary sex ratio profiles to consideration of the reproductive costs and consequences of raising sons. Our goal was to determine whether variation in male reproductive success, measured with genetic analysis, could be attributed to differential levels of maternal investment in rhesus macaques.

## Methods

### Study population and subjects

We collected data from two troops of rhesus macaques. One troop (group R) was resident on a 15-ha island, Cayo Santiago (CS; 18°09′ N, 65°44′ W), about 1 km off the coast of Puerto Rico, and the other troop (group M) resided in a 1-acre outdoor corral at the Sabana Seca Field Station, Puerto Rico (SSFS; 18°27′ N, 66°12′ W). Rhesus monkeys have inhabited Cayo Santiago since 1938 (Sade et al. 1985; Rawlins and Kessler 1986a) and group M was translocated from CS to SSFS intact in 1984 (Bercovitch and Lebron 1991). During this study, group R ranged in size from 140 to 250, while group M varied in size from about 110 to 160. Cliffs, forests, thickets, and scrub areas characterize CS, while group M resides in a grassland enclosure at SSFS containing structures for protection from the elements. In both locations, monkeys are provisioned once daily with monkey chow. At SSFS, the monkeys supplement their diet by foraging on the grass within the enclosure, while at CS they spend about half the day feeding on the natural vegetation (Marriott 1988). Provisioning provides a concentrated, high-quality food resource that is not available to all subjects on an ad libitum basis, but is inequitably distributed according to social status. At both locations, reproduction is seasonal and males reduce feeding time during the mating season (Bercovitch 1997).

All monkeys are recognized on an individual basis, and both troops are monitored almost daily. Birth dates are generally known to ±3 days. The primary dataset consists of longitudinal records collected from males between 4 and 6 years of age. Male rhesus macaques achieve sexual maturity at 4 years of age, skeletal maturity at 6 years of age, and accumulate body weight until 8 years of age (Bercovitch and Goy 1990). One cohort of males was followed in group R (*n*=7), while three cohorts of animals were followed in group M (*n*=11). Throughout the study, focal males remained resident in their natal troop. Sample sizes vary in the analyses because the secondary dataset consists of non-focal animals who contributed morphological, behavioral, demographic, and genetic data over the years.

### Morphological and behavioral data

Every monkey in group M is weighed twice per year, while only focal males were weighed in group R. Morphological measurements of focal subjects included body weight, abdominal skinfold thickness, and crown-rump length (Bercovitch 1992). Body condition is reflected in both abdominal skinfold level and the body mass index [BMI=weight (kg)/crown-rump length (cm)$^2$]. Although individual birth dates are known, it was not feasible to weigh each focal subject on his exact birth day, so weights were obtained at the time of routine veterinary examination. The eleven focal subjects in group M who provided the longitudinal data were initially weighed between 0.83 and 1.06 (mean±SD=0.98±0.07) years, with age at weighing not significantly different between future sires and non-sires (*t*=0.807, *df*=9, P=0.44). The precise age at weighing was comparable for males occupying high-, middle-, and low-rank positions (ANOVA: $F_{2,8}$ =1.646, P=0.25). Maternal preconception weight refers to weight of females immediately prior to the mating season.

Behavioral data included both ad libitum observations (Altmann 1974) of all monkeys and focal samples obtained from subject males (Bercovitch 1993). Male ranks were assigned on the basis of dyadic agonistic encounters, including threats, chases, fights, fear grimaces, avoidance of approaches, and supplants over resources (Bercovitch 1993; Bercovitch and Nürnberg 1996). In group M, we trifurcate the dominance scale into high, middle, and low status, whereas the reduced sample size of subjects in group R necessitated a division into either high or low rank. Natal male ranks are predictable from maternal ranks until adolescence (Sade 1967; Bernstein and Williams 1983) and no discrepancies emerged between relative maternal rank based on ad libitum records of female-female agonistic interactions and their son's rank. Given this consistency, combined with the absence of any revolutionary restructuring of male or female social relationships during the study, we assume that relative ranks of our male focal subjects were stable from 1 to 6 years of age.

### Genetic analysis

At both locations, all troop residents are bled for paternity analysis. Annual male reproductive output was established by incorporating all potential sires, i.e., males ≥4 years of age (Bercovitch and Goy 1990), into the genetic analysis. Blood samples for paternity were collected from the femoral vein in EDTA tubes, frozen, and stored at –20°C until analyzed. We determined paternity using both single-locus human-derived short tandem repeat (STR) marker typing (Kayser et al. 1995, 1996), and multilocus synthetic oligonucleotide DNA fingerprinting (Arnemann et al. 1989; Nürnberg et al. 1993). About a dozen human-derived STR markers are polymorphic in our study population. Potential sires were matched with infants and mothers according to allelotype based upon STR marker typing, and confirmation was achieved with DNA fingerprinting by running the probable sire on the same gel as mother and offspring. This dual approach circumvents the disadvantages associated with each technique and generates an unequivocal sire (Nürnberg et al. 1998). We identified the sire of 80% of infants (129/162) born between 1991 and 1995 in group M, and 77% of infants (90/117) born in group R between 1993 and 1995.

### Maternal investment

The two most common measures of maternal investment are suckling behavior and weight at independence, although both have been questioned as reliable indices of maternal investment (suckling: Cameron 1998; weight: Clutton-Brock 1991). In primates, weaning is a gradual process because infants mix maternal milk with solid food items for many months prior to cessation of nursing (Altmann 1980; Berman 1980, 1984; Lee 1987). Rhesus macaques allocate about 24 weeks to gestation (Silk et al. 1993), resume mating when infants are about 24 weeks of age (Berman et al. 1993), and conceive within 2 to 3 weeks of resumption of mating (Malik et al. 1992), or when infants are about 30 weeks of age (Bowman and Lee 1995). The interbirth interval in rhesus macaques is approximately 1 year (Rawlins and Kessler 1986b; Berman 1988). Nursing and carrying progeny essentially cease by 1 year of age, when mothers channel resources into direct investment in their next infant.

We restrict *maternal investment* to refer to expenditures incurred during the period of time when offspring are most dependent upon maternal resources for survival. We assume that 1 year of age demarcates the termination of direct maternal investment among rhesus macaques, such that weight at 1 year of age represents the maximum extent to which females invest resources in progeny. Maternal support of immature offspring in rhesus macaques is neither a function of progeny sex (Kaplan 1977; Schulman and Chapais 1980; Bernstein and Ehardt 1986) nor of dominance rank (Berman 1986). We view such behavior as maternal care, rather than a type of investment that extracts fitness costs. We examine fitness, not energetic, costs of investment by determining probability of infant survivorship and interbirth intervals of females according to the sex of their infants.

## Results

### Secondary sex ratios and infant mortality

In both populations, evidence of non-uniform sex ratios at birth was absent. The sex ratio in neither group M ($\chi^2$=2.63, *df*=4, *P*=0.62) nor group R ($\chi^2$=0.55, *df*=2, *P*=0.76) differed across years, allowing years to be combined. In both group M ($\chi^2$=1.24, *df*=1, *P*=0.27) and group R ($\chi^2$=0.36, *df*=1, *P*=0.36), the sex ratio at birth was uniform, a distribution identical to that reported for previous years in this population (Rawlins and Kessler 1986c; Berman 1988). At both locations, 44% of live births were female (Cayo Santiago: 51/117; Sabana Seca: 71/162).

Even though the population sex ratio at birth was unbiased, production of progeny could be sex biased as a result of maternal age, rank, or body condition. Maternal age had no significant effect on the sex ratio of progeny at birth (Table 1). Younger females tended to produce more sons than daughters, compared to older females, but the difference was not statistically significant (group M: $\chi^2$=1.38, *df*=1, *P*=0.24; group R: $\chi^2$=3.14, *df*=1, *P*=0.08). Even though young females at Cayo Santiago produced nearly twice as many sons as daughters, the distribution did not differ from chance ($\chi^2$=1.75, *df*=1, *P*=0.19).

The effect of maternal rank was scrutinized by comparing the extremes of the social hierarchy, due to limitations in the data. In group M, the five females comprising the alpha matriline produced 32 progeny during this study, of which 41% were female ($z=0.343$, $P>0.50$). The three females occupying the omega matriline in the troop produced 14 progeny, of which 43% were female (binomial $P>0.50$). In group R, data were insufficient to evaluate the omega matriline, but the three females in the alpha matriline produced an even sex ratio at birth ($n=13$, $x=6$, $P>0.50$).

The effect of body condition was evaluated by examining the association between maternal preconception weight and sex of subsequent infant. Body mass was comparable between those whose first born was a son and those who initially bore a daughter (5.08±0.74 vs 5.26±0.46 kg; $t=-0.591$, $df=18$, $P=0.56$). Similarly, preconception weight of parous females did not differ between individuals who subsequently gave birth to a son and those who produced a daughter (7.50±1.94 vs 7.69±1.55 kg; $t=0.491$, $df=75$, P=0.63). Stillbirths and neonatal mortality could bias the sex ratio prior to infant independence. Stillbirths are difficult to document on Cayo Santiago and unusual at Sabana Seca. During the 5-year study, 12 stillbirths were recorded in group M, with sex of the deceased known in 9 cases. Twice as many female fetuses were stillborn as male fetuses, but the difference was not statistically significant (binomial test: $x=3$, $P=0.51$). Between 1989 and 1995, infant survivorship to 6 months of age in group M was comparable for males and females ($\chi^2=0.55$, $df=1$, $P=0.46$). Infant mortality among young primiparous females (32%) was higher than among older females (19%), but the difference was not statistically significant ($\chi^2=1.58$, $df=1$, $P=0.21$). Almost half (5/11) the sons of primiparous females did not survive the first 6 months of life, while only 12% (1/8) of daughters succumbed during this period (Fisher exact $P=0.18$). Among the rhesus macaques on Cayo Santiago, 3-year-old females who raised their sons to 1 year of age were significantly more likely to fail to reproduce when 4 years of age than were 3-year-old females who raised daughters ($\chi^2=5.99$, $df=1$, $P=0.01$). Only 23% (3/13) of young primiparous females raising daughters forfeited the following birth season, while 69% (11/16) of young primiparous females rearing sons sacrificed the subsequent birth season.

**Table 1** The influence of female age on the secondary sex ratio. Values in each cell are the number of live births of each sex. Young females are 3–7 years of age; prime females are 8–11 years of age; old females are ≥12 years of age. Data for group M were collected between 1991 and 1995 ($\chi^2=1.39$, $df=2$, $P=0.50$), while data from group R were collected between 1993 and 1995 ($\chi^2=3.14$, $df=2$, $P=0.21$).

| | Male | Female | Total |
|---|---|---|---|
| Group M | | | |
| Young | 44 | 30 | 74 |
| Prime | 35 | 27 | 62 |
| Old | 12 | 14 | 26 |
| Total | 91 | 71 | 162 |
| Group R | | | |
| Young | 36 | 21 | 57 |
| Prime | 17 | 13 | 30 |
| Old | 13 | 17 | 30 |
| Total | 66 | 51 | 117 |

## Infant size and growth trajectories

Males weigh significantly more than females at birth (paired $t=-2.871$, $df=7$, $P=0.02$; Table 2), with relative female mass decreasing to 92% of male mass by 1 year of age (2.90±0.39 vs 2.68±0.29 kg; $t=2.937$, $df=95$, $P=0.004$). At 1 year of age, first-born males weigh the same as later-born males ($t=0.457$, $df=46$, $P=0.65$), a pattern identical to that of females ($t=-0.091$, $df=47$, $P=0.93$). By 1 year of age, males achieve 34%, and females 31%, the mass of fully adult females. Maternal preconception weight is predictive of weight of progeny at 1 year of age ($r=0.289$, $n=97$, $P=0.004$).

At 1 year of age, high-ranking males weighed significantly more than lower-ranking peers (Fig. 1; ANOVA: $F_{2,8}=4.823$, $P=0.04$), but, unlike their brothers, relative dominance rank among 1-year-old females was not associated with differences in weight (ANOVA: $F_{2,5}=0.181$, $P=0.84$). Among males, weight at 1 year of age was correlated with weight at 6 years of age ($r=0.665$, $n=11$, $P=0.029$), i.e., when a young adult, as well as being strongly predictive of weight at 8 years of age (Fig. 2), i.e., when body mass achieves an asymptote (Bercovitch and Goy 1990). On the other hand, female weight at 1 year of age was not associated with weight at either 3 years of age ($r=0.260$, $n=15$, $P=0.35$), i.e., immediately prior to the first mating season, or at 6 years of age ($r=0.184$, $n=15$, P=0.51), i.e., when adult body weight is attained (Bercovitch and Goy 1990).

**Table 2** Sex differences in birth weight (g) among rhesus macaques

| | Male | Female | Female/male ratio (%) | Reference |
|---|---|---|---|---|
| | 490 | 465 | 95 | van Wagenen and Catchpole (1956) |
| | 513 | 465 | 91 | Broadhurst and Jinks (1965) |
| | 480 | 460 | 96 | Roonwal and Mohnot (1977) |
| | 485 | 475 | 98 | DiGiacomo et al. (1978) |
| | 500 | 466 | 93 | Martin (1984) |
| | 480 | 450 | 94 | Small and Smith (1986) |
| | 486 | 470 | 97 | Silk et al. (1993) |
| | 453 | 473 | 104 | Bowman and Lee (1995) |
| Average | 486 | 466 | 96 | |

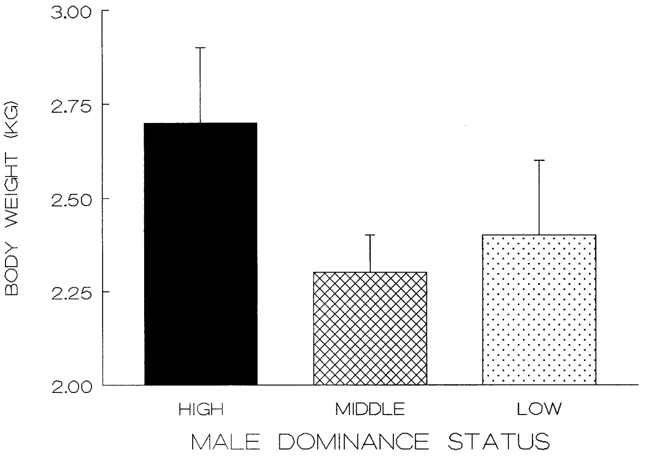

**Fig. 1** The influence of dominance rank on male mass at 1 year of age among subjects in group M. Histogram plots the mean+SD

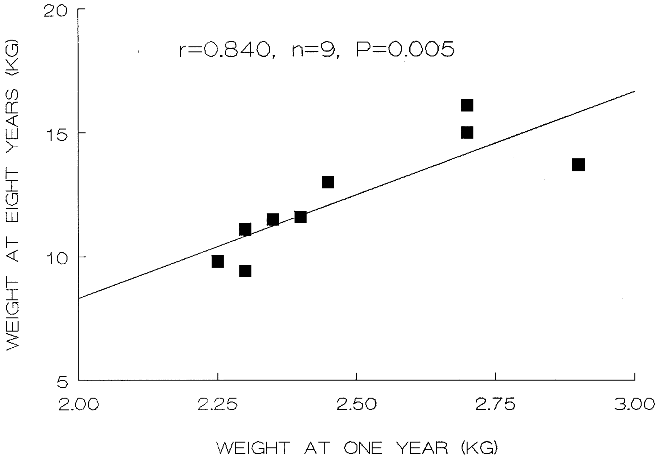

**Fig. 2** The relationship between male weight at 1 year of age and weight at 8 years of age in group M

## Body condition and reproductive output

Although females who conceived at 3 years of age weighed significantly more than barren peers ($t$=–5.201, $df$=34, $P$<0.001), weight at 3 years was unrelated to weight at 1 year of age, indicating that female body weight at the end of the period of maternal investment is an invalid indicator of age at first reproduction. On the other hand, male weight at 1 year of age was significantly correlated with number of offspring sired by 6 years of age in group M ($r$=0.702, $n$=11, $P$=0.02). Whether a son's mother was deceased or not by the time he arrived at his 6th birthday had no impact on his chances of siring offspring by young adulthood (Fisher exact $P$=1.00). One male who was orphaned at 2.83 years of age sired his first offspring when 5 years old.

In group M, weight of high-ranking 6-year-old males was significantly greater than that of their peers (ANOVA: $F_{2,11=}$9.203, $P$=0.004) and high-ranking males sired more offspring than their peers by 6 years of age (ANOVA: $F_{2,11}$=37.271, $P$<0.001). The BMI at 6 years of age differed between sires and non-sires ($t$=3.194, $df$=6, P=0.02) and was significantly correlated with number of progeny produced by 6 years of age ($r$=0.815, $n$=8, $P$=0.01). The BMI of high-ranking 6-year-olds (37.3±2.3) was about 20% greater than that of middle- (31.5±2.8) or low- (30.8±2.3) ranking peers (ANOVA: $F_{2,5=}$2.341, $P$=0.19). In group M, annual progeny output by males was a function of both body weight ($r$=0.493, $n$=21, $P$=0.02) and fat level ($r$=0.438, $n$=21, $P$=0.05; see Bercovitch and Nürnberg 1996).

In group R, only one individual was identified as a definite sire by 6 years of age, and none at an earlier age. He was responsible for siring 3 of the 48 offspring born in the 1995 birth season. The sole sire by 6 years of age was the highest-ranking male in his cohort, as well as the heaviest (11.50 vs 9.27±1.24 kg; $n$=6 peers). High dominance rank corresponded with both greater BMI ($t$=–2.850, $df$=5, $P$=0.04) and more fat ($t$=–2.988, $df$=5, $P$=0.03).

Combining cross-sectional and longitudinal data from both localities provides a crude, quantitative estimate of the role of maternal mass on son's reproductive success. Maternal preconception mass explained about 8% of the variance in offspring weight at 1 year of age, male weight at 1 year accounted for about 71% of the variance in adult weight, and adult weight was associated with about 25% of the variance in number of progeny produced. Therefore, maternal mass furnished less than 1.5% to the variance in sons' reproductive output. This value is probably overestimated because data are insufficient for using multiple regression analysis to compute partial $R^2$ values (see Sokal and Rohlf 1995).

## Sex differences in variance in reproductive success

Female rhesus macaques rarely bear more than a single offspring during the birth season, so annual reproductive output of females ranges from 0 to 1. On the other hand, annual reproductive output of males ranged from 0 to 11 in group M and from 0 to 7 in group R. Variance in per annum actual reproductive output of males in group M was threefold greater than that of females during the 5-year study (mean±SD of male:female coefficient of variation=3.0±0.9; Fig. 3a). In group R, male variance in annual progeny production across the 3-year study was fourfold higher than female variance (Fig. 3b).

Variance in lifetime reproductive success among males is unknown at both sites. Over the 5 year study in group M, males produced between 0 and 26 offspring. The five most productive males sired an average of 18.2 (±6.9) offspring during the 5-year study. During the 3-year investigation of group R, the most successful male sired a minimum of 12 offspring, while the least successful males sired no offspring. Among the rhesus macaques on Cayo Santiago, 30 years of longitudinal data revealed that lifetime reproductive success of females ranges from 0 to 14 progeny, with an average of

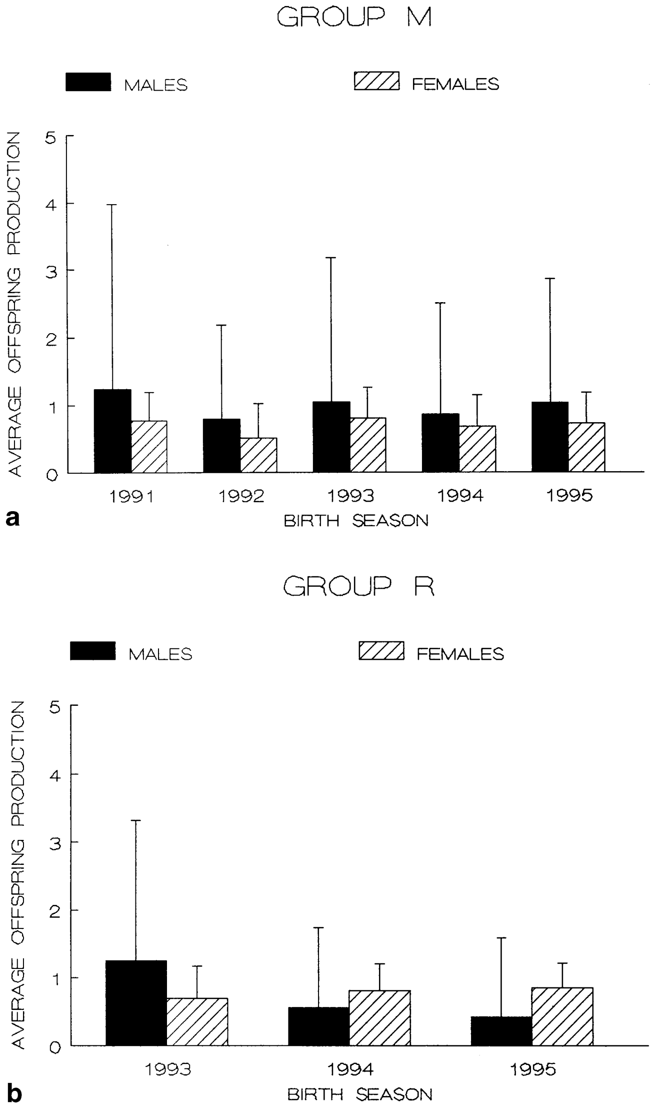

**Fig. 3a,b** Mean+SD in annual reproductive output of males and females in the two study groups. Male reproductive success is based upon genetic analysis of paternity (see Methods). Coefficients of variation for group M are: 1991 M=221%, F=55%; 1992 M=173%, F=99%; 1993 M=205%, F=56%; 1994 M=190%, F=69%; 1995 M=177%, F=62%. Coefficients of variation for group R are: 1993 M=166%, F=69%; 1994 M=211%, F=48%; 1995 M=279%, F=42%

about 4 offspring surviving to the age of reproduction (Bercovitch and Berard 1993). These data imply that sex differences in variance in lifetime reproductive success among males will be higher than among females.

## Discussion

Throughout their lives, male rhesus macaques are heavier than females. Females weigh 96% as much as males at birth, 92% when 1 year of age, and 78% when fully grown (8.6 vs 11.0 kg; see Rawlins et al. 1984; Schwartz and Kemnitz 1992; F.B. Bercovitch, unpublished data). Sex differences in length of gestation are absent (DiGiacomo and Shaughnessey 1972; Silk et al. 1993) and birth weight correlates with maternal weight (DiGiacomo and Shaughnessy 1972; Bowman and Lee 1995). Among males, those who are heavy at birth and grow rapidly have the highest survivorship rate, while among females, those huddling the norm at birth have the highest survivorship prospects (Small and Smith 1986). Mother's social status impacts son's, but not daughter's, weight at 1 year of age, and male, but not female, body weight at the end of the period of maternal investment is a reliable predictor of adult body weight. While male mass has an impact on progeny production, neither body size nor fat levels are related to fertility differences among adult female rhesus macaques on Cayo Santiago (Berman 1988). We suggest that maternal mass contributes to variation in son's reproductive success and that maternal investment in rhesus macaques is partitioned according to expected reproductive returns. However, we conclude that sex-biased maternal investment is limited and that male social skills supersede the degree of maternal investment as determinants of lifetime reproductive success.

### Sex-biased maternal investment or sex differences in metabolic efficiency?

The strongest evidence in support of the metabolic-efficiency model for rhesus macaques is the finding that sex differences in suckling behavior are absent (Gomendio 1990, 1995), but sex differences in growth rates are present. However, suckling frequency and duration could provide misleading cues regarding levels of maternal investment if milk intake is affected by offspring suckling force, milk compostion, and milk yield of mothers (Cameron 1998). For example, male fallow deer, *Dama dama*, fawns grow faster than female fawns, despite an absence of sex differences in suckling time, because more intense suckling by males triggers a greater milk yield per unit time (Birgersson et al. 1998). Data on potential sex differences in nutritional intake among rhesus macaques while suckling are unavailable.

The metabolic-efficiency model would not predict delayed reconception due to patterns of male infant growth rates because such rates are deemed to be independent of extraction of extra maternal resources that postpone resumption of cycling. However, among the rhesus macaques at the Yerkes Primate Center, Wilson et al. (1983) reported that 86% of primiparous rhesus macaques failed to conceive the subsequent year if they successfully raised sons, and we found the same pattern among 70% of primiparous females. Multiparous females on Cayo Santiago are also more likely to forfeit a year of reproduction if they successfully rear sons (Berman 1988). In rhesus macaques, the accelerated growth rate of infant males, combined with an increased likelihood of sacrificing a year of reproduction to nurture a male, especially among primiparous females, suggests that maternal investment in sons exceeds that in daughters and that sex-biased growth rates are not dependent on sex differences in infant metabolic efficiency (see also Small and Smith 1986).

Among rhesus macaques, the conclusion that maternal investment in sons is greater than in daughters can be questioned based upon findings from the Madingley colony indicating a greater likelihood of delayed subsequent conception when daughters are reared (Simpson et al. 1981). However, this is the sole site where the birth weight of females is greater than that of males (see Table 2). The social groups at Madingley are tiny, consisting of a single adult male, two to four adult females, and their offspring (Berman 1980; Simpson et al. 1981; Nevison et al. 1996), while those at Cayo Santiago are quite large, between 50 and 300, and multimale in composition. The results from Madingley have often been adopted as the model for maternal investment in rhesus macaques, but the original report suggests caution in interpretation because the pattern might be due to the „special conditions in captive colonies“ (Simpson et al. 1981). The small male infants at Madingley are unlikely to extract substantial maternal resources, which result in fitness costs, while the small matrilines and captive conditions might be factors that affect the sex ratio and maternal investment differently than in more natural settings (Rawlins and Kessler 1986c; see also Nevison et al. 1996).

Maternal investment patterns in primates vary with resource availability, maternal rank, mortality risk, maternal and offspring condition, parity, infant growth rate, birth order, and age (Lee 1984; Johnson and Southwick 1987; Hauser 1988; Hauser and Fairbanks 1988; Berman 1992; Fairbanks and McGuire 1995), which complicates detecting universal patterns. For example, in toque macaques, *M. sinica*, the extent of resource competition regulates the relationship between maternal condition and dominance rank, generating a situation where variation in secondary sex ratio is a function of socioecological surroundings (Dittus 1998; see also Myers 1978). Among Barbary macaques, *M. sylvanus*, infant sex had no effect on interbirth intervals among dominant females, but raising of a daughter by subordinate females tended to postpone subsequent breeding (Paul and Kuester 1990). Both nutritional and social status influence reproductive processes by mediating metabolic profiles regulating reproductive endocrinology (Bercovitch and Strum 1993; Bercovitch 1997). Flexibility in distributing maternal nutritional and social support to offspring as a function of dominance rank and body condition probably maximizes reproductive returns on investment.

Although the preconception weight of females did not influence the sex of progeny, maternal mass added during pregnancy could be a function of fetal sex. Passive diffusion of fetal hormones through the placenta can inform the mother of the sex of the occupant of the womb. Upon receiving signals that she is carrying a male, her body might adjust its metabolism and fat storage to prepare for nursing a son. Prenatal androgen injections to pregnant female rhesus macaques cross the placenta and influence both the behavior and morphology of their daughters (Goy et al. 1988). Fetal testosterone commences circulation by 40–50 days in rhesus macaques (Resko and Ellinwood 1981). Fetal androgens could enter the maternal circulation and modify maternal adiposity because testosterone is the precursor to estrogen, which encourages adipose tissue deposition (Norman and Litwack 1997). Fetal manipulation of maternal physiology could provide a mechansim to reduce the relative energetic costs of nurturing sons. Fat accumulation during late gestation is a mechanism minimizing the energetic costs of lactation.

In summary, sexual size dimorphism among infant rhesus macaques probably accrues from differential levels of maternal investment more than from sex differences in metabolic efficiency. Energetic costs imposed by nurturing sons translate into fitness costs, but abundant resources can probably ameliorate reproductive costs. We suggest that the costs of reproduction will be most substantial among young, primiparous female mammals, especially those who initate their reproductive careers prior to attaining adult body size. Primiparous females seem to be less efficient at channeling resources to offspring than are multiparous females (Künkele and Kenagy 1997), and therefore have the highest likelihood of sustaining the greatest investment costs in raising sons.

## Costs and consequences of raising sons and daughters

Cercopithecine social structure has been reasoned to influence sex-biased maternal investment in opposite directions. Female philopatry could favor investment in daughters, due to factors favoring recruitment of kin in the formation of alliances designed to enhance reproductive output, or it could favor investment in sons, due to factors intensifying food competition in the non-dispersing sex, which could impinge upon reproductive maturation and output (see Silk 1983, 1988; Johnson 1988; van Schaik and Hrdy 1991; Hiraiwa-Hasegawa 1993; Nevison et al. 1996). Both scenarios assume that maternal-rank effects on son’s reproductive success are diminished, due to natal dispersal of males.

Natal dispersal by high-ranking male rhesus macaques occurs at later ages than natal dispersal by low-ranking peers (Koford 1963; Colvin 1986). The copulatory behavior of male rhesus macaques follows an arch-shaped trajectory which peaks during the 2nd to 3rd year of residency in a non-natal troop or when 6–8 years of age in a natal troop (Berard 1999). Production of progeny by high-ranking young adult males in their natal troop may be more common than often assumed. Genetic analysis of paternity has revealed that sons of high-rank female rhesus macaques (Smith and Smith 1988; this study) and Barbary macaques (Paul and Kuester 1996) have a greater reproductive output in their natal troop than sons of low-rank females. Copulatory behavior by natal adult males in their birth troop occurs among a variety of wild primates (e.g., Packer 1979; De Ruiter et al. 1992; Pope 1992; Alberts and Altmann 1995a), and evidence for probable sirehood by high-ranking, natal males emerges from a number of studies of savanna baboons across Africa (Packer 1979; Smuts 1985; Bulger and Hamilton 1988; Altmann et al. 1996). In some mammals, genetic analysis has revealed that non-dispersing males sire offspring in their natal groups (Stockley et al. 1993; Keane et al. 1994; Hoogland 1995). If maternal investment in sons raises prospects for reproduction prior to natal departure, then male cercopithecine life history patterns raise an evolutionary irony: delayed dispersal is associated with *postponement* in the age at first reproduction among cooperative breeding species (e.g., Koenig et al. 1992; Solomon and French 1997), but can be associated with *accelerated* age at first reproduction among males residing in multimale social systems.

Maternal rank effects on sons' progeny production could also function subsequent to natal dispersal. Sons of dominant female Barbary macaques are more likely to sire progeny in non-natal troops than are sons of subordinate females (Paul et al. 1992). The sons of high-ranking female macaques have an increased chance of attaining dominance status in non-natal troops compared to sons of low-ranking female macaques (Walters and Seyfarth 1987; van Noordwijk and van Schaik 1999). Maternal rank could influence development of social skills among males, with experience as the son of a high-rank female enabling males to more rapidly integrate into new troops.

Finally, even in male dispersal species, maternal rank effects could mediate sons' reproduction if male survivorship to independence is a consequence of dominance rank. If, on average, sons of high-rank females have increased survivorship prospects compared to sons of low-rank females during the dependent period, then their reproductive value will be greater at the end of the period of parental expenditure. One component of reproductive value is age-specific survivorship, i.e., $l_x$, from age $x$ to $x$+1 (see Fisher 1930), which is usually assumed to be equal for all members of the same sex, but this need not be the case. Altmann et al. (1988) found that sons of low-rank female baboons had increased survivorship prospects, while Wasser and Norton (1993) uncovered the opposite pattern. Among semi-free-ranging rhesus macaques, Meikle and Vessey (1988) found that sons of high-rank females experienced increased survivorship during the 1st year of life. Because the underlying premise of parental adjustment in expenditure in offspring is based upon statistical averages, one would expect greater investment by high-rank females in sons if, on average, their sons had an increased chance of surviving the dependent period. Sons of high-ranking female rhesus macaques (Bercovitch 1993; Dixson and Nevison 1997) and savanna baboons (Alberts and Altmann 1995b) exhibit accelerated reproductive maturation, while immature sons of high-rank Japanese macaques, *M. fuscata*, are heavier than their peers (Mori 1979). Mothers might invest more in sons than in daughters in trying to ensure that they achieve an early high growth trajectory (Dunbar 1988), enabling them to capitalize on reproductive opportunities prior to their peers.

In summary, social systems characterized by natal male departure do not necessarily diminish the impact of maternal rank on sons' progeny production *when* dominance status influences morphological and social development germane to reproductive success. Body size and dominance status in non-human primates modulate male fitness, but their leverage is shackled by demographic, social, and ecological restraints (Bercovitch 1991, 1997; Strum 1994; Hamilton and McNutt 1997). Body size plays a role in male-male competition, but it operates in conjunction with social strategies to influence male reproductive succes (Bercovitch 1989, 1991; Clutton-Brock 1991, 1994; Strum 1994; Hamilton and McNutt 1997). Under these types of conditions, maternal investment in augmenting sons' body size is not expected to be overwhelming, but is not expected to be absent. Body size among male primates varies with local resource availability (Bercovitch 1989; Dunbar 1990; Strum 1994), and differences in male capability and efficiency to accumulate fat reserves prior to the mating season influence male reproductive success (Bercovitch 1997). Progeny production by male primates is much more dependent upon socioecological conditions, demographic factors, and social strategies than upon attributes such as body size (Bercovitch 1991; Clutton-Brock 1994; Strum 1994; Alberts and Altmann 1995b). Maternal investment in sons is a „bet-hedging“ strategy designed for remunerating reproductive success with little extra effort. When maternal investment has a limited impact on traits responsible for sex differences in variation in reproductive success, one does not expect large sex biases in maternal investment patterns.

In conclusion, maternal investment by rhesus macaques in sons is slightly greater than in daughters, with infant male body size exerting an impact on future reproductive success. However, the value of large sex biases in investment is diminished because the influence of body size on sons' reproductive success is constrained by ecological, social, and demographic forces. Parents are unable to dictate the reproductive destiny of offspring, but can provide a foundation that attempts to maximize the return on investment. At some point in the life cycle, offspring will be more responsible than their mothers for embracing a reproductive route that incorprates strategies to maximize fitness. Social skills involved in reproduction are likely to supersede the degree of maternal investment as determinants of progeny production in many primate species.

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