

# First-time macaque mothers bias milk composition in favor of sons

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Mammalian females invest heavily in each of their offspring, but little is known about the magnitude and sources of variation in the most energetically expensive form of maternal investment; milk production [1–5]. Investment strategies may change as females mature because females often begin to reproduce before they have completed their own growth [5]. Milk production may also be an important mechanism for sex-biased investment [5,6]. Here, I present data from 106 rhesus macaque (*Macaca mulatta*) mothers which show that primiparous mothers produce richer milk for sons than daughters, above a general sex bias among all mothers. This difference seems to reflect the tradeoffs between the benefits derived from additional investment in sons and the costs of diverting energy from maternal growth and development.

Milk samples were collected once during peak lactation from subjects of known age and social rank housed in large outdoor enclosures at the California National Primate Research Center (CNPRC). Analyses of milk constituents were conducted in the Nutrition Laboratory at the Smithsonian National Zoological Park and gross energy (GE) calculated using standard methods [3]. Milk variables were log transformed to achieve symmetry and stabilize variance and data were analyzed by ANCOVA, multiple regression and Chi-Square; significance accepted at  $p \leq 0.05$  and estimated effects and standard errors are presented on the log scale.

As found in red deer [2], there was a significant main effect of

infant sex on milk GE (estimated effect = 0.06, SE = 0.02,  $p = 0.002$ , Table 1); however, an interaction effect between parity and sex revealed that sons born to primiparous mothers (PM) get an additional gain in GE (estimated effect = 0.06, SE = 0.02,  $p = 0.007$ ). Similarly, sons received higher fat concentration in milk (estimated effect = 0.05, SE = 0.01,  $p = 0.002$ ) with an interaction between parity and sex (estimated effect = 0.04, SE = 0.01,  $p = 0.008$ ). Although there was no main effect for sex in protein concentration, an interaction effect between sex and parity showed that sons of PM received significantly higher protein concentration than all other groups (estimated effect = 0.02, SE < 0.01,  $p = 0.03$ ). Sugar is negatively correlated with fat in milk and therefore there was a main effect of sex; sons received milk with lower sugar concentration (estimated effect = -0.004, SE = 0.002,  $p = 0.043$ ). Maternal weight, BMI and social rank were not associated with milk composition or infant sex in this study.

At 3–4 months of age, infant weight showed a main effect for sex (estimated effect = 0.05, SE = 0.01,  $p < 0.001$ ), but not parity; sons of PM did not differ significantly in weight from sons and daughters of MM; however, daughters of PM weighed significantly less than the other three groups ( $p < 0.05$ , Figure 1). Milk production was associated with infant weight after controlling for infant age and maternal weight; there was a

main effect of milk gross energy (slope = 0.15, SE = 0.07,  $p = 0.04$ ) and milk yield (slope = 0.11, SE = 0.03,  $p = 0.001$ ) on infant weight.

Infants of PM represent a higher reproductive cost relative to maternal body size than offspring of MM. There are main effects of both infant sex and parity on infant size relative to maternal size (sex estimated effect = 0.81, SE = 0.25,  $p = 0.001$ , parity estimated effect = 1.25, SE = 0.26,  $p < 0.0001$ ). ANCOVA revealed that sons of PM weighed 15% of maternal body weight at 3–4 months of age, significantly higher than other groups ( $p < 0.05$ ), whereas daughters of MM weighed 11% of maternal weight; significantly less than the other three groups ( $p < 0.05$ ), daughters of PM and sons of MM are intermediate and weigh 13% and 12% of maternal body weight, respectively.

Given these data, it may be difficult for PM rearing sons to sustain the high costs of lactation. Colony records from 1973–2006 show an unbiased birth sex ratio for primiparous mothers (48.53% male,  $z = -1.21$ , 95% CI = 0.46–0.51,  $N = 1706$ ,  $p = 0.226$ ), but first-born sons are 1.6 times more likely to die post-natally than first-born daughters ( $\chi^2 = 10.34$ , 95% CI = 0.08–0.37,  $N = 1329$ ,  $p = 0.001$ ). If this reflects higher male vulnerability overall [7,8], then similar sex biases in mortality should be observed among the offspring of fully-grown prime-age females. However, this was not the case ( $\chi^2 = 0.66$ , 95% CI = -0.5–0.36,  $N = 756$ ,  $p = 0.418$ ).

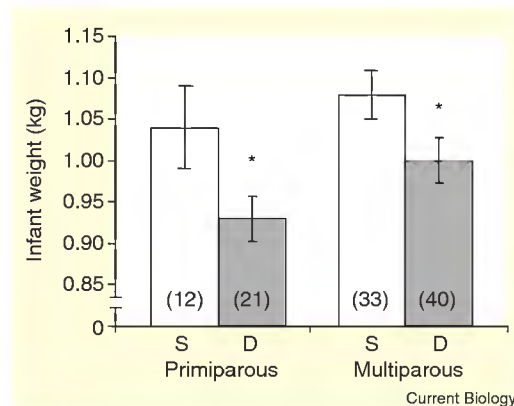


Figure 1. Mean ( $\pm$  SEM) infant weight (kg) at 3–4 months of age. Infant weight showed a main effect for sex (estimated effect = 0.05, SE = 0.01,  $p < 0.001$ ), but not parity; sons of PM did not differ significantly from sons and daughters of MM; however, daughters of PM weighed significantly less than the other three groups (asterisk:  $p < 0.05$ ).

Table 1. Summary statistics.

Milk Mean±SE	Primiparous mothers		Multiparous mothers		Effects
	S	D	S	D	Main/Interaction
Gross Energy (kcal/g)	1.14±0.07	0.90±0.03	1.00±0.03	0.98±0.03	sex <sup>2</sup> , sex x parity <sup>2</sup>
Fat (%)	7.7±0.75	5.3±0.4	6.5±0.4	6.2±0.3	sex <sup>2</sup> , sex x parity <sup>2</sup>
Protein (%)	2.5±0.16	2.2±0.08	2.1±0.05	2.1±0.07	sex x parity <sup>1</sup>
Sugar (%)	7.3±0.12	7.5±0.06	7.4±0.07	7.4±0.06	sex <sup>1</sup>

The table shows the raw data summary statistics for milk gross energy (kcal/g±SE) and fat, protein, and sugar concentrations (%±SE) for sons (S) and daughters (D) of primiparous and multiparous mothers. Statistical analysis was conducted after log transformation of milk variables and the results of the tests are denoted in the final column. <sup>1</sup>p < 0.05; <sup>2</sup>p < 0.01

These results suggest that sons of primiparous females are vulnerable because their mothers are less able to sustain the high costs of rearing them.

In polygynous species, like macaques, male reproductive output is highly skewed, and heavier males are at an advantage over smaller males [5,6,9,10]. In contrast, female macaques inherit their rank from their mothers [5,6], and differences in size among adult females have relatively little impact on reproductive success. If the incremental effects of additional investment have a greater impact on the growth and subsequent reproductive success of one sex than the other, then mothers are expected to direct additional resources to the sex that benefits most [6]. These tradeoffs may be muted in well-fed captive animals that are released from energetic constraints, but the lactation strategies of primiparous females, who are still growing themselves, bring these tradeoffs into sharp relief.

#### Supplemental data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/17/22/R958/DC1>

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## The heritability of attractiveness

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Sexual selection is responsible for the evolution of numerous conspicuous and extravagant displays observed in nature — from cricket choruses to peacock's tails. A key assumption of many models of sexual selection is that attractive males father attractive sons<sup>1</sup>. However, while particular traits under sexual selection have been shown to be heritable [1,2], the evidence for the heritability of attractiveness *per se* is far less compelling [1,3]. This dearth of information has led to disagreement about the existence and importance of this fundamental link between sire and sons' attractiveness [4]. Here we demonstrate in *Drosophila simulans* that attractive fathers sire attractive sons, as assumed by theory.

That attractive males father attractive sons is assumed by many sexual selection models; both by models based on genetic benefits — whereby females gain fitness benefits through their offspring — and by models based on sexual conflict — whereby attractive males are manipulating females for male benefit irrespective of the fitness consequences for females. This crucial link has been convincingly established in guppies [5] and sticklebacks [6], but in general, there is a lack of evidence for this fundamental genetic association [1,3]. We, therefore, investigated the heritability of male attractiveness in *Drosophila simulans* using a full-sib/half-sib design. Briefly, 68 sires were each mated to 2–3 dams (n = 185) and we assessed the attractiveness of a total of 527 sons (mean per dam = 2.85). The sons from each dam were collected as virgins at emergence and housed together for three days before being placed into individual mating vials with a three day-old virgin female (one male and one female per vial)