Dominance rank and reproductive maturation in male rhesus macaques (*Macaca mulatta*)

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The timing of reproductive maturation in females has been linked to differences in dominance status and exposure to males, but less information is available regarding the effect of dominance rank and exposure to females on the pace of reproductive maturation in males. A two-year study of a cohort of nine male rhesus macaques was undertaken to document potential social factors influencing variation in rates of reproductive maturation. The males lived in a large heterosexual group housed in a 0.3 ha outdoor enclosure. Every four weeks the focal subjects were isolated from the group to collect morphometric measurements and blood samples. The results revealed that dominance rank was not significantly correlated with average testosterone concentrations during the mating season. However, the highest ranking adolescent male had higher testosterone concentrations at a younger age, earlier in the mating season, and for a longer duration than did the lowest ranking male. Relative testicular weight was significantly correlated with dominance rank during the premating season, but not the postmating season, among adolescent males. The highest ranking adolescent male also engaged in more affiliative and sexual activity with nonkin, sexually receptive females than did lower ranking conspecifics. These patterns of development provide evidence that high dominance status accelerated reproductive maturation in male rhesus macaques.

Introduction

Subordinate social status hampers female reproductive maturation in many primate species (Abbott and Hearn, 1978; Epple and Katz, 1984; French *et al.*, 1984; Ziegler *et al.*, 1987, 1990; Bercovitch and Goy, 1990), whereas exposure to a male accelerates reproductive maturation among many female mammals (Vandenbergh, 1969a; Epple and Katz, 1980; Fadem, 1985; Ziegler *et al.*, 1987; Izard, 1990; Stonerook and Harder, 1992). The consequences of low dominance rank and exposure to females for reproductive maturation among male mammals are less well documented. Subordinate male dwarf mongooses, *Helogale parvula*, have smaller testicles but the same testosterone concentrations as higher ranking conspecifics (Creel *et al.*, 1992), whereas nonbreeding naked mole rats, *Heterocephalus glaber*, have suppressed testosterone concentrations in the absence of deficient spermatogenesis (Faulkes and Abbott, 1991). Unlike in females, suppressed endocrine concentrations in males are not necessarily associated with reduced gametogenetic function or reproductive success (Bercovitch and Goy, 1990).

Testosterone concentrations in male stump-tail macaques, *Macaca arctoides*, were not correlated with dominance rank, sexual activity or aggressive behaviour, but the lowest ranking adult male had the lowest testosterone concentrations and received the greatest number of attacks (Niewenhuijsen *et al.*,

1987). Eaton and Resko (1974) reported that dominance rank was not correlated with testosterone concentrations or amount of aggressive activity in Japanese macaques, *M. fuscata*, but Dessi-Fulgheri *et al.* (1981) found that the highest ranking male Japanese macaque in their study had double the testosterone concentration of subordinate individuals. Dominance rank was not correlated with testosterone concentrations among adult male vervet monkeys, *Cercopithecus aethiops*, but rates of aggression were correlated with testosterone concentrations in dominant males (Steklis *et al.*, 1985). Among adult male savanna baboons, *Papio cynocephalus*, in Kenya, testosterone concentrations were correlated with patterns of aggressive activity, not sexual behaviour, and dominance rank was correlated with levels of sexual activity, not with aggressive behaviour (Sapolsky, 1982). Alpha male lesser mouse lemurs, *Microcebus murinus*, living in heterosexual groups had testosterone concentrations comparable to those of isolated males, whereas the two or three subordinate males residing in the same heterosexual groups had testosterone concentrations about two-thirds that of the alpha male and comparable to each other (Perret, 1985). Testosterone concentrations climbed with elevations in dominance status and plummeted with declines in dominance status among male talapoin monkeys, *Miopithecus talapoin* (Eberhardt *et al.*, 1980). In sum, androgenic effects on sexual and aggressive behaviour appear to be facilitatory, and social factors determine suppression or expression of these types of behaviour (see Dixon, 1980; Bernstein *et al.*, 1983; Keverne, 1983; Bercovitch and Goy, 1990). Testosterone concentrations in male rhesus

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macaques are extremely responsive to social and sexual stimuli (Rose *et al.*, 1972).

The potential link between dominance status and reproductive maturation among male primates has not been subject to very intense scrutiny. High dominance rank is associated with a younger age of testicular descent and an earlier onset of seasonal testosterone profiles in some macaques (Bercovitch and Goy, 1990). Among adolescent male bonnet macaques, *M. radiata*, testosterone titres correlated with both dominance rank (Glick, 1980), and levels of sexual activity (Glick, 1979).

A lengthy adolescent stage of development is a widespread characteristic of primates, and few studies have tracked developmental patterns on a longitudinal basis (Caine, 1986). The primary goal of this report is to document the role of social status on reproductive maturation in adolescent male rhesus macaques residing in a heterosexual group in a large outdoor enclosure. Reproductive maturation refers to changes in testicular mass and plasma testosterone concentrations that accompany the adolescent stage of development. The relative testicle size of rhesus macaques is one of the highest among primates, probably because of the multimale mating system coupled with seasonal patterns of sexual activity (Harcourt *et al.*, 1981; Dixon, 1987). Two consequences of this pattern are paternal uncertainty and intense sperm competition (Bercovitch, 1992a). The effect of differential rates of reproductive maturation were examined in the context of mating system of the rhesus macaque to explore how dominance status can affect the onset of reproduction in male rhesus macaques.

Materials and Methods

Animals

Nine rhesus macaques were the focal subjects of this investigation. The males lived in a heterosexual social group (Group M) in a tri-sectioned 0.3 ha outdoor enclosure housing approximately 150 monkeys at the Sabana Seca Field Station, Puerto Rico (18°27'N, 66°12'W). The study site was located in a subtropical karst forest about 15 km west of San Juan. Water was available *ad libitum* and monkeys were fed daily with commercial monkey chow. Diet was occasionally supplemented with fresh fruit and the monkeys foraged on the grass within the enclosure. The entire social group had been translocated from Cayo Santiago to Sabana Seca in 1984 (Bercovitch and Lebrón, 1991), and the former site was inhabited by rhesus macaques since 1938 (Sade *et al.*, 1985; Rawlins and Kessler, 1986). Reproductive seasonality is a characteristic of the Cayo Santiago rhesus macaques (Rawlins and Kessler, 1985). For unknown reasons, the median birth month has shifted among the Group M rhesus macaques from February (1985) to December (1987) to July (1989).

About six months after birth, monkeys were tattooed with an identification number, but individual recognition was usually based upon general physiognomy. The alpha and omega males within the study cohort were born 6 days apart, with all of the adolescent subjects born between 30 October 1986 and 3 January 1987. The adolescent stage of development in rhesus macaques begins at about 3–3.5 years based upon commencement of production of fertile spermatozoa (Bercovitch and Goy, 1990). Data collected for this project were obtained between

January 1990 and December 1991, spanning the ages of 3–5 years among the study cohort.

Sampling procedures

Thirteen times per year, that is once every four weeks, the males were removed from their social group to collect blood samples and make morphometric measurements (Bercovitch, 1992b). Subject monkeys were encouraged to enter a small hallway (140 cm × 40 cm × 56 cm) connected to the large outdoor enclosure and leading to a gate that opens into an individual holding cage (62 cm × 48 cm × 64 cm). In addition to the nine adolescent male subjects, adult males were captured four times per year (January, April, July and October) to establish physiological and morphometric characteristics of adult males living in the same enclosure. Males are defined as adults after they reach 6 years of age, or the average age when skeletal maturation is complete (Turnquist and Kessler, 1989; Watts, 1990; Schwartz and Kemnitz, 1992). All monkeys were anaesthetized with approximately 10 mg ketamine HCl kg⁻¹ (Ketaset®: Aveco, Fort Dodge, IA), and morphometric measurements and blood samples were usually collected before 10:30 h from the subjects in a random order. This procedure is designed to control for diurnal rhythms characteristic of testosterone concentrations in rhesus macaques (Perachio *et al.*, 1977; Rose *et al.*, 1978; Chambers and Phoenix, 1981; Plant, 1981; Michael *et al.*, 1984; Sehgal *et al.*, 1986). On the afternoon of the same day, all males were released back into the large enclosure.

After immobilization, body weights were obtained using a battery operated scale that was accurate to the nearest 0.01 kg. Length and width of testicles, as well as canine size, were measured using a sliding caliper accurate to 1.0 mm. The scrotal sac was stretched to exclude the epididymis from measurement. Testicular volume (TV) in nonhuman primates is calculated using the formula for a regular ellipsoid (Abbott and Hearn, 1978; Dixon *et al.*, 1980; Wickings and Nieschlag, 1980; Steiner and Bremner, 1981; Plant, 1985; Bercovitch, 1989; Marson *et al.*, 1991):

$$TV = (\pi W^2 \times L)/6$$

where *W* is the width of the testis and *L* is the length of the testis. Testicular volume (TV) was calculated for both right and left testes and converted to weight using the regression equation $Y = 1.534x + 5.736$ (Bercovitch and Rodriguez, 1993). Canine size was measured from the gingival margin to the tip of the canine on the maxilla of the right side. Blood samples were collected from the femoral vein in 13 ml SST Vacutainer collection tubes (Beckton-Dickson, Rutherford, NJ), centrifuged (4470 *g* for 20 min) within 2 h of collection, and the plasma frozen at -20°C.

Behavioural observations were obtained 5 days per week on an *ad libitum* basis (Altmann, 1974) while walking within all three sections of the enclosure. These behavioural observations are inadequate for evaluating rates of activities, but valid for deriving directionality and patterns of social interactions (Altmann, 1974; Bernstein, 1991). Lindburg (1983) has shown a good concordance among various estimates of male reproductive success in rhesus macaques using *ad libitum* data collected on male sexual activity.

Table 1. Dominance hierarchy among the adolescent male rhesus macaques

Rank	ID	Loser								
		94	97	98	100	88	86	89	93	92
Winner										
1	94	—	8	2	5	3	3	1	4	0
2	97		—	7	7	6	5	1	0	2
3	98			—	2	1	1	0	2	0
4	100				—	1	1	0	0	1
5.5	88					—	1	4	1	0
5.5	86					1	—	1	1	0
7	89							—	1	0
8	93								—	4
9	92									—

Animals are listed in descending dominance rank order. ID refers to the tattoo identification code and is not indicative of birth order. The values reported in each cell are the number of dyadic agonistic encounters recorded during the study when the participant in the row was ranked the 'winner' over the participant in the column.

Relative dominance ranks were derived for the nine adolescent males on the basis of all dyadic agonistic encounters recorded between the subjects. Agonistic behaviours included threats, chases, fights, avoidance of approaches, fear grimaces, and supplants over resources. The terms 'alpha' and 'omega' refer to relative rankings within the adolescent cohort of this study, unless otherwise noted.

Testosterone radioimmunoassays

Analysis of hormone concentrations was undertaken at the Wisconsin Regional Primate Research Center using procedures previously described in detail (Robinson *et al.*, 1975). Plasma samples were extracted using diethyl ether and were then incubated with rabbit antitestosterone-BSA (Holly Hill Biomedicals, Hillsboro, OR), which crossreacts 30.8% with dihydrotestosterone, before radioimmunoassay. The final separation stage was accomplished with dextran-coated charcoal. Samples were assayed in duplicate, with the lower limit of detection 4.84 pg ml⁻¹. Recovery levels are about 96% for testosterone in the WPRC Assay Laboratory. The intra- and interassay coefficients of variation were 2.2 and 6.8%, respectively, for the high rhesus macaque male pool and 3.9 and 7.9%, respectively, for the low pool.

Statistical analysis

Both parametric and nonparametric statistical tests were performed, with the level of significance set at $P < 0.05$. For assessing the effects of dominance rank, data were transformed into linear rankings and the Spearman's correlation coefficient is reported. For comparisons using data obtained on a ratio scale, Pearson's product moment correlation coefficient is the statistic reported. The annual reproductive cycle was divided into two time points: premating (samples collected in October) and postmating (samples collected in April) periods (Bercovitch, 1992b). No reproductive activity was observed outside of the mating season. Reproductive seasonality among rhesus

macaques is associated with alterations in testosterone concentrations (Robinson *et al.*, 1975; Gordon *et al.*, 1976; Sehgal *et al.*, 1986; Bercovitch, 1992b), testicular size (Sade, 1964; Conaway and Sade, 1965), and sperm production (Zamboni *et al.*, 1974; Sehgal *et al.*, 1986). Comparisons of *premating* and *postmating* values were made using either independent or paired Student's *t* test. Measures of central tendency report the mean $\pm$ SEM. Analyses were undertaken using SYSTAT 4.0 (Wilkinson, 1988).

Results

Dominance relationships

A linear dominance hierarchy based upon dyadic agonistic interactions between adolescent males characterized the study cohort (Table 1). Male dominance rank was independent of age within the study cohort ($r_s = -0.058$, $n = 9$, $P > 0.50$).

Dominance rank and testosterone concentrations

Testosterone concentrations in adult males were over twice as high during the premating period as during the postmating period (4.32 ± 0.40 ng ml⁻¹ versus 1.80 ± 0.10 ng ml⁻¹; paired $t = 6.834$, d.f. = 4, $P < 0.01$). Four-year-old males had premating season testosterone concentrations that were significantly lower than those of adult males (2.29 ± 0.44 ng ml⁻¹; $t = 2.924$, d.f. = 10, $P < 0.02$), but significantly higher than their own testosterone concentrations when 3.5 years of age (1.33 ± 0.17 ng ml⁻¹; paired $t = 2.352$, d.f. = 8, $P < 0.05$), indicating that seasonal testosterone profiles occurred before attainment of adult male testosterone concentrations. Five-year-old males had testosterone concentrations that were not significantly different from those of adult males during the premating season (2.60 ± 0.88 ng ml⁻¹; $t = 0.805$, d.f. = 11, $P > 0.40$).

Profiles of endocrine maturation were associated with dominance rank (Fig. 1), but rank effects were generally non-linear and most apparent in comparisons between the alpha and omega male. In the six-month mating season subsequent to

Fig. 1. The relationship between changes in testosterone concentration and age according to dominance rank among adolescent male rhesus macaques. All males were born in November–December 1986. For purposes of clarity, the standard error bars have been excluded from the figure. Average testosterone concentrations for the entire cohort ($\square$) are compared with those of the alpha male (M94; $\bullet$) and the omega male (M92; $\circ$).

attainment of four years of age, the alpha male maintained the highest average monthly testosterone concentrations among his cohort (5.79 ng ml^{-1}), whereas the omega male was characterized by the lowest average concentrations (1.57 ng ml^{-1}). Of the twenty-six blood samples obtained per adolescent male between January 1990 and December 1991, the alpha male had testosterone concentrations in excess of 1.5 ng ml^{-1} on twenty occasions, whereas the omega male achieved this level only four times. Of the forty-four samples analysed from adult males, only one fell below this concentration.

At the onset of the mating season, dominance rank was significantly correlated with testosterone concentrations at both four and five years of age (Table 2). Testosterone concentrations during the premating period when four years of age were good predictors of levels at the premating period when five years of age ($r = 0.940$, $n = 8$, $P < 0.001$). However, dominance rank was not significantly correlated with average monthly testosterone concentrations during the mating season among the four-year-old males ($r_s = 0.571$, $n = 9$, $P > 0.10$). The top third of the hierarchy had testosterone concentrations comparable to the bottom third of the hierarchy during the mating season ($t = 1.063$, d.f. = 4, $P > 0.10$). Using dates of birth and approximate duration of gestation to assess the time of conception revealed that 71% (24 of 34) of conceptions during this mating season occurred between December 1990 and January 1991. During this two month peak conception period, dominance rank among the adolescent males was not correlated with testosterone concentrations ($r_s = 0.379$, $n = 9$, $P > 0.20$) and the top third and bottom third of the hierarchy maintained similar testosterone concentrations ($t = 0.984$, d.f. = 4, $P > 0.50$).

Dominance rank and testicular development

Estimated testicular weight of the adult male subjects during the premating period of October 1991 was $51.8 \pm 4.1 \text{ g}$ ($n = 5$), and the average testes:body weight ratio was 0.52. The largest testicles (61.4 g) and the greatest relative testicle size (0.63) characterized the highest ranking adult male in the troop, who was also the oldest male at 14.5 years.

The testicular weight of five-year-old males was 61% that of adult males ($31.8 \pm 5.1 \text{ g}$; $n = 8$) during the premating period, and their testes:body weight ratio (0.38) was significantly less than that of adult males ($t = 2.463$, d.f. = 11, $P < 0.05$). Among adolescent male rhesus macaques, testicular weight was significantly correlated with body weight, but testosterone concentrations were independent of testicle size (see Table 2). Despite the close link between testicle size and body weight, dominant males had larger testicles, but were not heavier, than subordinate males (see Table 2). At five years of age, the alpha adolescent male weighed 11.3 kg and his testes weighed approximately 49 g, while the omega adolescent male weighed 6.7 kg and his testes weighed about 11 g. As a consequence, the relative testicular size of five-year-old males was a function of dominance rank (Fig. 2) during the premating period. Dominance status was not correlated with testes:body weight ratio among these same males during the postmating period ($r_s = 0.251$, $n = 9$, $P > 0.20$).

Developmental patterns associated with canine growth proceeded at a pace independent of body growth. Size differences in canine length were virtually undetectable at four years of age, with seven of the nine males having right upper canine lengths of 4.0 mm. By five years of age, canine size had increased 2.5 fold ($1.1 \pm 0.2 \text{ cm}$; $n = 8$), but neither dominance rank ($r_s = 0.369$, $P > 0.20$) nor body weight ($r = 0.432$, $P > 0.20$) were significantly correlated with canine length.

Dominance rank and sexual activity

During the 1990–1991 mating season, the three lowest ranking adolescent males were never observed copulating with females, whereas their three highest ranking conspecifics were recorded copulating with fifteen of forty sexually mature females. Backdating from birth date to probable conception date, based upon duration of gestation, indicated that the alpha male in this cohort copulated with eight females at about the suspected days of conception, while the beta male copulated with two. Because of data collection methods, rates of sexual activity cannot be ascertained, but the patterns noted are considered to reflect rank-related differences in sexual behaviour accurately. In general, the lower ranking males ranged on the periphery of the group, whereas their higher ranking counterparts engaged in much more social activity. In the 1990–1991 mating season, nonkin sexually mature females were never observed grooming the omega male, whereas the alpha male was groomed by twelve nonkin, sexually mature females.

Discussion

Some 3.5-year-old male rhesus macaques have systemic testosterone concentrations comparable to those of adult males during the mating season, but others do not achieve this concentration until 5.5 years of age (Bernstein *et al.*, 1991). During this study, the highest ranking adolescent male had high testosterone concentrations at a younger age, earlier in the mating season, and for a longer duration than did the lowest ranking adolescent male. In accordance with the findings of Bernstein *et al.* (1991), dominance rank was not linearly correlated with

Table 2. Correlation coefficients between morphometric measurements, testosterone concentrations, and dominance rank in adolescent male rhesus macaques

Characteristic	Age (years)			
	3.5 ^c	4.0 ^c	4.5 ^c	5.0 ^d
Rank: testosterone ^a	-0.628	-0.778*	-0.603	-0.850*
Rank: body weight ^a	-0.251	-0.536	-0.370	-0.491
Rank: testes weight ^a	-0.377	-0.720*	-0.703*	-0.790*
Body weight: testes weight ^b	0.815**	0.774*	0.752*	0.875**
Body weight: testosterone ^b	0.313	0.186	-0.199	0.041
Testes weight: testosterone ^b	0.280	0.329	-0.054	0.316

^aSpearman's rank order correlation coefficient in row. ^bPearson product moment correlation coefficient in row. ^c*n* = 9; ^d*n* = 8; **P* < 0.05; ***P* < 0.01. Significance levels refer to correlations between the two traits linked in each row. High ranking individuals are generally assigned the *lowest* numbers, so a negative correlation coefficient between dominance rank and a trait indicates that the trait is elevated in the dominant individuals. The correlation coefficients in each cell were obtained during the postmating periods of April 1990 (3.5 years) and 1991 (4.5 years) and the premating periods of October 1990 (4.0 years) and 1991 (5.0 years).

Fig. 2. The association between relative testicle size and dominance rank among five-year-old male rhesus macaques during the premating period. The highest ranking male within the cohort has been assigned the lowest number. Among the same males when four years of age, an identical pattern emerged ($r_s = -0.703$, $n = 9$, $P < 0.05$).

testosterone concentrations among adolescent males throughout the mating season, but the highest ranking male within a cohort had the greatest testosterone concentrations.

The impact of courtship activity on reproductive endocrinology among nonprimates has been well documented (see, for example, Lehrman, 1964; Harding, 1983; McComb, 1987), but the potential role of 'courtship' behaviour on male reproductive maturation among nonhuman primates has not been addressed. Circumstantial evidence indicates that proceptive activities of females can influence the timing of reproductive maturation among male primates. Testosterone concentrations and levels of sexual activity are higher among pubescent male rhesus macaques housed with three females compared with those of conspecifics of the same age housed with only a single female (Goy *et al.*, 1992). During this study, both testosterone concentrations and the extent of sexual and affiliative behaviour with females were greater in the alpha adolescent male than in the omega adolescent male.

Exposing adult male rhesus macaques to oestrogenized females during the nonmating season results in an increase in testosterone concentrations (Vandenbergh, 1969b; Bernstein *et al.*, 1977), and testosterone concentrations increase in male pigtail macaques, *M. nemestrina*, when a female is introduced into a group (Bernstein *et al.*, 1978). Similarly, introduction of an oestrogen-primed long-tail macaque to peer groups of adolescent, or adult, males increases testosterone concentrations (Glick, 1984). Under conditions of rank instability, the male vervet monkey who engaged in the most affiliative behaviour with females emerged as the new alpha male in the group (Raleigh and McGuire, 1990). Chimpanzees, *Pan troglodytes*, that have higher testosterone concentrations are involved in more genital inspections (Nadler *et al.*, 1987) than those with lower concentrations and the degree of sexual stimulation is correlated with testosterone concentrations among humans (Knussman *et al.*, 1986). Given that intersexual courtship patterns prime reproductive hormones, and that visual and tactile exposure to females increases testosterone concentrations in many primate species, the testable prediction can be made that the timing of male reproductive maturation is a function of the degree of affiliative and sexual activity with females. The patterns of activity documented in the present investigation indicate that a synergistic effect between dominance status and intersexual social activity can determine the timing of reproductive maturation.

High testosterone concentrations could be a cause, or a consequence, of social conditions. Among male nonhuman primates, sexual activity is strongly suppressed following castration (Wilson and Vessey, 1968; Resko and Phoenix, 1971; Dixon, 1980; Schenk and Slob, 1986). However, sexual behaviour in males depends upon surpassing threshold concentrations of testosterone (Michael *et al.*, 1984) and does not directly reflect absolute concentrations of testosterone. Glick (1980) found that the most sexually active adult male bonnet macaque had the lowest testosterone concentrations. Among rhesus macaques, annual monthly mean testosterone changes parallel annual mean monthly mount rates, but individual testosterone concentrations are not correlated with individual mount rates (Gordon *et al.*, 1976). In both primates (Gordon *et al.*, 1976;

Rose *et al.*, 1978; Bercovitch and Goy, 1990) and nonprimates (for example *Spermophilus beecheyi*, Holekamp and Talamantes, 1991), annual peaks in testosterone concentrations precede or coincide with the onset of the mating season. Keverne (1983) has reasoned that suppressed testosterone concentrations in subordinate male primates is unlikely to be the primary mechanism accounting for reduced sexual activity in these males.

Investigations of gonadectomized males has revealed that testosterone is unlikely to be the cause of differences among males in levels of aggressive behaviour. Prepubertally castrated males can fight and dominate intact males (Wilson and Vessey, 1968; Bernstein *et al.*, 1979). At the Yerkes Regional Primate Research Center, wounding in male rhesus macaques is most frequent during the nonmating season (Ruehlmann *et al.*, 1988), but testosterone is at its nadir during that time (Gordon *et al.*, 1976). The degree to which aggressive activity influences access to female rhesus macaques has probably been exaggerated (see, for example, Berenstein and Wade, 1983). High ranking males disrupt the mount attempts of lower ranking males (Ruiz de Elvira and Herndon, 1986), but male aggression is more often directed at the female consort partner than at other males (Lindburg, 1971, 1983). Lindburg (1971) never observed males fighting for access to females during his field study of rhesus macaques in India and he noted that "... males did not compete for females; partner change was the prerogative of the female ..."

In the present study, the alpha adolescent male had more sexual partners than did the omega adolescent male. The alpha male was a descendant of the highest ranking matriline in the troop, but this matriline had fewer members than the other two matriline in Group M. Hence, the alpha male had fewer matrilineal kin in the troop, so the greater number of mating partners could be a byproduct of the number of potential non-kin available rather than an outcome of his status. However, this is unlikely because the beta male and omega male were from the same original matriline (the great-grandmother of the omega male was the sister of the great-great-grandmother of the beta male), but the beta male engaged in both affiliative and sexual activity with more females than did the omega male.

High ranking adolescent males had larger testicles than did lower ranking males, but rank effects on body weight and canine size were absent. In addition, four-year-old males had testicle weights that were about half those of adult males, while their canine lengths were only about 25% that of adult males (Bercovitch, unpublished). Rank-related differences in testicle size, but not canine size or body size, coupled with the more rapid developmental trajectory of gonads compared with canines, support the idea that sperm competition may be more important than aggressive competition as a determinant of reproduction in male rhesus macaques (Bercovitch, 1992a). Spermatozoa from pubertal chimpanzees are less motile than those from adult males (Marson *et al.*, 1991), and efficiency of sperm production is lower among adolescent rhesus macaques than among adults (Amann *et al.*, 1976), but adolescent male rhesus macaques living in large outdoor heterosexual groups have sired offspring when 3.5 to 4.0 years of age (Bernstein *et al.*, 1991; Smith *et al.*, 1992; Bercovitch, unpublished). If males cannot exclude other males from access to sexually receptive females, or if surreptitious copulations occur, then relatively large testicles can be advantageous (Popp and DeVore, 1979). DNA fingerprint analysis of free-ranging rhesus macaques has

shown that furtive copulations have resulted in viable offspring (Berard *et al.*, 1990). Covariation among traits such as dominance rank, relative testicle size, and sexual activity with females provide evidence that the age at onset of reproduction in male rhesus macaques is likely to depend upon social status.

In summary, dominance rank influences reproductive maturation in males, but the effect is nonlinear and most pronounced at both ends of the hierarchy. Higher ranking adolescent males have relatively large testicles compared with lower ranking conspecifics, a morphological partitioning of resources that can provide dominant males with an edge in sperm competition. One impetus priming accelerated sexual maturation in males could be increased levels of affiliative activity with females. Enhanced rates of social activity with females may stimulate reproductive maturation in males, as well as providing adolescent males with access to individuals that are essential for initiating their reproductive careers. However, the impact of rank-related differences in timing of reproductive maturation on the age at first reproduction among males is unknown owing to the paternal uncertainty that characterizes the mating system of rhesus macaques. Current analysis of sirehood based upon DNA fingerprint profiles (Bercovitch, unpublished) should provide the information required for linking reproductive maturation with reproductive success.

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