

Grooming and Consort Partner Selection in a Troop of Japanese Monkeys (*Macaca fuscata*)

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The Arashiyama West troop of Macaca fuscata consists of 150 monkeys transported from Kyoto, Japan, in February 1972 to their present location near Laredo, Texas. At this site the animals range over 108 acres and during the study period were only minimally provisioned and disturbed. In the report of a 3-year study of consort partner selection it was suggested that yearlong social bonds within the troop appeared to be distinct from consort bonds formed during mating season. Like Sade, we consider grooming to be a good measure of yearround affinitive bonding in macaques. This study compares the pairs formed for consorting with those formed for yearlong grooming activities, by the 94 individuals who formed consort relationships during the mating season of 1973-1974. It was found that yearlong grooming involved pairs of monkeys which were significantly different from those for consorting. Grooming was relatively frequent between related monkeys, while consort partners were seldom related. In addition, yearlong grooming patterns were not disrupted during mating season. These results suggest that consort and grooming activities are behavioral expressions of two important social networks, involving mutually exclusive social bonds.

KEY WORDS: primate; *Macaca fuscata*; incest; sex; grooming.

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INTRODUCTION

Two forms of social interaction in primate groups, allogrooming and consorting, have individually received a great deal of attention in studies concerned with primate affiliative bonding patterns. We believe that the choice of partners for each of these activities is highly structured by, and hence should illuminate, its own set of underlying relationships, or what Hinde (1974) has called the "infrastructure" of a primate group.

GROOMING

Social grooming is thought to be important in promoting, maintaining, and reinforcing cohesive bonds within a group of primates (Lindburg, 1973; Rosenblum *et al.*, 1966; Drickamer, 1976). In most groups of Old World primates, grooming is the most frequent form of overt social interaction (Sade, 1965; Rowell, 1972). As a result, it has been fundamental in our assessment of primate social relationships.

It is generally agreed that selection of grooming partners is associated with such variables as sex, rank, kinship ties, and the season in which the interaction occurs. For example, Oki and Maeda (1973) found that grooming in Japanese monkeys occurred primarily between females, especially between mothers and their offspring; while Drickamer (1976) reported that in rhesus monkeys both adult females and juveniles groomed most frequently with members of their own age-sex class and that these incidents accounted for 85% of the grooming for the entire year.

Special preference for grooming partners within kinship groups has been found in most studies of macaques. Sade (1965) reported that, within free-ranging rhesus groups on Cayo Santiago, related pairs, which constituted 15% of the total possible grooming combinations, accounted for 62-64% of the observed grooming bouts. Loy and Loy (1974) found that matrilineally related rhesus monkeys, which constitute only 6.6% of all possible pair combinations, accounted for 34.3% of the total grooming episodes. They went on to suggest the possibility of a mathematical constant between the number of related monkeys in a group and the amount of interrelative grooming which will occur.

Sade (1965) also reported that even during the mating season a high percentage of grooming continued to occur between related monkeys. Somewhat differently, Drickamer (1976) determined that a significant rise in grooming during the mating season was primarily a reflection of increased grooming between adult males and adult females. However, he attributed the surge in grooming not just to the formation of consort pairs in which mutual grooming does occur but also to the fact that increased disturbance of yearlong social activities

requires a counteracting and appeasing force. Hence normal grooming relations may actually receive extra attention during the mating season. These two pieces of research suggest that for macaques the set of social relations within genealogies is important and exclusive enough not to be significantly disrupted by the seasonal formation of consort bonds.

CONSORTING

The variables associated with the selection of consort partners in macaques have not been so extensively and specifically studied as those influencing grooming. However, rank, kinship, and previous friendly bonds have all been suggested as determining factors in the choice of consort partners. Although the concept of "consort" is ubiquitous in the primate literature, until recently only two studies (Bernstein, 1963; Reynolds, 1970) had focused directly on the phenomenon.

More recently, Fedigan and Gouzoules (1979) examined consort partner selection in the Arashiyama West troop of Japanese monkeys at some length, testing the hypotheses that monkeys choose their consort partners on the basis of the following criteria: age, rank, year-round affiliative bonds, kinship bonds, and idiosyncratic features. Data were collected over three mating seasons and three birth seasons and generated a sample of 518 heterosexual consorts and 178 homosexual consorts and 60 resultant live births. The last were used to determine the probable conception period and the characteristics of consort partners around the time of conception.

Age was found to be a significant factor in heterosexual partner choice (monkeys choose partners of their own age group) but not in homosexual partner choice. Rank was found to be significant for only 1 of the 3 years and only in heterosexual partner choice. In addition, high-ranking individuals were not more likely to consort with females before or during their probable conception period. This differs from Stephenson's (1974) finding that high-ranking Japanese macaque males mate preferentially with high-ranking females and concentrate their consort activities on preconception females. However, it does substantiate Hanby *et al.*'s (1971) and Eaton's (1974) data for the Oregon troop of *Macaca fuscata*, which showed that conception had no discernable effect on the type of consort partner and that high-ranking males did not inseminate proportionately more females.

Consort partner selection in both Japanese and rhesus macaques has often been found to be associated with preferences for nonkin (Bernstein, 1963; Enomoto, 1974; Hanby and Brown, 1974; Stephenson, 1974). Fedigan and Gouzoules also found that the Arashiyama West monkeys chose both their heterosexual and their homosexual consort partners outside of their matrilineal group. In addition, they suggested that yearlong social bonds and previous

friendly bonds within the troop appeared to be distinct from consort bonds formed during the mating season. Even adult central males, which usually originate in other troops and thus do not have closely related kin in the troop, appear to form stable affiliative bonds with certain females (the Japanese call these "special relationships") but to consort in mating season with different females. Enomoto (1974) also suggested that in his study troop of Japanese monkeys the individuals who exhibited affiliative bonds during the majority of the year did not tend to form consort bonds during mating season. If true, this phenomenon in Japanese macaques may represent a contrast to other species such as rhesus monkeys and common baboons, where it has been suggested that individuals often choose their consort partners on the basis of previous long-term friendly bonds (Hinde, 1974; Lindburg, 1971; Rowell, 1972; Ransom and Ransom, 1971).

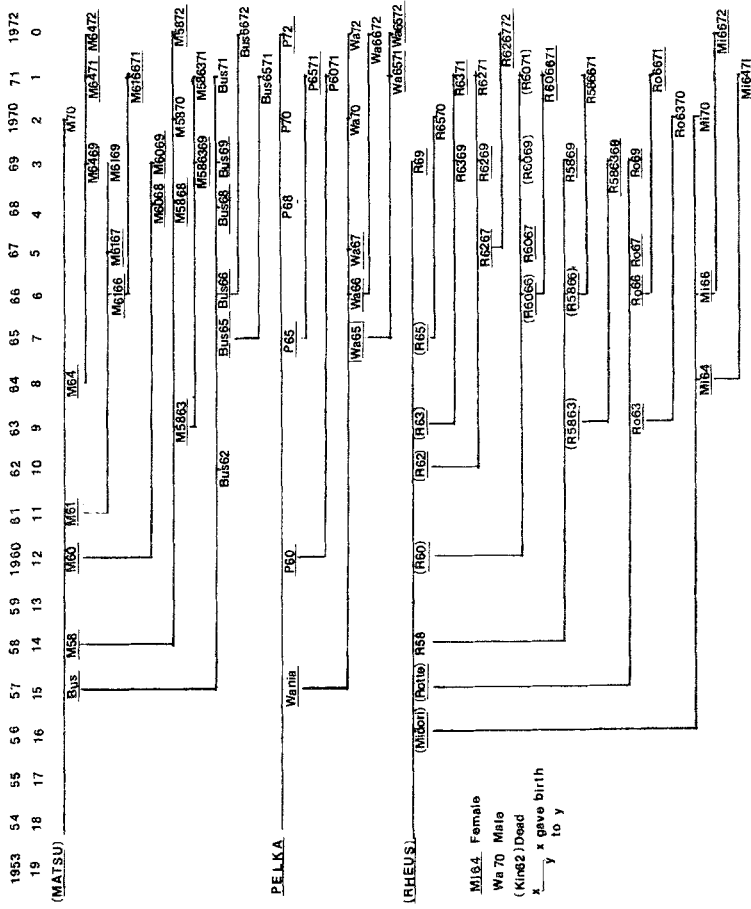
PURPOSE OF THIS STUDY

The present study continues the earlier one of Fedigan and Gouzoules, by testing their suggestion that yearlong social bonding is distinct from seasonal consort bonding in the Arashiyama West troop of Japanese monkeys. Since grooming is considered to be a good measure of long-term affiliative bonding (Sade, 1965), this study compares the selection of grooming partners throughout a year to the selection of consort partners during the mating season. The goal is to determine whether grooming and consorting reflect different or similar networks of social relationships and to assess the impact of seasonal consort bonding on yearlong grooming activities.

THE STUDY GROUP

The Arashiyama West troop of *Macaca fuscata* consists of 150 animals transported from Kyoto, Japan, in February 1972 to their present location near Laredo, Texas. At this site the animals are free to range over 108 acres of local arid brushland. Minimal provisioning and minimal human interference during the study period were maintained.

Japanese primatologists first contacted the troop near Kyoto in 1954, and these researchers were soon able to identify individuals and, over time, to chart genealogies for the troop. Since paternity is impossible to ascertain through observation alone, kinship is traced through female lines. The genealogies have been used in this study to assign individuals both to uterine groups ("kin") and to specific "family" groups. This "family" refers to a mother, sibling, or offspring. Individuals within a "kin" group, on the other hand, are those belonging to the same matrilineage. These relationships are shown in Fig. 1.



SUBJECT: Wa65
FAMILY: Wania, Wa66, Wa67, Wa70, Wa72, Wa6571, Wa6572
KIN: Pelka, P60, P65, P68, P70, P72, P6571, P6071, P6672
 of Koyama (1967).

For further information on this troop, both before and after transplantation, the reader is referred to Hazama (1964), Koyama (1967, 1970), Norikoshi (1971), Koyama *et al.* (1975), Clark and Mano (1975), Gouzoules *et al.* (1975), Fedigan (1976), and Fedigan and Fedigan (1977).

METHODS

The data used in this study were collected as part of a larger research project being carried out by the second author from 1972 to 1974 on the Arashiyama West troop. The grooming data utilized here were collected during the 12-month interval from April 4, 1973 to April 4, 1974, a period which included both a 5-month mating season and a 7-month nonmating season.

The consort data were collected daily during the 5 months (November 1973 to April 1974) of mating season, with samples taken at all hours of the day. For complete details, see Fedigan and Gouzoules (1979). For each sample the whole troop was surveyed on an *ad libitum* basis and all instances of consorting were recorded. Given the large size and free-ranging nature of the troop, it was virtually impossible to certify that every monkey was sampled on every survey. Nevertheless much time was devoted to searching the area on the periphery of the main body of the troop, in an effort to compensate for the "observability bias" of *ad lib* sampling and to locate and record the activities of the peripheral and less observable monkeys.

Grooming data were collected in the same manner, although sampling was performed every few days instead of daily, and it continued through both the 5-month mating season and 7-month nonmating season. Thus the two methods of collection were similar but the two sets of resulting data are independent.

The study sample was limited to the 94 members of the troop which formed consort relations, either homosexual and/or heterosexual, during the mating season (November 1973 until April 1974). It was possible to compare, using SPSS cross-tabulation, the selection of grooming partners made during the mating season, nonmating season, and the entire 12-month period of the study (April 4, 1973, to April 4, 1974) with the choice of consort partners made during the mating season of that year.

RESULTS

Grooming and Consorting Partners Compared

The following hypothesis was tested:

The partners chosen for grooming during a 1-year period (April 4, 1973, to April 4, 1974) differ significantly from

those chosen for consorting during the mating season of that year (November 9, 1973, to April 4, 1974).

As seen in Table I, the results of a χ^2 analysis comparing the formation of pairs for grooming and those for consorting show that the two activities involved significantly different pairs of monkeys. Only 49 of the 354 consort pairs were seen as grooming pairs. Similarly, while 345 different grooming pairs were formed, only 49 of these were also consort pairs. Thus it appears that the grooming partners chosen throughout the entire year were significantly different from consort partners chosen during mating season. These two social activities seem to reflect different affiliative bonds.

The nature of this difference in pair formations was then examined by analyzing the grooming and consorting patterns separately, in terms of kin and sex preferences for each behavior.

Patterns in the Selection of Grooming Partners

Table II shows how pairs of unrelated and related monkeys groomed, during the three test periods, nonmating season, mating season, and the entire year. It should be reiterated that a reference to "related" animals means that the individuals belong to the same matrilineage (Fig. 1). Thus pairs of animals belonging to the same "family" or "kin" group would be included under the title "related" in these tables. It should be noted that assignment of these relationships to pairs is to some extent an arbitrary interpretation by the authors of the available genealogy for the troop.

In terms of the number of grooming pairs formed in all test periods, unrelated pairs outnumber related pairs (e.g., 171 to 96 for nonmating season, 87 to 68 during the mating season, Table II). However, if we look at the per-

Table I. Comparative Analysis of Grooming Pairs and Consort Pairs^a

	Number of pairs which did not groom	Number of pairs which <i>did</i> groom	Total
Number of pairs which <i>did</i> not consort	3721 (85.1%)	296 (6.8%)	4017 (91.9%)
Number of pairs which <i>did</i> consort	305 (7.0%)	49 (1.1%)	354 (8.1%)
Total	4026 (92.1%)	345 (7.9%)	

^a Corrected $\chi^2 = 17.87100$, 1 df; significance = 0.0000.

centage of pairs formed out of the total number of possible pairs in each category, then quite a different picture emerges, one that resembles that drawn by Sade (1965) and Loy and Loy (1974). For example, while only 6% of the possible number of nonrelated pairs groomed during the total year, 20% of the total number of possible related pairs did groom. Further, when related monkeys are then divided into "kin" and "family," we find that 53% of the total number of possible family grooming pairs did, in fact, groom.

When the data from Table III are considered, an even clearer picture of grooming partner preference emerges. This table shows absolute frequencies of grooming bouts between related and unrelated monkeys (as opposed to the number of pairs and percentages of pairs shown in Table II). The number of observed grooming bouts between related monkeys is greater than the number

Table II. Analysis of Grooming Pairs

	Pairs of unrelated monkeys	Pairs of related monkeys	Kin	Family
Nonmating season				
Number of possible pairs within group	3818%	553%	451%	102%
Number of pairs formed	171	96	45	51
$\frac{\text{Pairs formed}}{\text{Pairs possible}} \times 100$	4%	17%	10%	50%
$\frac{\text{Pairs formed}}{\text{Total pairs}} \times 100$	64%	36%	17%	19%
Mating season				
Number of possible pairs within group	3818	553	451	102
Number of pairs formed	87	68	29	49
$\frac{\text{Pairs formed}}{\text{Pairs possible}} \times$	2%	12%	6%	40%
$\frac{\text{Pairs formed}}{\text{Total pairs}} \times 100$	56%	44%	19%	25%
Total year				
Number of possible pairs within group	3818	553	451	102
Number of pairs formed	229	116	62	54
$\frac{\text{Pairs formed}}{\text{Pairs possible}} \times 100$	6%	20%	14%	53%
$\frac{\text{Pairs formed}}{\text{Total pairs}} \times 100$	65%	35%	18%	17%

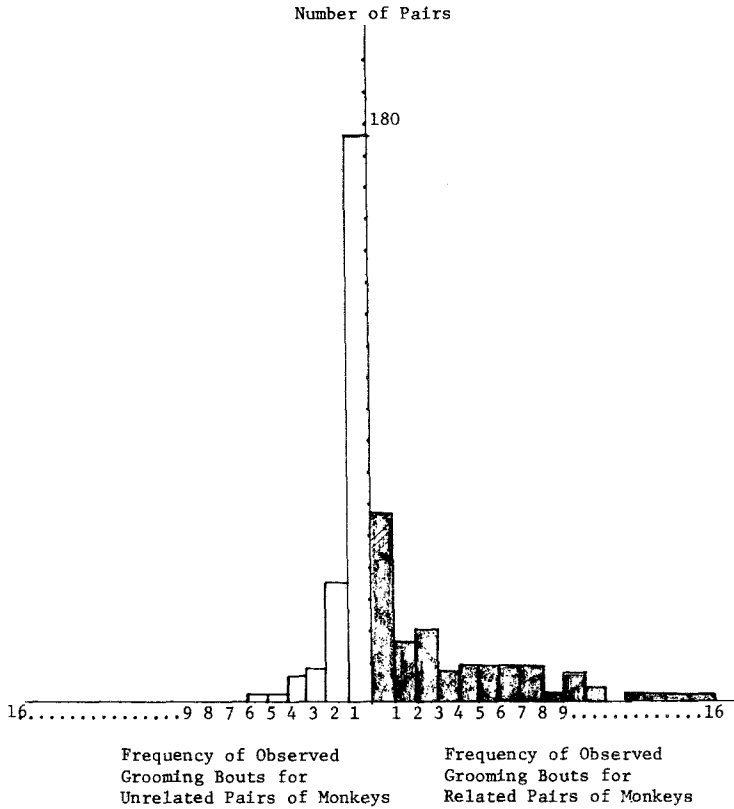


Fig. 2. Repetition of grooming pairs.

of observed grooming bouts between unrelated monkeys for all three tests periods. Thus while fewer related pairs were formed, those that were formed groomed more often than unrelated pairs.

Frequency of grooming bouts is illustrated in Fig. 2. A total of 180 unrelated pairs were observed grooming on one occasion only, and no pairs of unrelated monkeys were seen grooming more than six times. On the other hand, one pair of related individuals was seen grooming on 16 different occasions. Further, although duration of grooming bouts was not analyzed in the present study, we would suggest that related pairs appear to engage in longer grooming bouts than do unrelated pairs.

Thus the analysis of grooming pairs shows that more of the possible pairs of related monkeys were formed for grooming (reaching 53% of the total possible for family pairs over the whole year) than for unrelated monkeys (Table II). These related pairs groomed more often (Table III) and probably for longer

Table III. Observed Grooming Bouts

	Nonmating season		Mating season		Total year	
	Number of bouts	%	Number of bouts	%	Number of bouts	%
Pairs of unrelated monkeys	221	47	106	43	329	46
Pairs of related monkeys	250	53	141	57	393	54
Kin	56	12	32	13	88	12
Family	194	41	109	44	305	42

periods (from qualitative observation only) than unrelated monkeys, which generally groomed only once (see Fig. 2). However, these "transitory" unrelated pairs do outnumber the related pairs (Table II). A high degree of repetition in grooming between related animals, especially within family groups, would appear to be indicative of a set of relatively stable and consistent bonds.

Consort Partner Selection

Table IV shows the composition of the consort pairs during mating season. It can be seen that no male homosexual pairs were formed during this mating season. Only twice as many heterosexual pairs of both unrelated and related monkeys consorted as did female homosexual pairs (217 to 111 and 18 to 8).

In addition to preferences for consort partners based on sex, degree of relationship of animals also appeared to govern the choices of mates. In this

Table IV. Consort Pair Formations

		Male-male	Male-female	Female-female	Total
Pairs of unrelated monkeys	Number of pairs	0	271	111	328
	Percentage of total	0	61.3	31.4	92.7
Pairs of related monkeys	Number of pairs	0	18	8	26
	Percentage of total	0	5.1	2.2	7.3
Total					354

study no consort pairs were formed within family groups. In other words, there were no cases of consorting between mother and son, mother and daughter, brother-sister, etc. Only 26 pairs of matrilineally related animals were formed, compared to the 328 unrelated consort pairs observed during the 1973-1974 mating season. It is important to note that matrilineally "related" individuals may be monkeys which are fairly distantly related, and included may be relationships for which human kinship systems have no terminology.

DISCUSSION

Our analysis of grooming patterns within a troop of *Macaca fuscata* does support the idea that the selection of partners for grooming is partly a function of genealogical relationship throughout the year (Sade, 1965). Related pairs, which accounted for only 14% of the sample pairs, performed 53% of the year's grooming. These figures closely approximate those reported by Sade (1965), who found related animals constituted 15% of the total sample, and they accounted for 62-64% of the total grooming bouts. The suggestion made by Loy and Loy (1974), who found a similar ratio in a troop of rhesus macaques, that a constant exists between the number of related monkeys in a group and the amount of interrelative grooming which occurs, is supported by our results.

Year-round social bonds can be understood by analyzing grooming in terms of frequency and direction, since grooming is the best suited activity for demonstrating relations within a group of rhesus macaques (Sade, 1965, p. 5). A comparison of grooming as an indicator of year-round affinitive bonds and consort partner selection (Table I) did appear to show that in this troop the two activities involve independent and mutually exclusive social bonds. Even individuals with no close relatives in the troop chose to groom with one set of individuals and to consort with another set. This would seem in contrast to certain other primates, such as common baboons and some rhesus monkeys, where consort partners may indeed be chosen on the basis of previous or long-term affinitive bonds (Rowell, 1972; Hinde, 1974; Lindburg, 1973; Ransom and Ransom, 1971).

It was expected that grooming patterns during the mating season would reflect the formation of special consort relationships (Drickamer, 1976), possibly with an increase in grooming between unrelated adult males and females. However, our results showed that such was not the case and that grooming patterns during mating season were not significantly different from yearly patterns, although the special emphasis on repeated grooming between family members was somewhat *increased* during mating season when nonfamilial consort bonds were forming. Thus grooming in a consort context does not appear to have been sufficiently different in frequency to have a significant effect on year-round patterns of grooming. These, it will be recalled, were characterized by the emphasis on repeated grooming between related pairs and a high incidence of single grooming bouts between unrelated pairs of animals, all year long. Perhaps these

differences within grooming demonstrate different sorts of affinitive relationships between monkeys.

Our findings also substantiate the existence of kinship avoidance in choice of consort partners within macaque groups and suggest that the avoidance to some degree extends not only to the family but also to the entire matriline. The reluctance of nonhuman primates to engage in mating behavior with "family" members has often been seen as a form of incest taboo and has been the subject of much discussion (Imanishi, 1965; Tokuda, 1961-1962; Sade, 1968; Goodall, 1969; Hanby *et al.*, 1971; Demarest, 1977).

Demarest suggests that the incest taboo in primates "resonates with, and reinforces a biological tendency to outbreed" (1977, p. 324). He compiles data from studies of rhesus and Japanese macaques, savanna baboons, langurs, chimpanzees, gibbons, gorillas, and man to show that these species avoid mating with close family kin, that is, siblings, mothers, or offspring.

In Japanese macaques it appears that outbreeding not only is built into the species-specific social structure though the transfer of males out of their natal troop at some stage in adolescence but also is built into the behavior patterns themselves and is revealed through the avoidance of mating with close associates. It is of note here that male migrations out of home troops into new troops *peak* during mating seasons.

Several researchers (Westermarck, 1922; Wolf, 1966; Shepher, 1971) have suggested that, in humans, close associations, especially during development or childhood, do not enhance sexual attraction, but erode it. Demarest is of the opinion that in both human and nonhuman primates uninterest in inbreeding develops after many years of close association. Both human and nonhuman primates share the components of social organization which make close association an inevitable-prolonged part of maturation, with tightly knit group life and intensive socialization of the young.

Results of this study support the premise that kinship relationships are an important structuring principle in Japanese macaque social organization (Koyama, 1967). While it was found that the affinitive bonds associated with kinship had a positive effect on the choices of grooming partners, their very existence appears to negate the formation of related consort pairs. That these animals to some extent recognize degree of relatedness is suggested from their support system during agonistic interactions, in which more closely related monkeys tend to be supported against more distantly related individuals (Fedigan, 1976).

It is probably impossible for us to ever ascertain how these animals actually perceive kinship; however, we may suggest that they are aware of, and responsive to, the intensity of the affinitive bond. That is, the closer the association between the monkeys, the more likely they are to support each other in agonistic interactions and, given the results of our study, the less likely they are to mate

with each other. Grooming is the best measure of close association or year-round affiliative bonds, and we have shown that in the Arashiyama West troop of Japanese macaques grooming partners are significantly different from consort partners. This is not to go to the extreme of suggesting that Japanese macaques mate with "strangers" or "enemies"; the point we are making is that consorting and grooming are behavioral expressions of two *independent* social networks, both of which are integral parts of the social cohesiveness of the troop.

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