

A longitudinal analysis of reproductive skew in male rhesus macaques

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One of the basic tenets of sexual selection is that male reproductive success should be large in polygynous species. Here, we analysed 6 years of molecular genetic data from a semi-free-ranging population of rhesus macaques (*Macaca mulatta*), using Nonac's B index, to assess the level of male reproductive skew in the study troop. On average, the top sire in each year produced 24% of the infants, while 71% of troop males sired no offspring at all. Consequently, 74% of infants had at least one paternal half-sibling in their own birth cohort. Reproductive success was greatest for high-ranking males, males who spent the whole mating season in the troop and males of 9–11 years of age. Heterozygosity for major histocompatibility complex (MHC) class II gene *DQB1* was the strongest single predictor of male reproductive success. A negative relationship suggestive of female mate choice was noted between the B index and the proportion of extra-group paternities. Reproductive skew was not associated with relatedness among potential sires or with female cycle synchrony. We conclude that reproductive skew in male rhesus macaques is best accounted for by the 'limited-control' model, with multiple factors interacting to regulate individual reproductive output.

Keywords: rhesus macaques; male reproductive skew; kin structure; heterozygote advantage; mate choice

1. INTRODUCTION

Some disagreement has arisen about the effects of male dominance rank upon reproductive success in non-human primates (reviewed in Cowlshaw & Dunbar 1991; Bercovitch 1991, 1992; Bulger 1993; Alberts *et al.* 2003). High-ranking males generally sire more offspring than low-ranking males (e.g. red howler monkeys, Pope 1990; rhesus macaques, Berard *et al.* 1993; long-tailed macaques, de Ruiter & van Hooff 1993; Barbary macaques, Paul *et al.* 1993; savannah baboons, Altmann *et al.* 1996; toque macaques, Keane *et al.* 1997; and Hanuman langurs, Launhardt 1998), but the strength of the association between rank and reproductive output depends upon a number of factors, including the ability of males to monopolize sexually receptive females, the relative success of alternative male mating strategies and the impact of female mate choice (Bercovitch 1991; Alberts *et al.* 2003).

It was suggested by van Hooff (2000) that the differential reproductive success observed in male primates is evidence for 'reproductive skew', i.e. for conditions under which reproductive opportunities are not equally distributed among group members (Clutton-Brock 1998). The two basic models of reproductive skew are the 'concession'

model (Vehrencamp 1983a,b; Keller & Reeve 1994; Johnstone *et al.* 1999; Kokko & Johnstone 1999), whereby high-ranking individuals do not monopolize matings provided that matings by subordinates provide benefits to the high-ranking individuals, and the 'limited-control' model (Cant 1998; Clutton-Brock 1998; Reeve *et al.* 1998), whereby high-ranking individuals fail to monopolize matings because an assortment of factors (e.g. alternative male mating strategies, female choice, female cycle synchrony) interfere with their ability to do so. The models give different weights to the (genetic) relatedness of dominants and subordinates. The concession model predicts that a high level of kinship among breeders causes skew to increase because dominants allow distantly related individuals to have their own offspring as an incentive to stay in the group. More closely related individuals would increase their fitness merely by helping relatives (Vehrencamp 1983a; Keller & Reeve 1994). The limited-control model, in contrast, predicts that close genetic relatedness has the opposite or no significant effect on reproductive skew (Cant 1998; Clutton-Brock 1998; Reeve *et al.* 1998).

A multitude of quantitative measures of reproductive skew have been proposed (e.g. Vehrencamp 1983a,b; Cant 1998; Johnstone *et al.* 1999; Kokko & Johnstone 1999; Nonacs 2000, 2003; Kokko 2003; reviewed in Kokko *et al.* 1999), many of which are based upon reproductive output and highlight different statistical aspects of

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the observed distribution of offspring number. However, most empirical studies of reproductive skew undertaken to date have not been based upon quantitative approaches (e.g. Lundy *et al.* 1998; Cooney & Bennett 2000; Clarke *et al.* 2001; de Luca & Ginsberg 2001; Engh *et al.* 2002) and, out of the few studies that actually tried to measure skew (e.g. Jamieson 1997; Heinsohn *et al.* 2000; Reeve *et al.* 2000; Haydock & Koenig 2002; Seppä *et al.* 2002; Sumner *et al.* 2002), none was performed in primates. The most sophisticated longitudinal analysis of skew in male primates, a study of 32 group-years in a population of savannah baboons from Amboseli National Park, Kenya, made a convincing case for the limited-control model but did not provide a numerical index of skew (Alberts *et al.* 2003). Without precise data on reproductive output, however, the extent, causes and consequences of reproductive skew are difficult to assess.

We used paternity data collected over six consecutive breeding seasons in a group of semi-free-ranging rhesus macaques to provide the first quantitative analysis of reproductive skew in male primates. Our major goal was to relate temporal variations in reproductive output to changes in individual or group characteristics that might be indicative of the mechanisms underlying reproductive skew. Furthermore, while most studies of reproductive skew have so far focused upon the extent and possible causes of skew, none has examined its consequences. Our second goal, therefore, was to assess the effects of skew upon the kinship structure of our study group because genetic relationships are known to affect social relationships in group-living animals.

2. MATERIAL AND METHODS

(a) *Study population and study group*

Cayo Santiago is a 15.2 ha island located off the Puerto Rican coast. It is inhabited by *ca.* 800 rhesus macaques who are direct descendants of the 400 founder animals captured in India in 1938 (Rawlins & Kessler 1986). Although no animals have been added since the foundation of the colony, genetic analysis suggests that the population is not significantly inbred (Widdig *et al.* 2001). The study population lives in multi-male multi-female groups and breeds on a seasonal basis (Rawlins & Kessler 1986). The interbirth interval is *ca.* 1 year, and females give birth to a single offspring in more than 99% of cases (Bercovitch *et al.* 2002). The mating season on Cayo Santiago usually lasts from May to October, and is followed by the birth season from November to April. Animals can therefore be assigned to non-overlapping birth cohorts although the ages of infants born into the same cohort may differ by up to six months. The gender, date of birth, group membership and maternal identity of all animals are logged in a demographic database at the Caribbean Primate Research Center. The study troop, group R, consisted of a stable core of 42–61 adult females in each year, their offspring and some adult males who varied in number owing to dispersal. Some low-ranking females from group R split off into a sister troop, group BB, in June 1996 and were considered a different group thereafter.

(b) *Paternity analysis*

Female rhesus macaques are pregnant for an average of 167 days (Bercovitch & Berard 1993). Therefore, any adult male residing on the island any time during the 200 days prior to the

birth of a given infant was initially considered a potential sire of that infant. Paternity was determined using 15 microsatellites and occasional multilocus DNA fingerprinting (Nürnberg *et al.* 1998; Widdig 2002). Log_{10} -likelihood ratios (LR) for paternity versus non-relatedness were calculated as previously described by Krawczak (1999). Paternity of a given infant was regarded as established when the putative sire had an LR in favour of paternity that was larger than two (corresponding to a standardized paternity probability of 99%) and at least one unit larger than the LR of any other potential sire. Multilocus DNA fingerprinting was used in cases where no unequivocal sire could be identified using microsatellites alone (Widdig 2002).

(c) *Male reproductive skew*

All males who were at least 5 years of age and were members of group R for at least one month during a given mating season were considered potential troop sires for the corresponding birth cohort in the skew analysis. Reproductive output was determined for the mating seasons from 1992 to 1997 (i.e. the birth cohorts from 1993 to 1998), and its annual deviation from a uniform distribution among males was quantified using the binomial skew index ('B index') proposed by Nonacs (2000, 2003). The term 'reproductive skew' has been used in the literature to refer to both inequality in reproductive opportunities and variation in reproductive output. The B index is a quantitative measure of the variance in reproductive output and does not therefore allow direct causal inferences to be made (see Kokko *et al.* 1999; Nonacs 2000, 2003). However, indirect evidence for the mechanisms underlying reproductive skew can be obtained through the correlation between temporal changes in B index and changes in influential factors of interest. In contrast to other skew measures, the B index adjusts for individual differences in group residency, which is critical for rhesus macaques with their particular pattern of male dispersal. The B index allows the comparison of groups of different sizes and productivities. It is also highly sensitive to differences between low-productivity groups, as found in primates. Here, the B index was calculated once for all potential troop sires and once for actual troop sires alone. We confined our analysis to potential troop sires (29–62 adult males per season) and excluded non-troop potential sires (300–400 adult males per season) because large numbers of non-reproductive males tend to inflate skew indices.

(d) *Pairwise relatedness*

Relatedness of potential troop sires was assessed using the maximum-likelihood estimates of the pairwise kinship coefficients, obtained by an expectation maximization (EM) algorithm (Dempster *et al.* 1977) from the same microsatellite data as used for paternity analysis (see electronic Appendix A, available on The Royal Society's Publications Web site). We opted for this approach because the estimator of kinship in Queller & Goodnight (1989) has a high sampling variance (see Lynch & Ritland 1999) while the Lynch & Ritland (1999) algorithm may yield negative estimates when the number of loci with zero allele sharing is high. The respective estimates of kinship, albeit asymptotically unbiased and correct for very large numbers of animals, were therefore not deemed useful for the present purposes. To determine whether reproductive skew is kin specific, we compared the relative reproductive output of the close relatives of highly successful males with that of unrelated males. The two males with the highest reproductive output in each given year were identified (or the three most successful males, if the third most successful male had the same or one fewer offspring

than the second most successful male). All troop males with an estimated kinship coefficient larger than 0.0625 to one of these 'high reproducers' were classified as 'relatives' while all other potential troop sires were classified as 'non-relatives'. If n_r and n_n denote the respective total numbers of relatives and non-relatives in a given year, and if o_r and o_n are their respective offspring numbers, then $R = o_r n_n / o_n n_r$ is the relative reproductive advantage of relatives over non-relatives of high reproducers.

(e) Female cycle synchrony

The ability of a male to monopolize receptive females may depend upon the oestrous synchrony of the latter. If female oestrous synchrony is strong (i.e. all females ovulate within a short time period), a single male may be less capable of monopolizing all fertile females than if female synchrony is weak (i.e. females ovulate consecutively within a mating season). Asynchrony is therefore likely to promote reproductive skew. Since mating data were lacking for our study group, we assessed female cycle synchrony from the inferred synchrony of conception date. Assuming that gestation lengths were approximately equal and that females were impregnated during their first cycle in a mating season (Gordon 1981), infants born around the same time are likely to have been conceived around the same time. The level of female cycle synchrony (or asynchrony) within a birth season was therefore quantified by: (i) the mean time elapsed between consecutive births; and (ii) the percentage of days with at least one birth on which only a single birth occurred.

(f) Major histocompatibility complex class II genotypes

Animals on Cayo Santiago have been genotyped for major histocompatibility complex (MHC) class II locus Mamu-*DQB1* (Sauermann *et al.* 2001). This highly polymorphic locus, which plays a critical role in mediating a specific immune response in vertebrates, has at least 12 different alleles in the Cayo Santiago macaques. For the purpose of the present study, males were classified as either 'heterozygous' or 'homozygous' depending upon their Mamu-*DQB1* genotype.

(g) Statistical analysis

All statistical tests were carried out with a two-tailed error probability of 0.05. Where necessary, multiple testing was accounted for by Bonferroni adjustment (Sokal & Rohlf 1995). The B index (Nonacs 2000, 2003) was calculated using SKEW CALCULATOR 2002 (<http://www.obee.ucla.edu/Faculty/Nonacs>). All other statistical analyses were performed using SPSS 10.0.

3. RESULTS

(a) Paternity analysis

Paternity could be determined for 247 out of 263 infants (94%) born in group R between 1993 and 1998. The proportion of solved paternities varied between 86% and 98% across birth cohorts.

(b) Extent of male reproductive skew

On average, $71.1 \pm 3.9\%$ of troop males (mean \pm s.d.) did not sire any offspring in a given year, while $14.4 \pm 4.5\%$ of troop males produced a single offspring only (table 1). The remaining reproductive output was shared by between four and seven troop males who sired

an average of $79.7 \pm 6.8\%$ of infants (range of 66.7–87.0%). The troop male who produced the highest number of offspring in a given mating season ('top sire') was responsible for siring an average of $24.1 \pm 4.4\%$ of infants (range of 19.4–30.0%). The B index of reproductive skew differed significantly from zero in all years when all potential troop sires were taken into account, and in two out of six years (1995 and 1996) when only troop sires were considered (table 2).

(c) Skew and male dominance rank

Detailed rank data were unavailable for our study group except for the 1997 mating season (corresponding to the 1998 birth cohort). Here, the 45 potential troop sires could be subdivided into three equally sized rank categories based upon the outcome of dyadic agonistic interactions (data not shown). In 1997, the 15 high-ranking males sired 22 out of 31 offspring (71%), the middle-ranking males produced eight offspring (26%), and the low-ranking males collectively sired only a single offspring (3%). The difference in offspring number between classes was statistically significant (Kruskal–Wallis test: $\chi^2 = 7.248$, d.f. = 2, $p = 0.027$). Upon Bonferroni adjustment, subsequent multiple pairwise comparisons yielded a statistically significant difference in offspring number between high-ranking and low-ranking males (Mann–Whitney *U*-test: $z = 2.560$, $p = 0.010$), but not between high-ranking and middle-ranking males ($z = 1.014$, $p = 0.311$) or between middle-ranking and low-ranking males ($z = 2.141$, $p = 0.032$). The proportion of reproductively successful males also differed significantly between rank classes (high-ranking males, seven sires versus eight non-sires; middle-ranking males, six sires versus nine non-sires; low-ranking males, one sire versus 14 non-sires: $\chi^2 = 6.429$, d.f. = 2, $p = 0.040$).

(d) Extra-group paternities

Out of the 247 infants included in the analysis, 61 (24.7%) resulted from extra-group fertilization. The number of non-troop sires varied between one and 13 across years (table 2). The B index of reproductive skew among potential troop sires exhibited a strong negative correlation with both the percentage of extra-group paternities ($r_s = -0.928$, $N = 6$, $p = 0.008$) and the number of non-troop sires ($r_s = -0.886$, $N = 6$, $p = 0.019$). Likewise, the percentage of offspring sired by the top troop sire was negatively correlated with the percentage of extra-group paternities ($r_s = -0.986$, $N = 6$, $p < 0.001$) and the number of non-troop sires ($r_s = -0.943$, $N = 6$, $p = 0.005$).

(e) Male age

Non-troop sires in a given year were significantly younger (10.1 ± 4.1 years) than troop sires (12.3 ± 4.3 years) (Mann–Whitney *U*-test: $z = 2.826$, $N = 72$, $p = 0.005$). Within the troop, however, sires did not differ in age from non-sires (12.1 ± 4.5 years) (Mann–Whitney *U*-test: $z = 0.359$, $p = 0.720$). Similarly, no association was observed for the 1997 mating season between rank class and male age: the mean age of high-ranking males was 11.8 years, compared with 12.6 years for middle-ranking males and 11.6 years for low-ranking males (Kruskal–Wallis test: $\chi^2 = 0.732$, d.f. = 2, $p = 0.693$). The mean number of offspring per potential

Table 1. Reproductive output of potential troop sires. (N_x , number of troop males who sired x offspring.)

birth cohort	1993	1994	1995	1996	1997	1998
number of offspring sired by troop males	30	23	35	36	31	31
percentage of offspring sired by top troop sire	30.0	21.7	26.5	27.2	20.0	19.4
number of potential troop sires ^a	30 (11)	29 (9)	62 (21)	54 (14)	46 (11)	45 (7)
N_0^a	21 (10)	20 (8)	49 (18)	38 (13)	32 (9)	31 (6)
percentage of troop males with no offspring	70.0	69.0	79.0	70.4	69.6	68.9
N_1	4	3	6	12	7	7
N_{2-4}	2	4	5	2	4	5
$N_{\geq 5}$	3	2	2	2	3	2 ^b

^a Numbers in brackets refer to *Mamu-DQB1* homozygotes.

^b $N_{\geq 5}$ category includes the 'high reproducers', as defined in § 2d, except for the 1998 birth season where an additional male with four offspring was considered a high reproducer.

Table 2. Reproductive skew among male rhesus macaques.

birth cohort	1993	1994	1995	1996	1997	1998
B index (all troop males)	0.0935	0.0670	0.0885	0.1068	0.0508	0.0485
<i>p</i> -value	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
B index (troop sires only)	0.0161	0.0047	0.0508	0.0799	0.0043	0.0003
<i>p</i> -value	0.141	0.332	0.002	< 0.001	0.351	0.432
number of non-troop sires	1	11	4	3	7	13
percentage of extra-group paternities	3.2	36.1	19.1	10.0	36.7	36.7
average pairwise relatedness between potential troop sires	0.0262	0.0244	0.0246	0.0231	0.0240	0.0243
pairwise relatedness of high reproducers ^a	0.0830	0.1650	0.0610	0.0610	0.0150	0.0170
relative reproductive advantage of relatives of high reproducers ^b	1.08	3.00	2.61	1.50	0.52	1.56
female asynchrony (mean interval between consecutive births) (days)	4.7	3.0	3.1	3.1	2.6	4.7
female asynchrony (percentage of days on which there were births with one birth only)	93.1	75.9	60.6	82.4	72.5	71.4
odds ratio (reproducer versus non-reproducer) for <i>DQB1</i> heterozygotes	7.3	5.3	1.9	7.8	2.3	3.1

^a For seasons with more than two high reproducers, the average pairwise kinship coefficient is given.

^b Measured by parameter R , see § 2d.

troop sire was greater than one only for males aged 9–11 years (figure 1). Animals in this age group were responsible for 76 out of the 186 offspring (40.9%) sired by troop males. Males aged 8 or 12 years were slightly less successful (0.95–1.00 offspring per potential sire).

(f) *Male troop residency during the mating season*

Because of male inter-troop movement, group R comprised a variable number of potential troop sires (29–62 males) during the study period. The length of troop residency was always positively correlated with male reproductive success, but significantly so only in birth cohort 1995 (Spearman's rank correlation coefficient $r_s = 0.311$, $N = 62$, $p = 0.014$). A similar trend was observed in the birth cohorts of 1993 ($r_s = 0.357$, $N = 30$, $p = 0.053$) and 1997 ($r_s = 0.280$, $N = 46$, $p = 0.060$). Males who spent the whole mating season in the group were on average three times more successful than males who left or entered the group during the mating season, i.e. who spent five months or less in the group.

(g) *Male pairwise relatedness*

The mean pairwise kinship coefficient between potential troop sires was not correlated with the B index (table 2; $r_s = -0.147$, $N = 6$, $p = 0.781$), probably because the average pairwise relatedness of potential sires did not vary much over time. We therefore directly compared the reproductive success of the close relatives of high reproducers with that of non-relatives. The relative reproductive advantage of the former, measured by parameter R (see § 2d), was found to vary considerably over time (table 2). In 1994, for example, the six relatives of high reproducers sired six offspring, compared with seven infants sired by the 21 non-relatives ($R = 3.00$). In 1997, by contrast, the 14 relatives of high reproducers had only three offspring while the 29 non-relatives sired 12 offspring ($R = 0.52$). Overall, R was found to be larger than unity for all but one birth season. Over the 6 year study period, no statistically significant relationship emerged between R and the B index either among potential troop sires ($r_s = -0.200$, $N = 6$, $p = 0.704$) or among actual

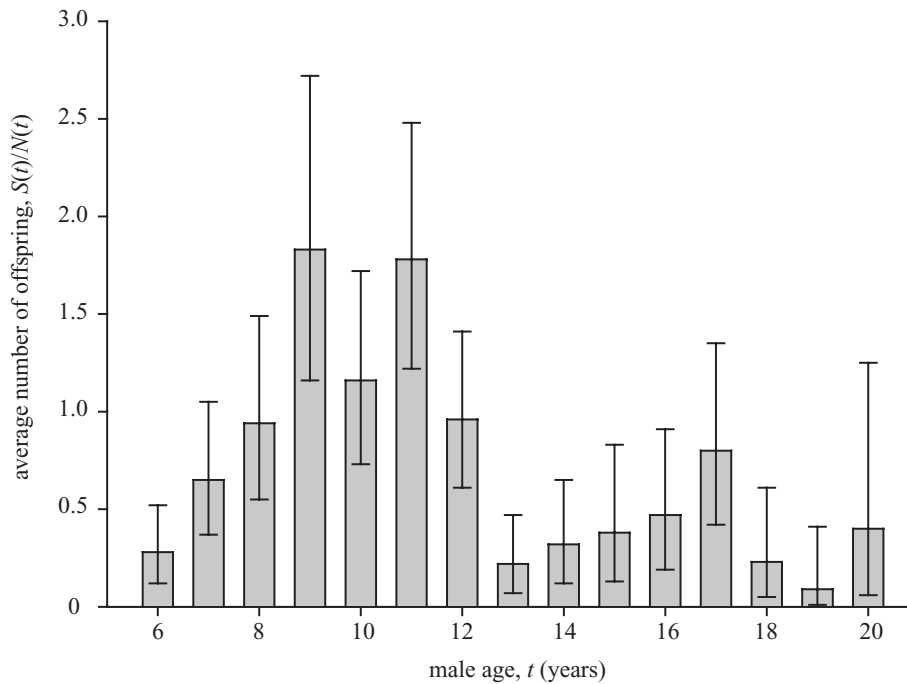


Figure 1. Age-dependent reproductive success of male rhesus macaques. $S(t)$, total reproductive output of males aged t years; $N(t)$, number of potential sires aged t years, summed over the whole study period. Error bars demarcate *ca.* 95% confidence limits for $S(t)/N(t)$, assuming that $S(t)$ is the sum of $N(t)$ independent Poisson variables.

troop sires alone ($r_s = 0.086$, $N = 6$, $p = 0.872$). However, the high reproducers were markedly less closely related to one another during the two mating seasons (1996 and 1997, corresponding to the 1997 and 1998 birth cohorts, respectively) in which the B index was lowest.

(h) Female cycle synchrony

We found evidence for female oestrous asynchrony (see Pereira 1991) in that births were widely distributed over birth seasons, with an average of 3.5 days between consecutive births and only 24% of days showing multiple births (table 2). Higher male reproductive skew is expected to be associated with higher female asynchrony (or lower synchrony). However, the mean interval between consecutive births was not correlated with the B index either among potential troop sires ($r_s = 0.147$, $N = 6$, $p = 0.781$) or among actual troop sires alone ($r_s = 0.029$, $N = 6$, $p = 0.956$). Similarly, the percentage of days with only one birth was not found to be associated with the B index among potential sires ($r_s = 0.600$, $N = 6$, $p = 0.208$) or among actual sires only ($r_s = 0.314$, $N = 6$, $p = 0.544$). No association was observed between the B index and the number of adult females in the troop (data not shown).

(i) MHC class II genotype

Males who were heterozygous at MHC class II locus *Mamu-DQB1* were more likely to reproduce than were homozygotes. The odds ratio of reproductive success for heterozygotes ranged from 1.9 to 7.8 (table 2). Among the 114 males considered potential sires, 38 heterozygotes and six homozygotes had at least one offspring. By contrast, 47 heterozygotes and 23 homozygotes never reproduced (odds ratio of reproductive success for heterozygotes: 3.10; 95% confidence interval: 1.05–9.51). Only 18 out of the 29 non-troop sires were *DQB1*

heterozygous, while 11 were homozygous. Because the frequencies of heterozygous males were virtually the same inside ($85/114 = 74.6\%$) and outside ($285/375 = 76.0\%$) group R, the odds ratio for reproductive success for non-troop heterozygotes (0.48, 95% confidence interval 0.21–1.15) was significantly lower than that of troop heterozygotes ($\chi^2 = 5.775$, d.f. = 1, $p = 0.016$).

(j) Consequences of male reproductive skew

When male reproduction is strongly skewed, infants born in the same year are likely to be paternal half-siblings (Altmann 1979). Since male rhesus macaques tend to remain in their troop for an average of 2 years before dispersing again (Manson 1995), paternal half-siblings within a social group are likely to be sired within a narrow time-window. Our paternity data revealed that 74% of individuals in group R had at least one paternal half-sibling of the same age, and an additional 15% had at least one paternal half-sibling within a 2 year age difference (Widdig *et al.* 2002). Among all 247 offspring with solved paternity, individuals had, on average, more paternal half-siblings (9.9 ± 9.7) than maternal half-siblings (2.6 ± 1.4) or full siblings (0.1 ± 0.4).

4. DISCUSSION

Based upon extensive longitudinal genetic data, we were able to demonstrate that male reproduction is significantly skewed in rhesus macaques. On average, the top sire in our study troop was responsible for 24% of the infants born during a given birth season, and approximately six males sired some 80% of infants, regardless of the number of males in the troop. Our data further provide evidence that the limited-control model of skew best accounts for the variable male reproductive success seen in this species.

Age, dominance rank and length of troop residency were all found to contribute to the observed variation in male reproductive output. Troop sires did not differ in age from troop non-sires, but the prime-age males (9–11 years of age) sired more offspring than did others (figure 1; also Bercovitch 1997; Bercovitch *et al.* 2003), a pattern also reported for Barbary macaques (Kuester *et al.* 1995) and savannah baboons (Packer *et al.* 2000). Dominance rank was independent of male age in the one year of our study with available rank data, and high-ranking males had the highest reproductive success. Nevertheless, middle-ranking and low-ranking males still sired almost one-third of infants, which corroborates earlier findings in a smaller group from the same population (Berard *et al.* 1994). Male group tenure in rhesus macaques tends to correspond to dominance (Vessey & Meikle 1987) so that high-ranking males are also older long-term residents. In our study, males who spent the entire six months of the mating season in the troop showed the highest reproductive output, which raises the question of why males would disperse from a troop at all during the mating season? Although most male-dispersal events occur at the onset of the mating season, some males nevertheless shift troops during the mating season (Lindburg 1969).

The results of our study suggest that female choice contributes to the variance in male reproductive success (see Manson 1992). An average of 25% of infants were sired by non-troop males, who not only were significantly younger than troop sires, but also had no position in the dominance hierarchy of the group. Their reproductive success therefore cannot be attributed to status. Furthermore, females often wander away from high-ranking consort partners and copulate with low-ranking novel group members in the shrubbery (Manson 1992; Berard *et al.* 1994). Given that surreptitious matings have produced offspring (Berard *et al.* 1994) and that females actively solicit other males for siring offspring, dominant males must have only a limited ability to control impregnation of sexually receptive females.

Distinguishing the limited-control model from the concession model of reproductive skew is difficult since circumstances under which the two models make opposite predictions, and could therefore be tested empirically, are not yet clear (Clutton-Brock 1998). Nevertheless, our findings conform with the predictions of the limited-control model in three pronounced ways. First, the concession model, as discussed in the literature, predicts that dominant males concede reproductive opportunities to more distantly related group members. We found, however, that the reproductive success of close relatives of the top sires tended to be higher than that of unrelated males. The effects of relatedness upon concession giving are likely to depend upon the sociobiology and the breeding behaviour of the species in question. Thus, concession giving by high-ranking males requires that incentives are cheap and that keeping subordinates in the group is beneficial to the dominants. Under such circumstances, which will arise for example in insects, close relatives would indeed require and receive fewer incentives than would distant relatives. In other species, where incentives are expensive (e.g. small numbers of receptive females, limited resources for rearing infants) and benefits are small (i.e. little defence or other assistance required by dominants), dominants might in

turn be able to increase their inclusive fitness more by benefiting their own kin. In any case, the present study revealed that the predictions originally made under a concession model do not hold true for rhesus macaques.

Second, under the limited-control model, one would expect that alternative male tactics and female choice would reduce the extent to which dominant males can monopolize sexually receptive females, and we found that a high number of infants were sired by non-troop males.

Finally, we observed that heterozygosity for MHC class II gene *DQB1* is a strong determinant of male reproductive success. Mechanisms of deliberate genotype-dependent concession are almost certainly less likely to influence relative male reproductive output than are factors that are intrinsic to the male genotype. MHC-associated overdominant selection potentially results from a higher resistance to the debilitating effects of injury and parasite infection in heterozygous males (Saueremann *et al.* 2001). Such a proviso does not, however, seem to be important under the specific physical and psychosocial circumstances of extra-group fertilization.

The key consequences of male reproductive skew in cercopithecine primates are that: (i) paternal half-siblings are likely to be of the same age or in close age proximity, depending upon the length of male tenure; and that (ii) most individuals can be expected to have more paternal than maternal half-siblings. A possible impact of paternal kinship on primate social relationships has recently been confirmed by three studies of baboons and macaques, which revealed that paternal relatedness influences male and female mating decisions (Alberts 1999) as well as the social relationships of adult females (Widdig *et al.* 2001, 2002; Smith *et al.* 2003). The mechanisms mediating this ability of kin discrimination are unclear, but, since reproductive skew tends to produce paternally related cohorts (see Altmann 1979), we suggest that future research into primate sociology should also focus upon the causes and consequences of male reproductive skew.

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