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Received 30 May 1983 and
accepted 5 July 1983

Keywords: Inbreeding avoidance, incest, dominance, sexual behavior.

The Role of Dominance and Intrafamilial Bonding in the Avoidance of Close Inbreeding

The patterns of stump-tail macaque heterosexual mounts recorded at the Yerkes Regional Primate Research Center Field Station demonstrate that consanguineous matings are avoided under conditions of restricted migration. The frequencies of both son/mother and maternal half-sibling mounts were found to be significantly lower than expected by chance. Contrary to earlier reports which suggest that maternal dominance inhibits mounting attempts by male offspring, intradyadic dominance is not a significant factor in the inhibition of mating between close kin. Close matrilineal association is regarded as the proximate mechanism for kin recognition. This behavioral aversion may function to promote migration in most mammalian species, and it may underlie the nearly universal avoidance of incest among human groups.

1. Introduction

The widespread existence of an incest taboo has received considerable attention in theories that address the evolution of human mating patterns. Recently, primatologists have also observed a parent, sibling and offspring mating avoidance through intergroup transfer among feral groups of monkeys and apes (Harcourt *et al.*, 1976; Packer, 1979; Pusey, 1980). While migration patterns undoubtedly decrease the likelihood of close inbreeding, studies on brown quail (Bateson, 1978), laboratory-housed deermice (Hill, 1974) and captive primates (Bramblett, 1983) have supported the recently resurrected hypothesis that early and intimate familial association fosters a sexual aversion which serves to minimize extensive inbreeding (Westermarck, 1891).

As an alternative hypothesis, some researchers suggest that the relatively higher social dominance of the mother may sufficiently inhibit mounting attempts by male offspring. Sade (1968) claims that since Cayo Santiago rhesus mothers usually are dominant to sons that do not migrate, a low son/mother mounting frequency is observed. Abernathy (1974) presents a supporting hypothesis that male dominance facilitates sexual expression while female dominance, including maternal dominance among the Cayo Santiago rhesus, suppresses it. Both Sade and Abernathy tend to dismiss the observed cases of son/mother mating avoidance as simple expressions of the intradyadic dominance relationship.

Others, expressing disbelief in the ethological reports, consistently maintain that incest avoidance is purely a cultural phenomenon. Livingstone (1980) suggests that instances of close inbreeding among non-human primates are less likely to be reported, and that this inherent bias has resulted in the erroneous belief in a panmammalian inbreeding avoidance mechanism. Harris (1980) also dismisses the primate field reports, claiming that the avoidance of consanguineous sexual activity among monkeys and apes is explicable in

terms of "male dominance and sexual rivalry". Harris further concludes that "there is no experimental evidence suggesting that there is an aversion to incest *per se* among monkeys and apes" (1980, p.268). On a purely theoretical basis, the avoidance of close inbreeding would be expected for sexually-reproducing species, given the cost of mate acquisition and the benefit of increased genetic variability accompanying the origin of biparental reproduction. Clearly, most genetic advantages of biparental reproduction over parthenogenesis would be unrecognized if sexually-reproducing species did not outbreed. From a behavioral viewpoint, the propensity to avoid mating with parents, siblings and offspring would be an unlikely addition to the existing cost of mate acquisition unless it offered concomitant and offsetting advantages, such as fitness increases from heterosis (Murray, 1980). Bengtsson (1978) has explored the cost/benefit relationship in the avoidance of inbreeding in primates, concluding that the costs of inbreeding usually exceed those costs of securing unrelated mates. While both genetical and behavioural aspects of inbreeding avoidance have been explored extensively in theory, few investigations have addressed these concerns experimentally.

The purpose of this investigation was

- (1) to determine the extent of son/mother and maternal half-sibling mounts in a captive group of non-human primates for which avoidance by means of emigration is not possible,
- (2) to test the role of intradyadic dominance in the inhibition of mating, and
- (3) to assess preliminarily the importance of intrafamilial bonding in the avoidance of close inbreeding.

2. Methods

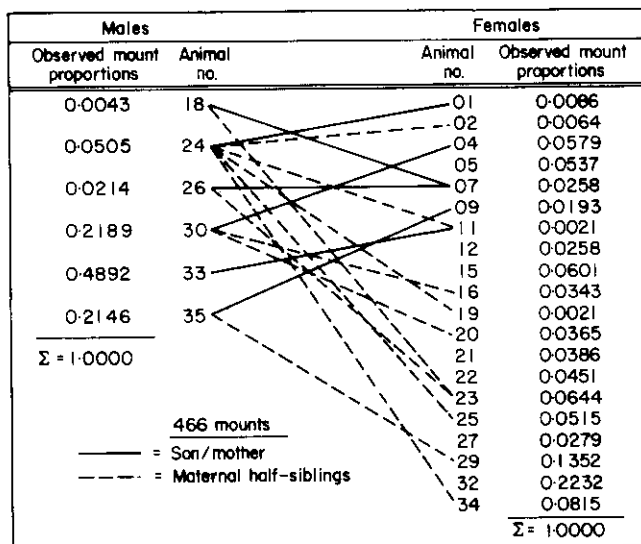
The subjects of the study were a captive group of stump-tail macaques (*Macaca arctoides*) housed at the Yerkes Regional Primate Research Center Field Station near Lawrenceville, Georgia. The group, numbering 39 animals, was housed in a 28.4 m × 32.7 m open-air compound, and was provisioned daily with monkey chow and fresh fruit. Observations were made from a tower overlooking the enclosure. All animals were in full view during data collection. The group and facilities are described in greater detail in Smith & Peffer-Smith (in press).

All observed adult heterosexual mounts were recorded on an *ad libitum* basis (Altmann, 1974). Technicians, who were not aware of the research design, were simply instructed to note separately any observed mounts during regular observation sessions. A total of 466 mounts was recorded between six focal adult males and 20 focal adult females. Mounts were defined minimally as intromission accompanied by pelvic thrusts. The scoring did not distinguish between mounts meeting these minimum criteria and mounts terminating with ejaculation and/or copulatory tie (Chevalier-Skolnikoff, 1975). These data represent an estimated 1100 hours of observation over a 21-month period. Dominance rankings were determined by dyadic food competition tests (Popp & DeVore, 1979) conducted on a daily basis. The dominance matrix was derived from over 3000 interactions over the same 21-month period. Three adult feral males were excluded from these analyses since they had no kin. Mounts and dominance interactions of juveniles and infants were not recorded.

Each animal's observed proportion of the 466 recorded mounts is shown in Figure 1. The mounting proportions are simply relative measures of overall mounting activity. The son/mother relationships are shown by the solid lines and opposite-sex maternal

half-siblings are indicated by broken lines. Paternal genetic relationships were not known, although the age distribution of the focal animals precluded father/daughter relationships.

Figure 1. Mounting proportions and maternal genetic relationships among the 26 focal animals.



In order to determine whether son/mother and sibling mounts were avoided, the observed son/mother, sibling and non-kin mounts were compared with those expected by chance. In determining expected mounting frequency, we proceeded from the premise that expected mounting frequency would be higher for those dyads whose members exhibit greater overall mounting activity. Therefore, the expected proportion of son/mother mounts was established by multiplying the observed proportion of a respective male's mounts by his mother's observed proportion. Each dyad's expected mount frequency was then derived by multiplying the respective proportion-product by the 466 total mounts.

The expected frequencies of sibling and non-kin mounts were computed in the same manner. Since one male (no. 33) had no female siblings, he was not included in the sibling analysis. In two cases where a male had more than one female sibling, the mount proportions for the female siblings were added before multiplying by the male's proportion. Similarly, expected non-kin mounts were derived by multiplying the pooled female non-kin proportions by the respective male's proportion. The predetermined level of significance for all statistical test was $P \leq 0.05$.

3. Results and Discussion

A G-statistic replicated test (log likelihood ratio test using multiple samples) was used to determine the relationship between each focal male's observed and expected mounting frequencies with the animal(s) from each category of relatedness. The G-statistic has several advantages since the data for several samples can be partitioned or pooled for goodness of fit as well as tested for sample heterogeneity using the interaction G-test (Sokal & Rohlf, 1981 p. 704). Since the expected frequencies in some cells were inadequate size

(<5), the goodness-of-fit test was not partitioned for individual samples. Two parts of the interaction G-test were analysed: the heterogeneity test to determine the variability among samples; and the pooled G-test to determine goodness of fit between the pooled observed and expected values.

The results of the analysis of heterogeneity of data for the son/mother and sibling data were compared to the respective critical values from the chi-square distribution. Neither the samples for the son/mother ($G_H = 9.19$, 5 d.f., $P > 0.05$) nor sibling ($G_H = 1.69$, 4 d.f., $P > 0.05$) data were significantly heterogeneous. This homogeneity among sample dyads demonstrates that whatever the relationship between observed and expected frequencies, the within-group samples do not differ significantly from one another.

In order to test whether the observed son/mother and sibling mounts differed significantly from the expected values, the results of the pooled G-tests were also compared to the respective critical values. The result of the pooled goodness-of-fit test showed that observed mounts were significantly lower than expected for both son/mother ($G_P = 5.28$, 1 d.f., $P < 0.025$) and sibling ($G_P = 6.31$, 1 d.f., $P < 0.025$) dyads.

These analyses demonstrate not only that the deviations of the observed from the expected are significant for both son/mother and sibling mounts, but also that all observed mounts for both groups are consistently lower than expected by chance. These combined analyses, therefore, eliminate the possibility that the significantly lower son/mother and sibling mounts were due to variation among experimental subjects.

In order to assess the role of dominance in this observed kin mating avoidance, relative dominance relationship and frequency of consanguine mounts were compared for all subject dyads (Table 1). Table 1 (a) shows the son/mother dominance relationships and the total number of observed mounts between each respective dyad. The dominant member of the pair is shown in bold type, with sons in the left column and the mothers on the right. The only son/mother dyad that was observed to mount was no. 30/no. 04. The mother in this case (no. 04) was clearly dominant to her son, despite the three mounts. The high-ranking male (no. 33) is particularly interesting since he mounted all unrelated

Table 1

Comparison of intradyadic dominance and observed mounting frequency. The dominant animal in each dyad is shown in bold type
(a) Son/mother dominance and mounting frequency (b) Male and female sibling dominance and mounting frequency

(a) Son/mother dyads		(b) Maternal half-sibling dyads	
♂ no./♀ (no.)	Number of mounts	♂ (no.)/♀ (no.)	Number of mounts
18/ 07	0	18 /23	0
24/ 01	0	24 /02	1
		24/ 11	0
		24 /19	1
26 /07	0	24 /25	0
		24 /34	1
30/ 04	3	26 /23	0
		30 /16	3
33 /11	0	30 /20	3
35 /09	0	35 /29	6

females in the group, but was never observed to mount or attempt to mount his subordinate mother.

The data for maternal half sibling dyads are illustrated in Table 1 (b). The relationship between the two variables is not as clear for these data, since for nine of the ten sibling dyads, the male-sibling was dominant to his sister. Recall, however, that despite this male-sibling dominance, males mounted their female siblings less than expected.

In order to assess quantitatively the relationship between dominance and mount, data were combined for all 16 son/mother and sibling dyads. A Point-Biserial test was used to determine the correlation between dominance and kin mounts. The Point-Biserial correlation coefficient (Hinkle *et al.*, 1979, p. 97–99) is designed to determine the association between a discrete characteristic (intradynamic dominance) and a corresponding variable on either the interval or the ratio scale (frequency of mounts). The result ($r_{pb} = 0.055$) is not significant ($t = 0.026$, 14 d.f., $P > 0.05$), clearly indicating that dominance is not an important variable in the suppression of kin mating in this group.

4. Conclusions

These data offer several conclusions. First, inbreeding avoidance among close maternal kin is exhibited in this group as a behavioural aversion and not simply as a consequence of intergroup transfer. Second, dominance, which undoubtedly plays an important role in the mating patterns within primate groups, cannot account for this observed inbreeding avoidance behavior.

If this and other accounts of non-kin mating preference in captive groups are validated as a general mammalian pattern, one of two proximate mechanisms may be involved: (1) the intimate familial association between the mother and male offspring, and between opposite-sexed siblings, may affect sexual expression at maturity—in other words, selection may have shaped behavior in such a way that the intimate bond within the matriline serves as a sufficient cue for consanguinity; or (2) animals may refrain from mating with relatives through kin recognition mechanisms, such as olfactory or other distinctive phenotypic signatures (Beecher, 1982). Innate recognition of paternal relatives has been shown with young pigtail macaques (Wu *et al.*, 1980), among other animals (Waldman & Adler, 1979), and is of central importance to Hamilton's (1964) kin selection hypothesis. However, among captive rhesus macaques where paternity is known, a high rate of father-daughter and paternal half-sibling inbreeding has been reported (Smith, 1982). Other investigators (Hoogland, 1982; Bramblett, 1983) have shown that the extent of sexual interaction between maternally-related kin is inversely proportional to the intensity and duration of the uterine-group social bond. These studies lead us to suggest cautiously that early and intimate uterine-group association, rather than direct phenotypic recognition, is the probable proximate mechanism for avoidance of mating between maternally-related kin.

The ultimate result of either a kin-mating aversion or the dispersal of one or both sexes is an increase in genetic variability. How these two behaviors interrelate is not yet clear, although Hoogland (1982) suggests that male dispersal patterns in black-tailed prairie dogs are secondary consequences of the female's refusal to mate with close kin. Maynard Smith (1978) also suggests that the availability of mates within the natal group likely influences dispersal patterns in all animals. The available evidence indicates that kin-mating aversion may function to promote migration in most mammalian species, and it may underlie the nearly universal avoidance of incest among human groups. Further

research is undoubtedly required on the proximate mechanisms as well as on the yet unexplored relationship between inbreeding avoidance behavior and the retention of genetic variability as a possible ultimate cause.

The authors thank Dr Curt D. Busse, Mr Thomas P. Gordon, Dr Frank E. Poirier and Dr Patricia L. Whitten for their helpful comments during the development of this paper. We acknowledge the statistical consultation of Dr Paul W. Sciulli and the technical assistance of Mr Eric S. Bour, Ms Frances W. Haman, Ms Susan P. Martin, Ms Patricia G. Peffer-Smith and Ms Peggy M. Plant. The research was supported in part by U.S. Public Health Service Grants DA-02128, RR-00165 and RR-00167 (Division of Research Resources, National Institutes of Health) to the Yerkes Regional Primate Research Center of Emory University. The first author acknowledges support from Sigma Xi, The Scientific Research Society and an Ohio State University Alumni Research Grant.

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