

Inbreeding Avoidance in Rhesus Macaques: Whose Choice?

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ABSTRACT Whether nonhuman primates avoid copulating with close kin living in their social group is controversial. If sexual aversion to relatives occurs, it should be stronger in females than in males because of females' greater investment in each offspring and hence greater costs resulting from less viable offspring. Data presented here show that adult male rhesus macaques breeding in their natal groups at Cayo Santiago experienced high copulatory success, but copulated less with females of their own matrilineages than with females of other matrilineages. Adult females were never observed to copulate with males of their own matrilineage during their fertile periods. Although natal males sometimes courted their relatives, examination of two measures of female mate choice showed that females chose unrelated natal males over male kin. Female aversion to male kin was specific to the sexual context; during the birth season, females did not discriminate against their male relatives in distributing grooming. Evolved inbreeding avoidance mechanisms probably produce different outcomes at Cayo Santiago than in wild rhesus macaque populations. Gender differences in sexual aversion to relatives may be partly responsible for differences between studies in reported frequency of copulations by related pairs. © 1993 Wiley-Liss, Inc.

Parent-offspring and sibling matings are rare in nonhuman primates, just as in humans (reviewed by Fox, 1980; Chapais and Mignault, 1991; but see Leavitt, 1990), and such matings decrease the viability of resulting offspring (Ralls and Ballou, 1982). Whether humans develop sexual aversions to close childhood companions, who are usually genetic relatives, is controversial (Shepherd, 1983; Thornhill, 1991; but see Hartung, 1985; Leavitt, 1990). If such aversions exist, their evolutionary history can be illuminated by asking whether similar aversions exist among nonhuman primates. Because sex-biased dispersal usually separates adult opposite-sex close kin into different social groups (Packer, 1979; Pusey and Packer, 1987), primatologists have few opportunities to address this question empirically. Kin dyads living in the same social group avoid copulating, or copulate rarely, in chimpanzees (Goodall, 1986), Barbary macaques (Paul and Kuester, 1985), Japa-

nese macaques (Takahata, 1982), and ring-tailed lemurs (Pereira and Weiss, 1991). Results are less clear for rhesus macaques (Sade, 1968; Missakian, 1973; Chapais, 1983a; Sade et al., 1984; McMillan, 1986).

Parental investment theory (Trivers, 1972) suggests that if sexual aversion to close relatives does occur, it should be stronger in females than males because of females' greater investment in each offspring and hence greater potential costs resulting from less viable offspring (Clutton-Brock and Harvey, 1976; Waser et al., 1986; Hammerstein and Parker, 1987; Chapais and Mignault, 1991). Specifically, selection should disfavor inbreeding in both sexes as long as unrelated mates are readily available, but a smaller decrease in the availability of unrelated mates will cause males,

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compared to females, to begin courting relatives. Among wild chimpanzees, females resist their sons' and brothers' courtship attempts (Tutin, 1979; Pusey, 1980; Goodall, 1986). Captive female Japanese macaques frequently engage in homosexual behavior, choosing unrelated partners exclusively (Chapais and Mignault, 1991), whereas the same animals occasionally engage in incestuous heterosexual copulations. Thus males may initiate most or all incestuous copulations.

In this work, we address two questions: (1) do free-ranging rhesus macaques avoid copulating with their matrilineal relatives residing in their social group? and (2) if so, are females more averse than males to copulating with their matrilineal relatives?

Question 1 can be resolved simply by comparing observed to expected frequencies of copulations between kin and nonkin heterosexual dyads. Question 2, however, requires examination of behaviors that demonstrably indicate mate choice, which may be defined as "any pattern of behavior, shown by members of one sex, that leads to their being more likely to mate with certain members of the opposite sex than others" (Halliday, 1983). Elsewhere, we have established two behaviors (proximity maintenance and cooperation with male hip-grasps) as female mate choice indicators (Manson, 1992).

Unlike females, who are philopatric, most male rhesus macaques leave their natal group upon reaching sexual maturity at age 4–5 years (Sade, 1972a; Drickamer and Vessey, 1973). Because in our study groups several males remained in their natal group as adults, we can test whether females chose unrelated natal males (i.e., natal males from other matrilineages) over male relatives as mates.

SUBJECTS AND METHODS

Study groups and site

The subjects of our study were 76 adult (4.5 years and older) and adolescent (~3.5 years old) female rhesus macaques of two social groups (groups T and Q) on Cayo Santiago, a 15-ha island 1 km off the southeast coast of Puerto Rico. Compositions of our

study groups are shown in Table 1. The monkeys of Cayo Santiago are provisioned and are trapped annually for identification marking. A biweekly census of the entire population updates a database of births, deaths, intergroup transfers, and group fissions covering the entire period since 1956. Periodic removal of entire social groups keeps the population between ~600–1,400. Otherwise, the monkeys are free-ranging and are not handled or interfered with (for more information about Cayo Santiago management and history, see Altmann, 1962; Sade et al., 1977; and Rawlins and Kessler, 1986).

Measures and definitions

During the 4–6 month mating season, female rhesus macaques undergo estrous cycles of ~30 days, during which they are sexually active for ~2 weeks. Behavioral endocrinological studies of captive rhesus macaques (Catchpole and Van Wagenen, 1978; Gordon, 1981) show that ovulation occurs during the 4 days preceding the "attractiveness breakdown" (Chapais, 1983b), i.e., the sharp decrease (usually from one day to the next) in the female's sexual attractiveness. The attractiveness breakdown is recognizable by either the end of all sexual activity or, less commonly, the beginning of a 1–2-day period culminating in the end of all sexual activity and characterized by: (1) marked decrease in proceptive behavior, (2) complete cessation of following and courtship by high-ranking males, and (3) toleration by these males of occasional copulations with low-ranking males in plain view (behavior that would have provoked male aggression earlier in the estrous period). The 4 days preceding the attractiveness breakdown will be called the peri-ovulatory period. We were unable to consistently determine the peri-ovulatory periods of adolescent females.

Rhesus macaques are series mounters. Mating pairs engage in up to 100 nonejaculatory mounts (including intromission and 1–7 pelvic thrusts) before the final ejaculatory mount, discernible by a characteristic pause and rigid posture by the male. We defined mount series culminating in ejacu-

lation, as well as (rare) single mounts culminating in ejaculation, as copulations. All analyses in this work that use copulatory frequency or rate as a variable refer to copulations as defined here; incomplete mount series are not included. Because rhesus macaque females do not exhibit reliable morphological signs of estrus, we regarded a female as being in estrus from the day she was first seen in a mount series, or with a mating plug (coagulated ejaculate on her perineum), until the day after her attractiveness breakdown.

A dominance interaction was scored whenever one animal supplanted another (approached and took its spot immediately after the approached animal vacated it) or when the approach of one animal caused another to grimace (retract the lips and cheeks, exposing the teeth), cower (lean downward and away from the approaching animal), or flee. We ascertained male and female dominance relationships separately by arranging individuals in matrices showing winners of dominance interactions along one axis and losers along the other.

An approach was scored when one animal decreased the distance between itself and another animal by at least one half m and stopped or sat, with the final distance between them being less than 4 m. A leave was scored when one animal increased the distance between itself and another animal by at least one half m, with the initial distance between them being less than 4 m. Approaches and leaves taking place at the artificial drinking stations were excluded from analyses, as were "leaves" during chases.

For each dyad, consisting of a male and an estrous female, in which we observed at least 10 summed approaches and leaves, we calculated Hinde's index (Hinde and Atkinson, 1970) by subtracting the proportion of all female leaves within the dyad from the proportion of all female approaches within the dyad. This index measures responsibility for maintaining spatial proximity. Its value can vary from -1.00 (the male is entirely responsible for maintaining proximity) to $+1.00$ (the female is entirely responsible for maintaining proximity). The cutoff of

10 summed approaches and leaves, set arbitrarily before data were analyzed, increases the reliability of Hinde's index as a measure of dyadic relationships. This procedure excluded most (67.8–87.7%, depending on mating season and social group) heterosexual dyads that included females on whom we conducted focal follows during peri-ovulatory periods.

A sexual refusal was scored when a female responded to a male's hip-grasp (grasping the female's hips with both hands from behind) by refusing to present (stand up to be mounted) to begin a mount series. Females refused by either remaining seated or moving away. A "muzzle-up" was scored when a male moved his face close to a female's face, smacked his lips, and then moved away. This is a courtship signal directed toward estrous females (Altmann, 1962).

We obtained individuals' ages and (for natal individuals only) matrilineage memberships from the long-term Cayo Santiago database. A matrilineage is a group of monkeys descended from the same founding ancestress among the females alive in 1956. Group Q contained members of three natal matrilineages. Group T contained members of two natal matrilineages. All references to "relatives" or "kin" in this paper are to matrilineal relatives only. Paternity is not known.

We defined all natal males that were observed to complete at least one copulation as actively breeding natal males. We divided dyads consisting of (1) a female that was a focal subject, and (2) an actively breeding natal male, into two categories: Related dyads consisted of a female and natal male from the same matrilineage. Unrelated dyads consisted of a female and natal male from different matrilineages. The mean coefficient of relatedness (assuming all siblings to be half-siblings) of related dyads was .138 (SD = .14) in 1988, and .117 (SD = .124) in 1989.

Data collection and analysis

One to four observers collected data on 162 days during one complete mating season (June–October 1988) and 7 weeks of a second mating season (June–August 1989).

TABLE 1. Compositions of study groups by age-sex-origin class

| Age-sex-origin class | Group Q | | Group T | |
|---------------------------------------|-------------------------------------|--------------------------------------|--------------------------------------|--------------------------------------|
| | June 1988 | June 1989 | June 1988 | June 1989 |
| Adult ¹ immigrant males | 21 (9.9, .52, 25.8) ⁶ | 18 (12.3, .48, 33.3) ⁵ | 28 (10.4, .59, 21.5) ⁵ | 30 (10.6, .53, 28.8) ⁵ |
| Adult ¹ natal males | 4 (7.0, .88) ⁶ | 6 (7.2, .73) ⁶ | 3 (5.5, .90) ⁶ | 7 (6.1, .50) ⁶ |
| Subadult ² immigrant males | 1 (4.5, .18, 0) ⁵ | 0 | 3 (4.5, .35, 0) ⁵ | 0 |
| Subadult ² natal males | 5 (4.5, .18) ⁶ | 3 (4.5, .13) ⁶ | 3 (4.5, .35) ⁶ | 5 (4.5, .15) ⁶ |
| Adult ³ females | 30 | 36 | 21 | 27 |
| Adolescent ⁴ females | 7 | 6 | 6 | 4 |
| Juveniles and infants | 58 | 74 | 40 | 53 |
| Total group size | 126 | 142 | 104 | 126 |

1. >4.5 years old.

2. 4.5 years.

3. >3.5 years.

4. 3.5 years.

5. (mean age [years], mean dominance rank [proportion of group males dominated], mean group tenure [months]).

6. (mean age [years], mean dominance rank [proportion of group males dominated]).

One observer collected data on 104 days of the intervening birth season. Ad libitum (Altmann, 1974) observations provided information about dominance relationships and cycling females' reproductive states. During the mating season, we conducted 2-hour focal individual follows (Altmann, 1974), divided into 30-minute sampling blocks with no more than 5 minutes between them, on females chosen randomly from those judged to be in estrus on the preceding day. Data from uncompleted 2-hour follows were used in the analyses described here, except for uncompleted 30-minute sampling blocks, which were discarded. During the birth season, JHM conducted 15-minute follows on females chosen according to a sampling schedule. See Manson (1992) for more details on data collection.

To ensure interobserver reliability, all observers were required to meet a standard of 90% concordant records with JHM's, over four consecutive 30-minute focal follows. This procedure established interobserver reliability regarding all behaviors analyzed in this paper. Data collected during these test sessions were not analyzed.

Dominance relationships

We have reported elsewhere (Manson, 1992) that adult males (5.5 years and older) in our study groups formed linear dominance hierarchies. The dominance relation-

ships of some dyads of low-ranking males could not be determined because we observed no interactions between the two animals. The dominance ranks of subadult (~4.5 years old) males were unstable and highly dependent on the presence of allies, usually kin. Females also formed linear dominance hierarchies, which were predictable from the females' genealogical relationships, as in previous studies of this population (e.g., Sade, 1967). Entire natal matrilineages could be ranked relative to one another. Table 1 shows mean dominance rank, age, and (for immigrant males) group tenure of males divided by age class (adult or subadult) and origin (immigrant or natal). Adult natal males tended to be younger and higher-ranking than adult immigrant males. In both study groups in both years of the study, at least 2 adult sons of females of the lowest ranking natal matrilineage held high rank (in the top 30%) in the male dominance hierarchy.

Mate choice behavior

Two behaviors by adult females were correlated with peri-ovulatory copulation rate and therefore qualify as mate choice (Manson, 1992).

Male-estrous female dyads in which smaller proportions of hip-grasps elicited sexual refusals had higher peri-ovulatory copulation rates. Because sample sizes of

TABLE 2. Copulatory success of natal and immigrant males

| Group, year, sample | N ₁ ³ | X ₁ ⁴ | N ₂ ⁵ | X ₂ ⁶ | U ⁷ | P |
|-----------------------------|-----------------------------|-----------------------------|-----------------------------|-----------------------------|----------------|-------|
| Q, 1988, all ¹ | 9 | .043 | 22 | .012 | 72 | .141 |
| T, 1988, all ¹ | 6 | .022 | 31 | .017 | 91 | >.50 |
| Q, 1989, all ¹ | 9 | .028 | 18 | .003 | 42 | .006 |
| T, 1989, all ¹ | 12 | .062 | 30 | .033 | 157 | .151 |
| Q, 1988, adult ² | 4 | .098 | 21 | .012 | 4.5 | .0012 |
| T, 1988, adult ² | 3 | .043 | 28 | .018 | 33 | .347 |
| Q, 1989, adult ² | 6 | .042 | 18 | .003 | 13.5 | .0004 |
| T, 1989, adult ² | 7 | .107 | 30 | .003 | 79.5 | .037 |

1. Includes adult and subadult males.

2. Includes adult males only.

3. Number of natal males.

4. Mean peri-ovulatory hourly copulation rate of natal males.

5. Number of immigrant males.

6. Mean peri-ovulatory hourly copulation rate of immigrant males.

7. Mann-Whitney U.

both dyads and hip-grasps per dyad were small, (1) groups Q and T were combined and (2) "proportion of hip-grasps refused" was treated as a categorical variable (all, some, or no hip-grasps refused). Mating seasons were analyzed separately (1988: Kruskal-Wallis test: $H = 12.33$, $df = 2$, $P < .01$; 1989: $H = 8.316$, $df = 2$, $P < .02$). Trends were in the same direction in both mating seasons when groups T and Q were analyzed separately.

In group Q, but not in group T, dyads with higher Hinde's indices (i.e., greater female responsibility for proximity maintenance) had higher peri-ovulatory copulation rates (1988: Kendall's $\tau = .197$, $N = 77$ dyads, $P = .011$; 1989: $\tau = .226$, $N = 139$, $P = .00008$). Reasons for intergroup differences in this relationship are discussed by Manson (1992).

We could not consistently determine adolescent females' peri-ovulatory periods, so we could not measure peri-ovulatory copulation rates for dyads that included adolescent females. Because mate choice behaviors are defined as those that influence the likelihood of potentially fertile mating, we were therefore unable to demonstrate that any behaviors of adolescent females indicate mate choice.

RESULTS

We collected 1,016 hours of focal data on 66 females during the mating seasons and 406 hours of focal data during the intervening birth season. Of the mating season data,

85 hours on 18 females, collected in August 1989, were discarded from all but one of these analyses because the study ended before the end of the focal female estrous periods, raising problems of data censorship (truncation). Data from truncated estrous periods were used only to classify natal males as actively breeding natal males. We observed 302 copulations, including 74 peri-ovulatory (i.e., potentially fertile) copulations, during focal observations of nontruncated estrous periods. All statistical tests are based on data collected during focal observation only. All tests are two-tailed.

Copulatory success of natal and immigrant males

Among adult and subadult males combined, natal males tended to have higher mean peri-ovulatory hourly copulation rates (averaged over all adult females that were focal subjects during their peri-ovulatory period) than immigrant males, although this result was significant only in group Q in 1989 (Table 2). Considering adult males only, natal males had higher mean peri-ovulatory copulation rates than immigrant males in group Q in both years and in group T in 1989.

Frequency of copulations of matrilineal relatives

Related dyads were less likely than unrelated dyads to complete at least one copulation during focal observation (Table 3: 1988: Yates' corrected $\chi^2 = 25.533$, $P < .001$;

TABLE 3. Numbers of intralineage and interlineage dyads by occurrence of at least one copulation

| | 1988 Mating Season ¹ | | 1989 Mating Season ¹ | |
|----------------------------------|---------------------------------|-----------|---------------------------------|------------|
| | Related | Unrelated | Related | Unrelated |
| Copulating dyads ² | 3 (17.5) | 35 (20.5) | 6 (13.4) | 21 (13.6) |
| Noncopulating dyads ² | 93 (78.5) | 77 (91.5) | 106 (98.6) | 93 (100.4) |
| Copulating dyads ³ | 0 (12.2) | 26 (13.8) | 2 (10.4) | 19 (10.3) |
| Noncopulating dyads ³ | 77 (64.8) | 61 (73.2) | 91 (82.3) | 71 (79.7) |

1. All figures observed value (expected value).

2. Including adolescent females.

3. Excluding adolescent females.

TABLE 4. Responsibility for proximity maintenance in related and unrelated dyads

| Group, year | N ₁ ¹ | \bar{X}_1 ² | N ₂ ³ | \bar{X}_2 ⁴ | U ⁵ | P |
|-------------|-----------------------------|--------------------------|-----------------------------|--------------------------|----------------|-------|
| Q, 1988 | 7 | -.47 | 34 | .12 | 25 | .0012 |
| T, 1988 | 5 | -.33 | 12 | 0 | 19 | .11 |
| Q, 1989 | 20 | -.27 | 35 | -.02 | 224 | .0276 |
| T, 1989 | 1 | .07 | 4 | .16 | 2 | 1.00 |

1. Number of related dyads.

2. Mean Hinde's index of related dyads.

3. Number of unrelated dyads.

4. Mean Hinde's index of unrelated dyads.

5. Mann-Whitney U.

1989: $\chi^2 = 7.966$, $P = .0048$). We obtained similar results after removing adolescent females from these analyses (1988: $\chi^2 = 25.153$, $P < .001$; 1989: $\chi^2 = 14.374$, $P = .0001$). Related dyads that copulated tended to be less closely related than related dyads that were not observed to copulate (1988: \bar{X}_1 coefficient of relatedness of copulating dyads = .052, \bar{X}_2 of noncopulating dyads = .141; 1989: $\bar{X}_1 = .056$, $\bar{X}_2 = .12$). We observed no mother-son copulations and only one copulation between siblings. We observed no peri-ovulatory copulations by related dyads during focal (or *ad lib*) observation. We observed 39 peri-ovulatory copulations by unrelated dyads and 35 peri-ovulatory copulations involving immigrant males, during focal observation.

Male courtship toward kin vs. nonkin

Among natal males that were observed to perform at least one "muzzle-up" display; muzzle-ups were directed at lower hourly rates toward matrilineal kin than toward nonkin (1988: $N = 8$ males, \bar{X} rate toward kin = .157, toward nonkin = .327, Wilcoxon signed ranks test, $P = .025$; 1989: $N = 12$, \bar{X} rate toward kin = .043, toward nonkin = .226, $P = .0093$). Related dyads characterized by at least one hip-grasp were not less

closely related than related dyads in which hip-grasps were not observed.

Responsibility for proximity maintenance

In group Q, estrous adult females were less responsible for maintaining spatial proximity (i.e., Hinde's indices were lower) in related than in unrelated dyads (Table 4). Because female proximity maintenance did not correlate with peri-ovulatory copulation rate in group T, we could not use female proximity maintenance to determine whether females in that group chose unrelated natal males over male relatives as mates. In group T in 1988, there was a nonsignificant trend toward lower Hinde's indices in related than in unrelated dyads. Within the sets of related dyads, coefficient of relatedness was not significantly correlated with Hinde's index in either mating season.

Sexual refusals

We divided dyads in which we observed at least one hip-grasp into three categories depending on what proportion of hip-grasps elicited sexual refusals: all, some, or none. Because sample sizes were small, we combined the "some" category with the "all" and "none" categories for separate Fisher's Exact tests (Table 5). In 1988, related dyads

TABLE 5. Numbers of related and unrelated dyads by proportion of male's hip-grasps refused by the female

| Proportion of hip-grasps refused | 1988 Mating Season | | 1989 Mating Season | |
|----------------------------------|--------------------|-----------|--------------------|-----------|
| | Related | Unrelated | Related | Unrelated |
| All | 5 | 3 | 4 | 2 |
| Some | 0 | 6 | 2 | 10 |
| None | 1 | 24 | 1 | 17 |

had higher proportions of sexual refusals than unrelated dyads, regardless of how the "some" category was collapsed (Fisher's exact probability = .001 or .016). In 1989, the significance of this result depended on how the "some" category was collapsed (Fisher's exact probability = .088 or .008). Within the sets of related dyads, there was no tendency for females to refuse higher proportions of hip-grasps in more closely related dyads.

Birth season grooming relationships

During the birth season, actively breeding natal males that were groomed by adult and/or adolescent females tended to receive grooming at higher hourly rates from females of their own matrilineages than from females of other matrilineages, although this result was not statistically significant (Wilcoxon signed ranks test, $N = 13$ males, \bar{X} grooming by kin = .114 min/hr, \bar{X} grooming by nonkin = .046 min/hr, $P = .101$). There were six related dyads in which we observed at least 10 summed approaches and leaves in both (1) the birth season and (2) the female's estrous period during at least one mating season. In all six, the female was more responsible for proximity maintenance (i.e., Hinde's index was higher) in the birth season than in the mating season (Sign Test, $P = .016$).

DISCUSSION

In this study of free-ranging rhesus macaques: (1) natal males, compared to immigrant males, had equally high or higher copulatory rates with fertile females, (2) natal males copulated less than expected by chance with females to whom they were matrilineally related, (3) natal males courted their matrilineal relatives less than nonrelatives, (4) in one social group, estrous adult females maintained proximity preferen-

tially to unrelated natal males, compared to related males, (5) estrous females refused more hip-grasps of related than unrelated natal males, and (6) females did not groom their male relatives less than unrelated natal males during the birth season. Considering proximity maintenance and sexual refusals in related dyads only, females were equally averse to close and distant relatives. However, related dyads that completed copulations tended to be less closely related than related dyads that were not observed to copulate.

Our finding that estrous females in group Q maintained proximity preferentially to unrelated natal males, compared to related males, does not stem from estrous females' tendencies to maintain proximity preferentially to lower-ranking males (Manson, 1992). Mean male dominance rank did not differ between unrelated and related dyads in group Q.

These results strongly suggest that behavioral propensities inhibit copulations between matrilineal relatives, when they reside in the same social group, in rhesus macaques. Natal males had high copulation rates with fertile females, although this may have occurred because natal males 5 years and older were mostly high-ranking (Table 1), and male dominance rank correlated positively with mean peri-ovulatory copulation rate (Manson, 1992). In any case, natal males certainly did not have lower peri-ovulatory copulation rates than immigrant males. But natal males' mating partners tended to be from matrilineages other than their own. Although more than half of observed peri-ovulatory (potentially fertile) copulations involved natal males, we observed no peri-ovulatory copulations between matrilineal relatives.

Female rhesus macaques appear to be more averse than males to copulating with relatives. Although natal males courted their relatives less intensely than unrelated females, they occasionally sought copulations with relatives (e.g., by grasping their hips), but were rebuffed. Female aversion to adult and subadult male kin is specific to the sexual context. During the birth season, females did not disfavor their male relatives

in forming and maintaining grooming relationships. Limited evidence suggests that females are more responsible for maintaining proximity to their male relatives during the birth season than while they are in estrus.

These results, which are consistent with data on heterosexual interactions in chimpanzees (Tutin, 1979; Pusey, 1980; Goodall, 1986) and homosexuality in Japanese macaques (Chapais and Mignault, 1991), raise three interrelated questions. First, are they generalizable to wild rhesus populations? Second, what proximate psychological mechanisms are responsible for the observed behavioral patterns? Third, why do Cayo Santiago rhesus macaques avoid mating with distant matrilineal relatives, which are unlikely to pose a threat of inbreeding depression?

Published accounts (e.g., Teas et al., 1981; Melnick et al., 1984) suggest that wild rhesus macaque males do not breed in their natal groups, although sample sizes are much smaller than at Cayo Santiago. We speculate that maturing female rhesus macaques develop sexual aversions to males that frequently groom or rest near them and/or their matrilineal relatives. In small wild groups, males reaching sexual maturity experience these aversions, which severely limit their access to mates, and almost invariably emigrate quickly. At Cayo Santiago, provisioning and the absence of predators have produced unusually large social groups and large matrilineages, and an abundance of "leisure" time for grooming and relaxed proximity. Nevertheless, a disproportionately large amount of affiliative behavior still occurs among matrilineal relatives (e.g., Sade 1972b). Thus females develop sexual aversions to matrilineal relatives, even distant ones, based on the proximate cues of grooming and spatial proximity. Because males have sexual access to many unrelated females in their natal groups, some males remain and breed for several years before emigrating. However, adult natal males sometimes face situations in which the only sexually receptive unrelated females in their group are (1) actively seeking copulations with other males (Man-

son, 1992) or (2) being monopolized by higher-ranking males. They may then court their female relatives, although this tactic has a low probability of success.

Gender differences in sexual aversion to relatives may explain why some researchers (e.g., Missakian, 1973) have found no evidence of inbreeding avoidance in Cayo Santiago rhesus macaques. Males frequently attack estrous females that are accompanying lower-ranking males (Chapais, 1983b; McMillan, 1983; Manson, 1991). The effect of this coercive mating tactic on the frequency of intralineage mating probably varies with the dominance relationships and demographic structure of the social group. For instance, if the alpha male and other high-ranking males are from the same natal matrilineage, and most of the group's females are from that matrilineage, natal high-ranking males may harass and sequester their relatives intensively enough to obtain numerous copulations with them. A mere examination of the distribution of copulations among heterosexual dyads would show no tendency toward inbreeding avoidance, whereas detailed behavioral records might show female sexual aversion toward related males.

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LITERATURE CITED

- Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* 49:227-265.
- Altmann SA (1962) A field study of the sociobiology of rhesus monkeys (*Macaca mulatta*). *Ann. N.Y. Acad. Sci.* 102:338-435.
- Catchpole HR, and van Wagenen G (1978) Reproduction in rhesus monkeys, *Macaca mulatta*. In GH Bourne (ed.): *The Rhesus Monkey*. New York: Academic Press, pp. 118-139.
- Chapais B (1983a) Matriline membership and male rhesus reaching high ranks in their natal troops. In RA Hinde (ed.): *Primate Social Relationships: An Integrated Approach*. Oxford: Blackwell, pp. 200-208.
- Chapais B (1983b) Reproductive activity in relation to male dominance and the likelihood of ovulation in rhesus monkeys. *Behav. Ecol. Sociobiol.* 12:215-228.
- Chapais B, and Mignault C (1991) Homosexual incest avoidance among females in captive Japanese macaques. *Am. J. Primatol.* 23:171-183.
- Clutton-Brock TR, and Harvey PH (1976) Evolutionary rules and primate societies. In PPG Bateson and RA Hinde (eds.): *Growing Points in Ethology*. Cambridge: Cambridge University Press, pp. 195-237.
- Drickamer LC, and Vessey S (1973) Group changing in free-ranging male rhesus monkeys. *Primates* 14:359-368.
- Fox, R (1980) *The Red Lamp of Incest*. New York: Dutton.
- Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press.
- Gordon TP (1981) Reproductive behavior in the rhesus monkey: social and endocrine variables. *Am. Zool.* 28:1140-1162.
- Halliday TR (1983) The study of mate choice. In P Bateson (ed.): *Mate Choice*. Cambridge: Cambridge University Press, pp. 3-32.
- Hammerstein P, and Parker GA (1987) Sexual selection: games between the sexes. In JW Bradbury and MB Andersson (eds.): *Sexual Selection: Testing the Alternatives*. New York: John Wiley & Sons, pp. 119-142.
- Hartung J (1985) Book review of Shepher J (1983) *Incest*. A Biosocial View. New York: Academic Press. *Am. J. Phys. Anthropol.* 67:169-171.
- Hinde RA and Atkinson S (1970) Assessing the roles of social partners in maintaining mutual proximity as exemplified by mother-infant relations in rhesus monkeys. *Anim. Behav.* 18:169-176.
- Leavitt GC (1990) Sociobiological explanations of incest avoidance: A critical review of evidential claims. *Am. Anthropol.* 92:971-993.
- Manson JH (1991) Female mate choice in Cayo Santiago rhesus macaques. Ph.D. dissertation, University of Michigan.
- Manson JH (1992) Measuring female mate choice in Cayo Santiago rhesus macaques. *Anim. Behav.* 44:405-416.
- McMillan CA (1983) Factors affecting mating success among rhesus macaque males on Cayo Santiago. Ph.D. dissertation, SUNY Buffalo.
- McMillan CA (1986) Lineage-specific mating: Does it exist? In RG Rawlins and MJ Kessler (eds.): *The Cayo Santiago Macaques*. Albany: SUNY Press, pp. 201-217.
- Melnick DJ, Pearl MC, and Richard AF (1984) Male migration and inbreeding avoidance in wild rhesus monkeys. *Am. J. Primatol.* 7:229-243.
- Missakian EA (1973) Genealogical mating activity in free-ranging groups of rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. *Behaviour* 45:224-240.
- Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim. Behav.* 27:1-36.
- Paul A, and Kuester J (1985) Intergroup transfer and incest avoidance in semifree-ranging Barbary macaques (*Macaca sylvanus*) at Salem (FRG). *Am. J. Primatol.* 8:317-322.
- Pereira ME, and Weiss ML (1991) Female mate choice, male migration, and threat of infanticide in ringtailed lemurs. *Behav. Ecol. Sociobiol.* 28:141-152.
- Pusey AE (1980) Inbreeding avoidance in chimpanzees. *Anim. Behav.* 28:543-582.
- Pusey AE, and Packer C (1987) Dispersal and philopatry. In BB Smuts, DL Cheney, RM Seyfarth, RW Wrangham, and TT Struhsaker (eds.): *Primate Societies*. Chicago: University of Chicago Press, pp. 250-266.
- Ralls K, and Ballou J (1982) Effects of inbreeding on infant mortality in captive primates. *Int. J. Primatol.* 3(4):491-505.
- Rawlins RG and Kessler MJ (1986) The history of the Cayo Santiago colony. In RG Rawlins and MJ Kessler (eds.): *The Cayo Santiago Macaques*. Albany: SUNY Press, pp. 13-45.
- Sade, DS (1967) Determinants of dominance in a group of free-ranging rhesus monkeys. In SA Altmann (ed.): *Social Communication Among Primates*. Chicago: University of Chicago Press, pp. 99-114.
- Sade DS (1968) Inhibition of mother-son mating among free-ranging rhesus monkeys. *Sci. Psychoanal.* 12:18-38.
- Sade DS (1972a) A longitudinal study of social behavior of rhesus monkeys. In R Tuttle (ed.): *Functional and Evolutionary Biology of Primates*. Chicago: Aldine-Atherton, pp. 378-398.
- Sade DS (1972b) Sociometrics of *Macaca mulatta*. I. Linkages and cliques in grooming matrices. *Folia Primatol.* 18:196-223.
- Sade DS, Cushing K, Cushing P, Dunaif J, Figueroa A, Kaplan JR, Lauer C, Rhodes D, and Schneider J (1977) Population dynamics in relation to social structure on Cayo Santiago. *Yrbk. Phys. Anthropol.* 20:253-262.
- Sade DS, Rhodes DL, Loy J, Hausfater G, Breuggeman JA, Kaplan JR, Chepko-Sade BD, and Cushing-Kaplan K (1984) New findings on incest among free-ranging rhesus monkeys. *Am. J. Phys. Anthropol.* 63:212-213.
- Shepher J (1983) *Incest. A Biosocial View*. New York: Academic Press.

- Takahata Y (1982) The socio-sexual behavior of Japanese monkeys. *Z. Tierpsychol.* 59:89–108.
- Teas J, Richie TL, Taylor HG, Siddiqui MF, and Southwick CH (1981) Natural regulation of rhesus monkey populations in Kathmandu, Nepal: rhesus monkey groups near Kathmandu, Nepal show demographic profiles of intrinsic population stability. *Folia Primatologica* 35:117–123.
- Thornhill NW (1991) An evolutionary analysis of rules regulating human inbreeding and marriage. *Behav. and Brain Sci.* 14:247–293.
- Trivers RL (1972) Parental investment and sexual selection. In B Campbell (ed.): *Sexual Selection and the Descent of Man 1871–1971*. Chicago: Aldine, pp. 136–179.
- Tutin CEG (1979) Mating patterns and reproductive strategies in a community of wild chimpanzees (*Pan troglodytes schweinfurthii*). *Behav. Ecol. Sociobiol.* 6:29–38.
- Waser P, Austad S, and Keene B (1986) When should animals tolerate inbreeding? *Am. Nat.* 128:529–537.