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Short-term consequences of different breeding histories for captive rhesus macaque mothers and young

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Summary. Life histories of rhesus monkey mothers (*Macaca mulatta*) were classified in terms of (1) whether the mothers were top ranking or not, (2) gave birth to more daughters than sons or vice versa, and (3) gave birth at intervals of one year or of more than a year. Bearing daughters at intervals of more than a year was the most common history among top ranking mothers, while bearing sons annually was most common among other mothers. The consequences for the infants and mothers of such histories were examined and (1) infants were more likely to die as neonates if they had an older sister, especially if the sister had been born in the previous birth season; (2) dyads with daughters received more aggression from other adults in the daughter's first year, but not necessarily through the year following the birth of the next infant; (3) when mothers of daughters gave birth of the next infant after at least one fallow year, their daughters directed considerable amounts of harassing aggression to their next-born sibling; and (4) mothers of sons but not of daughters delayed longer when they received more aggression from other adults.

We discuss the views that birth sex ratios may be affected by a mother's rank rather than how often she is involved in aggressive encounters with other adults; and that in top-ranking mothers, birth intervals may be controlled more by the infant's sex than aggression the family received. Fitting the data into a life history strategy model is done as a provisional and speculative exercise.

Introduction

Breeding data from the Madingley colony of captive one-male groups of rhesus macaques have shown that mothers gave birth to more daughters than sons if top ranking, and to more sons than daughters if not top-ranking (Simpson and Simpson 1982). Mothers were also slower to breed again after bearing dauthers than after bearing sons (Simpson 1983; Simpson et al. 1981). In this paper we consider the consequences of different breeding histories of mothers through the births of two consecutive infants, up to the end of the second infant's first year.

Birth sex ratios skewed towards females for high ranking mothers and to males for low ranking were also found by Altmann (1980) in free ranging yellow baboons. In captive bonnet macaques, Silk (1983) found that low ranking mothers gave birth to more males than females, although mothers from the top half of the hierarchy did not produce more daughters than sons. Meikle et al. (1984) reported a non-significant trend towards producing more daughters than sons in top ranking females or "matriarchs" within genealogies, but in comparisons *between* genealogies found that females in genealogies ranking higher than mid-rank within a large group produced more daughters than sons. Our results could be reconciled with those of Meikle et al. (1984) if our small one-male groups were regarded as comparable to high ranking genealogies who are never defeated by other genealogies visible to them in adjacent runs, and our top ranking mothers are equivalent to "matriarchs".

In explaining biased sex ratios in functional terms, their consequences may be invoked (Altmann 1980; Clutton Brock and Albon 1982; Simpson and Simpson 1982; Silk 1983; Meikle et al. 1984). Meikle et al. (1984) have contrasted two models. Their data support a model derived from Trivers and Willard (1973) where mothers in high ranking genealogies can invest much in offspring, and invest in sons who repay the highest levels of investment most effectively. Meikle et al.'s data (1984) cannot support a local resource competition model (e.g. Silk 1983), which states that daughters receive more benefit from high maternal rank, because they are better protected as infants and ultimately inherit their mother's ranks.

Testing both theories requires data and inferences about long-term consequences for the mothers, ideally in terms of the reproductive success of their offspring. In deciding which theory applies to a particular group, data about short-term consequences can also be used and in this paper we consider neonatal deaths, and aggression received by a mother and infant from other adults and from other young, including her own older infants, as potential costs of particular kinds of breeding history. We show that mothers' histories, described in terms of the sexes of their offspring and whether they are spaced annually or at longer intervals, tend to be appropriate to their ranks, and to minimise the effects of aggression received from other adults.

Methods

Colony conditions. The subjects were rhesus macaques, living in 6 social groups, each having 2 to 5 adult females (at least 4y) and their young, and one fully adult male (at least 5y). Families were kept in their original groups so far as possible. The colony had 6 separate outdoor runs each connected with its own indoor room, which was provided with background heat. All colony members could hear, see and smell each other. In 1982 a new colony was formed, using young adults and young from the previous colony (Anderson and Simpson 1979) together with a few imported animals. Its runs were similar to but larger than those of the original colony.

Rank. Top-ranking mothers dominated all other females in their groups, while non-top mothers could be dominated by at least one female. Some non-top mothers were medium ranking (Figs. 2 and 3) and able to dominate at least one lower-ranking female. Evidence of dominance was provided by attacking, supplanting, avoiding, fear-grinning and presenting in non-sexual contexts. In any pair, one mother was regarded as dominant to the other if their aggressive actions occurred in one direction only. If aggressive actions were exchanged, the mother who gave at least three times more than she received was regarded as dominant. If no aggressive acts occurred between two individuals, they were deemed to be equal in rank unless data were available about their aggressive relationships with a common third individual.

Birth interval data. Birth interval data use births after 1972, when we no longer did experiments involving frequent removal of mothers and infants from their social groups (Anderson and Simpson 1979; Simpson et al. 1981). Thereafter mothers were excluded if temporary removal from their group (for health reasons) could have interfered with their access to adult males when they were in estrus.

Births in the old colony since the analyses in Simpson et al. (1981) are included in this paper.

Sex ratio data. Sex ratio data came from all mothers living in social groups after 1959 and having known dominance ranks at the time of conception (see also Simpson and Simpson 1982).

Neonatal deaths. Neonatal deaths (1959–1980) include stillbirths and infants dying within 2 weeks occurring in the social groups in 1959-1980, and exclude miscarriages. Here we do not consider the rarer cases of deaths of older infants, most of which were difficult to interpret because they occurred when the colony was less settled (Anderson and Simpson 1979) and when mothers and/or their infants were being experimentally separated from each other and from their social groups.

Primiparous mothers were excluded from the analysis of neonatal deaths because their relative inexperience (Hooley and Simpson 1981) was seen as making them especially likely to lose neonates, and because of potentially confounding effects (Ruppenthal et al. 1976) of primiparae's initial experience with male infants. (In the present study 4/16 male and 1/8 female neonates were lost by primiparae).

Aggression received. Data on aggression and harassment received by mothers and young were taken between 1972 and 1978.

Aggression received by mothers from other adults was a composite category. In each hour of observation a mother scored 1 only for 1 or more occurrences of the categories "supplant", "threaten" or "chase" received from one companion, and "fear grin", "avoid" or "non-sexual present" directed at a companion. At least six hours of observation were used at each age of the infant (Figs. 2 and 3). This "one-zero" scoring method (used with 1 h intervals here) is discussed by Simpson 1979; Simpson and Simpson 1977; and Altmann 1974).

Harassment received by the mother and infant from *other young* was relatively rare and was counted during at least 16 h observation through the infant's first 16 weeks of life. Scores in Fig. 3 included episodes involving direct aggression from older siblings to the mother-infant dyad, and incidents judged to cause risk and/or distress to the infant. For example, a 2y sister took its mother's nipple out of its infant sister's mouth, the mother pulled the infant away, the infant squeaked, and the sister had a tantrum.

Statistics. Two-tailed statistical tests were taken from Siegel (1956). Ninety five per cent confidence limits for percentage measures were based on β-distributions expected of the ratios providing percentages and probabilities. (Phillips 1973, and Numerical Algorithm Group, NAG Central Office, Mayfield House, 256 Banbury Road, Oxford, OX2 7DE, and see Fig. 1).

Family terminology. Neonates were infants of 14 days or less, and infants were young up to one year old. Infants were classified according to sex, and also according to the sex of their closest aged older sibling. Mothers bearing infants and conceiving in the next birth season (Anderson and Simpson 1979) were called "quick", the others being "slow". Siblings born in the previous birth season were called yearlings and those born earlier were called older than yearling siblings. Infants whose mothers had been slow to conceive them had older than yearling closest siblings, while infants of "quick" mothers had yearling siblings. Some infants with yearling sibilings also had older than yearling siblings. All siblings considered in this paper were less than 4 years old.

Results

Table 1 sets out 8 possible histories of mothers bearing 2 successive infants, and the number of

Table 1. Eight histories of mothers who bear two successive infants

History	Mother's rank	Sex of older infant	Subsequent inter-birth interval	Cases
a	Top	♀	Slow	7[a]
b	Top	♀	Quick	2[a]
c	Top	♂	Slow	0
d	Top	♂	Quick	6
e	Non-top	♀	Slow	7[b]
f	Non-top	♀	Quick	7[b]
g	Non-top	♂	Slow	6
h	Non-top	♂	Quick	15

[a] Among Top mothers, those with daughters as the older of the two successive infants are more likely to be Slow, those with sons to be Quick ($P<0.02$, Fisher exact probability test)

[b] Among Non-top mothers, those with sons as older infants may be quick (NS, $\chi^2=0.86$). Among all mothers, those with sons as first infants are more likely to be quick ($P<0.05$, $\chi^2=4.14$). Top mothers are more likely to bear daughters, non-top mothers to bear sons (NS, $\chi^2=0.95$, but see Table 2 for the results from a larger sample)

Table 2. The numbers of female and male infants born to top-ranking and non-top-ranking mothers, including mothers in Table 1 (Birth Interval Sample), mothers bearing only one infant and/or bearing their last infant before the colony was renewed, and mothers who conceived their infants in the new colony

Maternal rank	Infant sex	Birth interval sample	New colony	Total sample
Top	Female	9	8	46
	Male	6	1	16[a]
Non Top	Female	14	2	34
	Male	21	4	58
	$n=$	50	15	154

[a] Birth sex ratio skewed to females in top-rank mothers and to males in non-top mothers ($\chi^2=19.11$, $P<0.001$, total sample)

actual cases of each history observed in our colony for the 50 mothers with all the relevant information. The most common history for top ranking mothers was history (a) – bearing a female infant, and being slow to bear the next infant. In contrast, top ranking mothers who bore sons were all quick to bear another infant (history (d)). The most common history (h) for non-top mothers was to bear a son, followed quickly by another infant.

Table 2 shows the relation of mother's rank to sex of infant at birth for a much larger sample than was available in Table 1. For the total sample, we can see that nearly 3 times as many female as male infants were born to top rank mothers while non-top rank mothers bore about two-thirds again as many males as females ($P<0.001$). In the new colony this sex ratio finding is confirmed: of 9 births to mothers who conceived their infant when they were top-ranking in their social groups, 8 were daughters ($P=0.022$, Binomial Test), while of 6 births to non-top mothers conceiving their infants in their social groups only 2 were daughters.

Interbirth intevals, shown roughly as "quick" and "slow" in Table 1 are set out in 3 months periods in Table 3 and Fig. 1 which also gives birth-to-conception intervals. Mothers were more likely to be "slow" to conceive after bearing daughters ($P<0.001$). This effect is seen in top-ranking mothers alone ($P<0.02$ in Histories a to d). Table 3 and Fig. 1 show that mothers of sons were especially likely to bear their next infant between 12 and 15 months later.

Consequences

Here we follow out some of the consequences for mothers who bear male or female infants, and go on to be slow or quick in bearing their next infants.

Neonatal deaths. Mothers lost more sons than daughters as neonates (NS, Table 4a), but the effect of the infant's sex on the next infant may have been more important. Thus infants with female closest older siblings were more likely to die as neonates than those with male closest older siblings ($P<0.05$, Table 4b). (More infants would be needed to analyse the effects of the neonate's sex as well as that of its sibling.) Among neonates with yearling siblings, the effect of having a sister was especially severe (Table 4c). Female neonates with yearling sisters were more likely to die as neonates than female neonates with yearling brothers ($P<0.01$) or with closest older than yearling sisters ($P<0.01$). For these reasons, daughters could be more costly to mothers in terms of their effects on the survival of their next neonatal siblings, especially when the mothers bear their next infant in the next birth season. Although direct violence to neonates was seldom seen, 6 of 8 older infants

Table 3. Birth-to-conception and interbirth intervals following the birth of a female or male infant. The numbers of cases falling into each 3-month period are shown[a]

Birth to conception interval (days):	105–197	197–288	288–379	379–471	471–562	562–653	>653	Row total	
Interbirth interval (months):	9–12	12–15	15–18	18–21	21–24	24–27	>27		
Sex of infant									
Male	2	7	2	2	4	1	5	23	*
Female	6	15	0	1	1	2	2	27	

[a] Each infant whose birth defined the start of a birth interval survived beyond the date when the next infant was conceived, or at least 30 months, whichever was the shorter. An interval from a birth to a next conception of 253 days (the median for the whole sample) will produce a median interbirth interval of 421 days if 168 days is regarded as the gestation period (from van Wagenen 1972). In this table the median interbirth interval of 421 days falls within the 12–15 month interval

[b] Birth intervals following the births of daughters were longer than those following the births of sons ($P < 0.001$, Median Test)

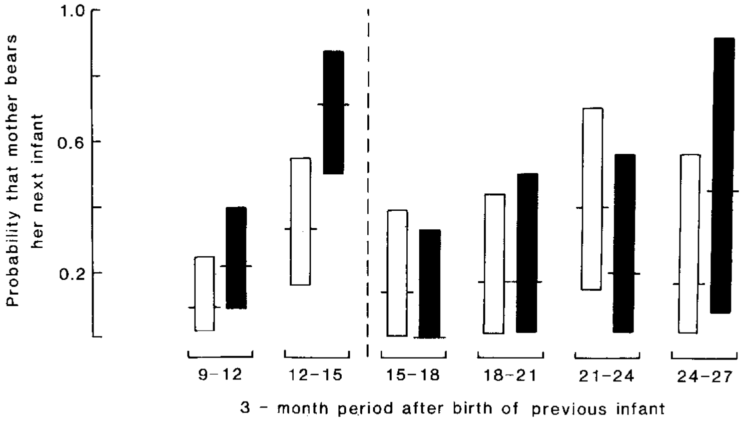

Fig. 1. For mothers of surviving daughters (*open bars*) and sons (*closed bars*), probabilities that the next infant will be born in the 3 month intervals shown, with 95% confidence intervals, based on data in Table 3. Thus, by the end of the 12th month after giving birth to sons, 21 mothers had not yet given birth, but 15 of these did so in the 12–15 month interval, making a probability of 15/21 (0.71) and suggesting that 95% of future comparable samples would produce probabilities between 0.52 and 0.89

who showed signs of harassment *post mortem* were female. It follows that bearing two daughters in successive birth seasons could be especially costly to mothers (Histories b and f in Table 1).

Aggression received by mothers from other adults. Mothers with infant daughters received more attacks, chases and threats from other adults than mothers with sons (Fig. 2). Fifteen of 17 mothers with 8 week-old female infants received at least one episode per hour, compared with 10 of 21 mothers with sons ($P < 0.02$, $X^2 = 5.88$). Figure 2 also shows the ranges of the four scores of aggression, taken through the infant's first year. In 11/17 mother-daughter pairs all 4 scores exceeded 1/6 h, compared with 7/21 mother-son pairs (NS, $\chi^2 = 2.56$).

Figure 2 suggests that being top-ranking reduced the levels of aggression received by some mother-infant dyads (e.g. JOS, CEL, NIM, EBE, DEN and ROM). But even top-ranking mothers with daughters received considerable amounts of aggression (LOL and AND).

The sex of the closest older sibling was not related to the amount of aggression received by mothers from other adults when their infant was 8 weeks old. Similarly, a gap between siblings of one year rather than two or more years did not necessarily increase the amount of aggression received, although one female infant whose female sibling had been born in the previous year had the highest score among female infants with female siblings.

Harrassment and aggression received from other young. Mothers with daughters did not receive more aggression from other young than mothers with sons. But sisters (♀>1y in Fig. 3) directed more aggression to subsequently born young than did brothers ($P < 0.02$, Mann-Whitney U test, and Hooley and Simpson 1983), especially if more than a year passed before the subsequent infant was born. Thus especially high levels of aggressive harassment were likely to be associated with a sister who had been the youngest in the family for at least two years. Figure 3 displays the scores received from closest siblings only (lower 6 lines of data), and from all young including the closest older sibling (top 4 lines). When all young are included, sex and age effects associated with closest older siblings are not significant, partly because of the aggression directed to sons by young other

Table 4. The numbers of neonates who die or survive[a], according to A the sex of the neonate; B the sex of the closest older sibling; and C the sex and age of the closest older sibling

	Probability of dying				
	Die	Survive		95% limits[b]	
A) Sex of neonate:					
Female	8	26	0.24	0.12–0.40	NS,
Male	3	32	0.09	0.02–0.21	$\chi^2=1.87$
B) Sex of closest older sibling:					
Female	9	24	0.27	0.14–0.44	$P<0.05$,
Male	2	34	0.06	0.01–0.17	$\chi^2=4.55$
C) Sex and age of closest older sibling:					
Yearling female[c]	6	5	0.55	0.31–0.84	$P<0.01$, Fisher
Yearling male[d]	0	21	0.00	0.02–0.12	
Older than yearling female[c]	3	19	0.14	0.02–0.28	NS, Fisher
Older than yearling male[d]	2	13	0.13	0.00–0.30	

[a] First born infants are excluded from this analysis (see Methods, Section 3)

[b] See Methods, Section 7

[c] Neonates with closest yearling female siblings were more likely to die than those with closest older than yearling female siblings ($P<0.01$, Fisher's exact probability test)

[d] The ages of male closest older siblings did not affect neonatal death

than the closest sibling. When the closest older siblings were considered alone, few siblings born in the previous year were aggressive (Fig. 3, middle), but closest siblings who were female and born before the previous birth season contributed at least one episode of aggression per 6 h in 7/12 cases (♀>1y in Fig. 3), compared with only 2/18 comparable brothers ($P<0.02$, $\chi^2=5.56$).

Receiving high levels of aggression from all young when the closest older sibling is female and born before the previous birth season may have been a strong effect in female infants (open circles, top two lines of Fig. 3). The single score of the infant with a yearling sister lies below the 95% confidence limits for the 5 scores of female infants with older than yearling sisters as closest siblings (mean = 5.22, SD = 2.68, 95% limits from 1.98 to 8.55).

The aggression from a non-yearling closest older sibling may be a result of the age-gap between sibling and infant, rather than the sibling's age (see also Hooley and Simpson 1983). For having an older than yearling sibling did not lead to high levels of aggression received if a yearling was also present. Only three of 11 such older siblings produced non-zero aggression scores, compared with 8/14 yearlings (whose scores were nevertheless low, as Fig. 3 shows) ($P<0.02$ Fisher exact probability test).

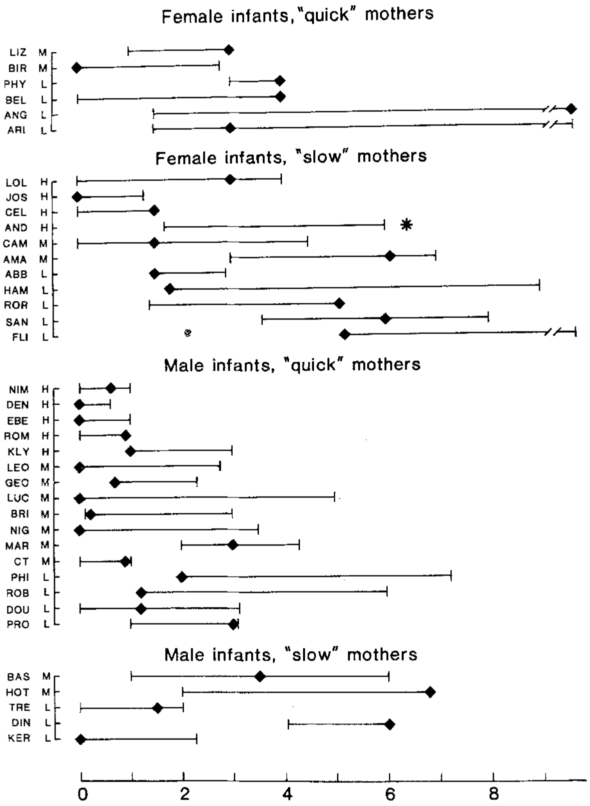

Fig. 2. Aggression received from other adults by mothers of female and male infants, who subsequently give birth in the next year ("quick"), or later ("slow"). Diamonds mark the scores during infants' 8th weeks, and the bars indicate the ranges of the 4 scores taken through the infants' first years (at 8 weeks, 16 weeks, 20–50 weeks and 52 weeks). Mothers' ranks through the four observation periods in the infant's first years are shown as "*H*" for top, "*M*" for middle and "*L*" for low. * No 8-week data were available for AND; bar indicates range of scores between weeks 16 and 52

Mechanisms controlling birth sex ratios and birth intervals. Provisionally we believe that mothers conceive daughters or sons (Simpson and Simpson 1982) in response to whether or not they are top ranking rather than to such potential stressors as levels of aggression received from others. To be top-ranking is never to be supplanted by other females, except when they are supported by the adult male, but it is not necessarily to avoid involvement in giving and receiving aggression (e.g. LOL and ANG in Fig. 3). It can also be argued that any response to levels of aggression in mothers with daughters should be inhibited. For a low ranking female currently receiving little aggression because

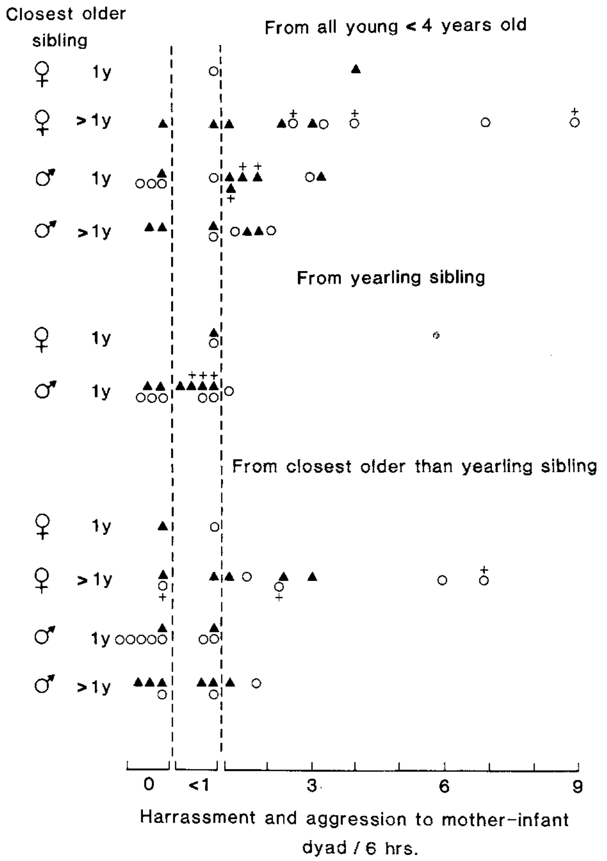

Fig. 3. Harassment and aggression received from other young (individuals under 4 years old) by mother-infant dyads through the infant's first year, according to the sex and age of the closest older sibling. Circles refer to female infants, triangles to males, and " + "s mark infants with dominant mothers through their first year

she has a son (e.g. LUC or CT in Fig. 3), responding to this low level by subsequently giving birth to a daughter could then meet dangerously high levels of aggression (e.g. ANG, ARI in Fig. 3).

Once a mother has an infant daughter, the infant's female sex and possibly her lower level of independent activity in the early weeks (Simpson et al. 1981) may delay subsequent conception in our captive groups, even in mothers who receive low levels of aggression (e.g. LOL, JOS, CEL, Fig. 3) and in top ranking mothers (e.g. History a rather than b in Table 1). In these cases "stress" may not be involved in delaying subsequent conception (Altmann et al. 1978; Dunbar 1980), which can be quick in mothers with daughters in spite of high levels of aggression received (ANG and ARI in Fig. 3). For non-top ranking mothers who currently have daughters, to be "quick" can be of survival value, if their low rank makes them likely to conceive sons next time (Table 2).

The timing of the subsequent conceptions of mothers with sons may be more directly influenced by stress. Unlike mother-daughter pairs, mother-son pairs receiving higher levels of aggression from other adults are slower to conceive in weeks 8, 16 and 2 to 50 ($P<0.05$, Table 5).

Table 5. Spearman correlation coefficients for interbirth intervals and the aggression received by mothers from other adults during their infants' first year of life

	Age of infant (weeks)				
	8	16	20–50	52	
Females	0.02	0.16	0.10	−0.13	$n=19$
Males	0.64*	0.45*	0.45*	0.32	$n=20$

* $P<0.05$

Discussion

Short-term costs were greater for mothers of daughters than mothers of sons. Daughters were at considerable risk of dying within 14 days of birth, especially when they were the second of two daughters born in successive birth seasons. Surviving daughters together with their mothers could receive higher levels of aggression from other adults through their first years than mother-son dyads. If mothers could choose their life-histories freely, they should accordingly produce sons rather than daughters. Mothers, however, have good reasons for bearing daughters. Thus they should avoid becoming producers of the most abundant sex of offspring (Fisher 1930) and it is possible in some groups of macaques that high ranking mothers should produce daughters to inherit their high rank and contribute to the mothers' fitness by adding to the family's fighting strength as they mature (Silk et al. 1981a, b; Simpson and Simpson 1982; but cf Meikle et al. 1984). In this view, top ranking mothers better able to afford and counter the effects of aggression accompanying young daughters should rear the daughters, doing so at intervals of more than a year, to avoid bearing another infant while their first is still a relatively vulnerable yearling. Because maternal rank is relatively stable in our colony (Simpson and Simpson 1982), mothers top in one year can expect to be top in the next, and can therefore expect to bear series of daughters. Because neonatal deaths are especially likely when the older sibling is a yearling daughter (Table 4), dominant mothers should avoid producing infants annually. The relative abundance of History a in Table 1 among the dominant mothers supports this view. Non-top mothers, in contrast, should produce sons annually, (History h in Table 1), unless subjected to very high levels of aggression (Table 5).

Such *post hoc* speculation is a convenient framework for assembling a number of results, but it is not by itself strong evidence that mothers do indeed choose futures. Moreover, the finding that bearing infants at intervals of more than a year can result in high levels of harrassment from other young for the mother-infant dyad if the closest older sibling is a daughter (Fig. 3) suggests a possible cost of being slow to conceive. At this stage we cannot weigh such costs to older infants against the benefit of avoiding high risks to neonates by bearing infants at intervals of more than a year.

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References

Altmann J (1974) Observational study of behaviour: Sampling methods. Behaviour 49:337–367

Altmann J (1980) Baboon mothers and infants. Harvard University Press, Cambridge, Ma

Altmann J, Altmann SA, Hausfater G (1978) Primate infant's effects on future reproduction. Science 201:1028–1030

Anderson DM, Simpson MJA (1979) Breeding performance of a captive colony of rhesus macaques (*Macaca mulatta*). Lab Anim 13:275–281

Clutton-Brock TH, Albon SD (1982) Parental investment in male and female offspring in mammals. In: King's College Sociobiology Group, Cambridge (eds) Current problems in sociobiology. Cambridge University Press, Cambridge, pp 223–247

Dunbar RIM (1980) Determinants and evolutionary consequences of dominance among female gelada baboons. Behav Ecol Sociobiol 7:253–265

Fisher RA (1930) The genetical theory of natural selection. Oxford University Press, Oxford

Hooley JM, Simpson MJA (1981) A comparison of primiparous and multiparous mother-infant dyads in *Macaca mulatta*. Primates 22:379–392

Hooley JM, Simpson MJA (1983) Influence of siblings on the infant's relationship with the mother and others. In: Hinde RA (ed) Primate social relationships: an integrated approach. Blackwell Scientific Publications, Oxford pp 139–142

Meikle DB, Tilford BL, Vessey SH (1984) Dominance rank, secondary sex ratio, and reproduction of offspring in polygynous primates. Am Nat 124:173–188

Phillips LD (1973) Bayesian statistics for social scientists. Nelson, London

Ruppenthal GC, Arling GL, Harlow HF, Sackett GP, Suomi SJ (1976) A 10 year perspective of motherless-mother monkey behavior. J Abnorm Psychol 85:341–349

Siegel S (1956) Nonparametric statistics for the behavioural sciences. McGraw Hill, New York

Silk JB (1983) Local resource competition and faculative adjustment of sex ratios in relation to competitive abilities. Amer Nat 12:56–66

Silk JB, Clark-Wheatley CB, Rodman PS, Samuels A (1981a) Differential reproductive success and faculative adjustment of sex ratios among captive female bonnet macaques (*Macaca radiata*). Anim Behav 29:1106–1120

Silk JB, Samuels A, Rodman PS (1981b) The influence of kinship, rank and sex on affiliation and aggression between adult female and immature bonnet macaques (*Macaca radiata*). Behaviour 78:111–137

Simpson MJA (1979) Problems of recording behavioral data by keybord. In: Lamb ME, Suomi SJ, Stephenson GR (eds) Social interaction analysis: methodological issues. University of Wisconsin Press, Wisconsin, pp 137–156

Simpson MJA (1983) Effect of the sex of an infant on the mother-infant relationship and the mother's subsequent reproduction. In: Hinde RA (ed) Primate social relationships: an integrated approach. Blackwell Scientific Publications, Oxford, pp 53–57

Simpson MJA, Simpson AE (1977) One-zero and scan methods for sampling behaviour. Anim Behav 25:726–731

Simpson MJA, Simpson AE, Hooley J, Zunz M (1981) Infant related influences on birth intervals in rhesus monkeys. Nature 290:49–51

Simpson MJA, Simpson AE (1982) Birth sex ratios and social rank in rhesus monkey mothers. Nature 300:440–441

Trivers RL, Willard D (1973) Natural selection of parental ability to vary the sex ratio of offspring. Science 179:90–92

Van Wagenen G (1972) Vital statistics from a breeding colony: reproduction and pregnancy outcome in *Macaca mulatta*. J Med Primatol 1:3–28