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AFFILIATION AS AN INTERVENING VARIABLE: COVARIATION IN MEASURES OF AFFILIATION IN A REPRODUCTIVE AND A NONREPRODUCTIVE GROUP OF RHESUS MACAQUES *(Macaca mulatta)*

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ABSTRACT: Affiliation is often used as an intervening variable in behavioral studies of nonhuman primates. Variables used to measure affiliation should be strongly correlated if it is a valid intervening variable. Social context also should not strongly influence relationships between variables used to measure affiliation. Few studies have, however, reported either the correlations between variables used to assess affiliation or the influence of social context on relationships between the variables. Correlations between affiliative variables were therefore calculated on data from two groups of rhesus (*Macaca mulatta*) and influences of social context on these correlations were assessed.

Affiliation was measured with 7 variables. Two methods were used to investigate the influence of social context: Analyses were made of interactions between several age/sex categories of individuals. Comparisons were made between an experimental group and a matched control group. There were higher rates of sexual behavior in the experimental group. The mature males in the experimental group were vasectomized so females did not conceive. In this group females had repeated nonpregnant estrous cycles. Males were intact in the control group. In this group the mature females conceived and were pregnant during data collection.

The variables were significantly correlated across all social contexts. Affiliation may therefore be a useful intervening variable. The magnitude of the correlations between variables did vary considerably across social contexts. Sometimes the sign of the correlations between measures changed as a function of social context. Analyses of individual variables and their interrelationships may therefore be necessary for detailed understanding of the meaning of affiliative interactions in nonhuman primates.

Primatologists often define affiliation by elaboration of the measures used for its assessment (O'Keeffe, Lifshitz, & Linn, 1983;

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Baker & Estep, 1985; Ehardt & Bernstein, 1987; Crooks & Rasmussen, 1991). Proximity and grooming are probably the most universally used measures of affiliation (Carpenter, 1942a; Rasmussen, 1984; Hill, 1986; Byrne, Whiten, & Henzi, 1989). Measures of behavioral patterns associated with proximity (such as approaches, leaves and follows) and grooming presents, presents, and mounts are sometimes used to assess affiliation (Rasmussen, 1984; Chadwick-Jones, 1989). Vocalizations have also been used to assess affiliation (Biben, Symmes, & Masataka, 1986; Masataka & Biben, 1987). These affiliative variables share three characteristics: They are associated with either distance reduction or proximity maintenance, they do not evoke escape responses, and they are not agonistic behavioral patterns.

Affiliation is an intervening variable (MacCorquodale & Meehl, 1948; Miller, 1959; Hinde, 1985) since it is a tendency that is assumed to be assessed by variables having these three characteristics. An intervening variable is a convenient label used to describe several variables that are closely related to each other (Deese & Hulse, 1967).

Affiliation might be defined as a social centripetal tendency responsible for individuals forming into groups and staying in groups that is not agonistic. This definition does not make a necessary link between affiliation and an influence on an individual's Darwinian or inclusive fitness (Hamilton, 1964; Tinbergen, 1965; Rasmussen, 1988). This definition does not exclude sexual interactions.

If affiliation is a useful intervening variable, it must provide a fuller understanding than if the variables used for its measure are not assumed to assess aspects of the same tendency. The process of assessment of the validity and usefulness of an intervening variable involves many steps (Suen & Ary, 1989).

Dominance is an intervening variable that has both gone through some of these steps and that has been often used in studies of nonhuman primates (Altmann, 1962; Bernstein, 1981; Boyd & Silk, 1983; Cowlishaw & Dunbar, 1991). Much less attention has been directed to evaluation of affiliation as an intervening variable. There are many reasons why greater attention should be devoted to this task. The results of the analyses in this article bear on four of these reasons.

First, an intervening variable is a label used to describe a number of variables that are closely interrelated. Only incomplete information is available on the relationships between measures used to assess affiliation. Many who use measures of affiliation have spent years watching their subjects and hence have an excellent sense of the appropriate measures to use to assess affiliation. Yet a quantitative knowledge of the interrelationships between variables would provide useful additional support for choice of appropriate measures.

Second, the distinction between affiliative and sexual behavior is ambiguous in the literature. Sexual behavior is functionally defined as behavior that has been associated with conception during the phylogenetic past (Scott, 1956; Tinbergen, 1965; Rasmussen, 1984). Presents and mounts are patterns of behavior that are sometimes sexual that have received considerable attention as measures of affiliation. Perhaps this is so because they do not neatly fit into any single behavioral category (Marler, 1968). This is particularly true for intrasexual presents and mounts (Reinhardt, Reinhardt, Bercovitch, & Goy, 1986; Chadwick-Jones, 1989) since they are not sexual within a functional definition of sexual behavior (Rasmussen, 1984).

Third, knowledge of the social context of an affiliative interaction may be essential for understanding its meaning. Sex of interactants may, for example, influence the meaning of an affiliative interaction. Male => male or female => female mounts could, for example, have a different association with other measures of affiliation than do male => female mounts or female => male mounts. [=> symbolizes directional behavioral interactions. Male grooms of females are therefore symbolized as male => female grooming. <=> symbolizes bidirectional behavior or a measure of the distance between a dyad. When, for example, analyses are focused on grooming of males by females and grooming of females by males this is symbolized as male <=> female grooming.] It also may be necessary to know the reproductive status of the interactants and the reproductive state of the group in which they interact to evaluate affiliative interactions. Adult male grooming of adult females in estrus could, for example, have a different meaning than adult male grooming of pregnant females (Smuts, 1985). If social context does have a strong influence on the relationship between measures of affiliation then assessment of the measures, and the context in which they occur, may be necessary for accurate assessment of affiliation.

Fourth, if an intervening variable is found useful, it may help us to understand underlying design features (Tooby & Cosmides, 1990) of primate social organization. Intervening variables help group variables that together characterize possible adaptive aspects of primate social organization, such as their coherence (Zuckerman, 1932).

Analysis of the correlations between several measures of an intervening variable is an essential step toward evaluation of its utility (Hinde and Datta, 1981). If several measures are strongly related, then there is greater confidence in the intervening variable as an explanatory tool.

All the analyses presented here are centered on the correlations between 7 measures of affiliation. Five of these are frequently used to

measure affiliation: Two are measures of mean distance between pairs, the third is the combined rate of approaching, leaving and following, the fourth is grooming and the fifth grooming presents. The other two are presents and mounts. Presents and mounts are sometimes used as measures of affiliation, sometimes as measures of sexual behavior and sometimes as measures of agonistic behavior.

The analyses focus on the degree to which one measure of affiliation between pairs predicts their affiliation by the other measures: If, for example, monkey "A" grooms monkey "B" more than monkey "C", does monkey "A" also more frequently solicit grooming with grooming presents to monkey "B" than to "C"? That is, if there is a transitive (Boyd & Silk, 1983) grooming relationship between "A", "B" and "C", does this transitive relationship also hold for solicitations of grooming?

The measures of affiliation are initially assumed to be reciprocal (Hinde, 1987). This is only an initial assumption. More complex relationships are both possible and probable (Seyfarth, 1977). If, for example, monkey "A" both presents to and mounts monkey "B", then the presents and mounts are reciprocal. If monkey "A" presents to monkey "B" and is mounted by monkey "B", but neither receives presents from monkey "B" nor mounts monkey "B" then the presents and mounts are complementary (Hinde, 1987).

Focus on the correlations between variables provide information on the first two reasons why affiliation should be more closely examined as an intervening variable. First, examination of the magnitude of the correlations assesses the degree to which several measures of affiliation are related and hence the extent to which they may all measure a shared affiliative tendency. Second, examination of the strength of correlations between presents and mounts and the other measures helps show the degree to which these variables assess similar affiliative tendencies.

Analyses of the data as a function of interactants' age and sex is one method used to investigate influences of social context, the third reason affiliation should be more closely examined as an intervening variable. Comparisons are also made between a sexually active group and a matched reproductive group. Females in the sexually active group did not conceive because the reproductively mature males were vasectomized. Mature females in this group had repeated nonpregnant estrous cycles and engaged in sexual behavior during each cycle (Michael & Zumpe, 1988). Sexually mature females in the reproductive group conceived and were pregnant throughout the duration of observations. There were therefore significantly higher rates of sexual behavior in the group containing the vasectomized males (Rasmussen & Goy, 1988; Rasmussen, 1993 a,b).

METHODS

Animals and Housing

The sexually active group was composed of a 5 year old vasectomized male, a 4 year old vasectomized male, an intact 2 year old male, four 4 year old females, one 3 year old female, and three 2 year old females. The matched reproductive group had the same age and sex composition but all males were intact. Thus the experimentally manipulated difference between groups was male fertility.

There were 24 menstrual cycles among the mature females in the sexually active group. Forty-six consorts and 14 ejaculations occurred in the group during data collection. In the reproductive group, there were 4 menstrual cycles among the mature females. There were 27 consorts and 3 ejaculations in the group during data collection.

Subjects were selected so they could be closely matched with a paired individual. Matching was by sex, age, weight and housing history. All females were nulliparous and thus did not vary in parturitional, lactational, or infant rearing experience. One member of each matched pair was placed in the sexually active group and the other in the reproductive group.

The groups were housed in identical indoor pens. These were 6.7 m in length, 2.5 m in width and 2.6 m in height. The pens were separated by a minimum distance of 1.2 m and in a room with two additional identical pens containing breeding rhesus groups. Lights were automatically turned on at 6 am and turned off at 6 pm. Two frosted windows next to the pens let in ambient light.

The 5 and 4 year old males in both groups copulated to ejaculation. The 4 and 3 year old females in the reproductive group conceived. Although young, all group members, except 2 year olds, were sexually mature to the extent that they were potentially capable of reproduction.

Behavioral Sampling

All subjects were observed from outside the pens for more than a year before this experiment. I habituated them to my presence for 3 weeks before data collection. The data were collected from January 2, 1987 until the day before the birth of the first infant in the reproductive group, June 1, 1987. Data were collected on a lap top computer for 5 days each week from 15.00 to 18.00 hours. I collected all data except those on the menstrual cycles of the females. The latter are routinely collected on all rhesus at the primate center.

Individual group members were the focus of 14 min sampling

sessions. The sessions were divided into seven 2 min sampling intervals. A mean of 7.28 (SD=2.28) sampling sessions were conducted each day of data collection. The focal subjects of the sampling sessions were selected sequentially from a list of all individuals in both groups. Focal sampling (Martin & Bateson, 1993) was used for the variables requiring constant subject monitoring. Concurrent samples (Hausfater, 1974; Chapais, 1986) were collected on all occurrences of variables (Martin & Bateson, 1993) that could be simultaneously monitored for all group members. An auditory cue was programmed into the lap top 15 seconds before the beginning of the next 2 min interval to sharpen focus on variables sampled instantaneously at the onset of the next interval. The analyses are based on 2445 2 min interval samples collected during the 14 min sampling sessions.

The definitions of the affiliative variables used during data collection are provided in the appendix. The unit of observation and the method used to sample the variables are summarized in Table 1. All analyses are based on summary descriptive statistics. The present rate of "A" to "B" was, for example, calculated by dividing all observations of presents of "A" to "B" from focal sampling sessions on "A" and "B" by the sum of 2 min intervals collected during those sampling sessions.

Table 1. Variables, Observation Method and Sampling System

Variable	Unit of Observation	Sampling Method
1. Nearest Neighbor Distance	individual-focal	instantaneous
2. Close Distance to Nearest Neighbor	individual-focal	instantaneous
3. Approaches, Leaves & Follows (ALF)	individual-focal	frequency
4. Grooming	all individuals	1/0 (concurrent)
5. Grooming Presents	individual-focal	frequency
6. Presents	individual-focal	frequency
7. Mounts	all individuals	frequency (concurrent)

Statistical Control of Previous familiarity before Group Formation

In an ideal study there would be no differences between the sexually active group and the reproductive groups except those associated with

the experimental manipulation: vasectomization of the mature males in the sexually active group. Groups of nonhuman primates cannot yet, however, be as closely matched as, say, groups of inbred rodents. Previous studies in which matched groups are compared have seldom used subjects as closely matched as those in this project, matching made possible by the large population of rhesus maintained by the primate center.

A systematic difference was found between the two groups during data analyses: some pairs of individuals were housed with each other for more days before group formation. This nuisance variable is referred to as previous familiarity. The influence of previous familiarity was statistically controlled (Cohen & Cohen, 1983) by using the residuals from the regression of the affiliative interactions on this nuisance variable. Transformations were used, when appropriate, to normalize the residuals. Linear and quadratic fits were tried for every dependent variable. For all dependent variables, except grooming, the quadratic aspect of previous familiarity did not appreciably increase R^2; therefore only linear fits were used. Grooming rate was regressed on both the linear and quadratic aspects of previous familiarity. All descriptive and inferential statistics use the residualized variables. Tests of significance and interpretation of the influence of previous familiarity on affiliation have been published elsewhere (Rasmussen, 1993a).

Analytic Strategy

Several methods are used to describe and analyze relationships between measures of affiliation and differences in these relationships between groups. These methods were first applied to all members of each group and then to dyads composed of various age/sex classes, such as female => male interactions. As in Fisher's protected t-test, tests of significance were not conducted on subcategories of dyads unless the tests conducted on all dyads, and on the immediately higher dyad types, were significant (Cohen & Cohen, 1983; Rasmussen, 1984). Each set of analyses is followed by a brief discussion. A general discussion compares results across all dyad types.

Spearman Correlations between Variables: One analytic focus is the degree ordinal patterns of affiliation between monkeys are correlated with those evaluated by other measures of affiliation. If monkey "A" grooms "B" more than "C", is "A" also likely to more frequently grooming present to "B" than to "C"? Spearman correlation coefficients (Siegel & Castellan, 1988) are used to describe these relationships between all possible pairs of the 7 affiliative variables for directional dyads in each group. Interactions directed by one individual to another

are called directional dyads (Koyama, 1991). Affiliative interactions directed by the oldest male to the oldest female are therefore a directional dyad. There were 21 correlations possible between the 7 measures of affiliation.

The distance from "A" to "B" is the same as the distance of "B" to "A". There were therefore 55 ([11 x 10]/2) nondirectional dyads on which nearest and close neighbor distances could be calculated in each group. Duplicate values of neighbor distances were matched with directional behavioral interactions so relationships between distances and affiliative interactions could be described.

Trends in association between Measures of Affiliation within Groups: Overall trends in the association between measures of affiliation within groups were also evaluated. Was, for example, there a trend for stronger correlations between measures of male => male affiliation in the reproductive group than in the sexually active group? Three methods are used to evaluate such trends.

First the signs of the 21 correlations between the measures of affiliation within groups are used as a simple description of the direction of relationships. Distances to neighbors decrease with greater affiliation, and all the behavioral measures increase with greater affiliation. If the measures assess the intervening variable affiliation, then measures of distance to neighbors should be positively correlated; behavioral measures of affiliation should be positively correlated, and the measures of distance to neighbor and the behavioral measures should be negatively correlated.

Second, similarity in the way dyads were ranked by the affiliative variables is assessed with the Kendall Coefficient of Concordance, W (Siegel & Castellan, 1988). W provides a measure of the consistency with which the variables rank dyadic interactions. W was calculated by ranking dyads by Nearest Neighbor Distance and Close Nearest Neighbor Distance in descending order and the other variables in ascending order.

Third, the mean strength of agreement between each measure of affiliation and the 6 others was determined. The mean of the means of the squared correlations with the other variables was used for this task. The squared Spearman correlations indicate the proportion of variation shared in ranks of directional dyads as they are ordered by two variables. Correlations between variables opposite to those expected were given a value of 0 before calculating the mean. The mean squared correlation may be interpreted as the mean proportion of affiliative variation shared between dyads ranked by one variable and all others. This measure provides an empirical guide to determining which measure of affiliation tended to be most strongly associated with the others.

The three methods overlap. Each evaluates trends in the association between measures of affiliation. However, by looking at the patterns from different, but overlapping, perspectives it was possible to have a more complete knowledge of the complex patterns of rhesus affiliation.

Comparison of Patterns of Affiliation between Groups: Another focus of the analyses is similarity in relationships between measures of affiliation in the sexually active group and the reproductive group. Did, for example, the mature females in both groups tend to present at a higher rate to the females who they also mounted at higher rates?

A Pearson correlation was calculated between the Spearman correlation matrices from the groups in order to assess the overall similarity in the relationships between the variables. This correlation between paired values of correlation coefficients is called the matrix correlation. Like all correlations (Cohen & Cohen, 1983), matrix correlations are not influenced by linear transformations of the coefficients in either matrix. Similarities in relative values of correlation coefficients are therefore assessed. The significance of the matrix correlations was determined on the basis 10,000 random permutations of the matrices (Dow, Cheverud, & Friedlaender, 1987; de Waal, 1991).

Differences between groups in the mean squared correlations for each measure of affiliation are also calculated. These show the degree relationships between the measures were influenced by differences between groups. The greatest difference in correlations between groups is used to show the relationship between variables most influenced by the difference in social contexts between groups.

RESULTS

All Dyads

The first set of analyses was conducted on all 110 directional dyads in each group. The matrix correlation was +.95 ($p<.001$). In both groups all 21 correlations between the variables were in the expected reciprocal direction (Table 2). The coefficient of concordance was slightly less in the sexually active group (W =+.50, $p<.001$) than in the reproductive group (W=.55, $p<.001$).

All affiliative measures in the reproductive group, except close neighbor distance, had stronger mean squared correlations. The correlation between grooming present and present rates differed most between groups. There was a moderate reciprocal relationship (+.47) between these variables in the reproductive group. There was only a weak tendency in this direction in the sexually active group (+.10).

Table 2. Affiliation between All <=> Dyads.

Spearman Rank Order Correlation Coefficients between the Variables and the Mean Squared Correlations of the Variables. Upper Half Matrix, Reproductive Group; Lower Half Matrix, Sexually Active Group; Sr^2 and Rr^2 are the mean of the squared correlation coefficients between the row variable and the other 6 variables for the Sexually active (S) and Reproductive (R) groups; Diff=Sr^2 - Rr^2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.69	-.88	-.79	-.45	-.38	-.21	+.35	+.38	-.03
2. Close Neighbor	+.79		-.58	-.59	-.45	-.25	-.14	+.27	+.24	+.03
3. ALF Rate	-.80	-.66		+.75	+.48	+.49	+.35	+.33	+.38	-.05
4. Grooming Rate	-.70	-.60	+.65		+.29	+.47	+.19	+.25	+.31	-.06
5. Grooming Present Rate	-.27	-.13	+.37	+.16		+.47	+.38	+.09	+.18	-.09
6. Present Rate	-.46	-.36	+.44	+.46	+.10		+.55	+.13	+.20	-.07
7. Mount Rate	-.28	-.17	+.41	+.04	+.50	+.19		+.09	+.11	-.02

The relative values of correlation coefficients in the matrices from the two groups were remarkably similar. Monkeys who tended approach, follow or leave each other, for example, also tended to be closer to each other in both groups.

The rank orders of directional dyads by each of the 7 measures of affiliation were significantly concordant in both groups. Variables in the reproductive group were slightly more concordant, and the mean squared correlations were larger in the reproductive group for 6 of the 7 variables.

Sexually Mature Dyads

The sexually mature group members seemed likely to be those whose affiliative interactions might differ most between groups since these were those whose reproduction differed. Analyses were therefore conducted on the 42 directional dyads in each group that did not contain 2 year olds.

The correlation between the two matrices was +.92 ($p<.001$). In the sexually active group, 19 of 21 correlations between variables were in the expected reciprocal direction; all correlations were in the expected direction in the reproductive group (Table 3). The concordance in the reproductive group was identical with that calculated on all dyads

Table 3. Affiliation between All <=> Dyads not containing 2 Year Olds. Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.78	-.89	-.79	-.35	-.60	-.31	+.32	+.43	-.11
2. Close Neighbor	+.63		-.62	-.71	-.47	-.29	-.14	+.18	+.30	-.13
3. ALF Rate	-.82	-.54		+.81	+.36	+.59	+.24	+.29	+.39	-.10
4. Grooming Rate	-.71	-.53	+.64		+.32	+.58	+.20	+.28	+.38	-.10
5. Grooming Present Rate	-.37	-.12	+.38	+.28		+.32	+.14	+.10	+.12	-.01
6. Present Rate	-.42	-.26	+.32	+.62	-.13		+.33	+.12	+.22	-.10
7. Mount Rate	-.21	-.03	+.34	+.04	+.48	-.18		+.06	+.06	+.01

(W=.55, $p<.001$); the concordance of the variables in the sexually active group was smaller (W = .45, $p<.001$). There were larger mean squared correlations between all variables in the reproductive group except mount rate. The correlation between present and mount rates differed most between groups. Presenting and mounting were faintly complementary in the sexually active group (r=-.18). These measures were moderately reciprocal in the reproductive group (r=+.33).

Over 84% of the variation in correlation matrices was shared. ALF rate and nearest neighbor distance were, again, the variables with the strongest mean square correlations in both groups. Frequently used measures of affiliation (neighbor distances, grooming, and ALF rates) were more strongly related than were the affiliative interactions that are more closely associated with sexual interactions (grooming present, present, and mount rates).

Measures of affiliation in the sexually active group were more discordant. In the reproductive group, presents and mounts were reciprocal, whereas they were faintly complementary in the sexually active group.

Male => Male Dyads

There were 6 directional male => male dyads in each group. The matrix correlation was +.65 ($p<.001$). In the sexually active group, 17 of 21 correlations between measures of affiliation were in the reciprocal direction; in the reproductive group all correlations were reciprocal (Table 4).

Table 4. Male => Male Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		1.00	-.96	-.96	-.97	-.79	-.73	+.23	+.82	-.59
2. Close Neighbor	+.50		-.96	-.96	-.97	-.79	-.73	+.43	+.82	-.39
3. ALF Rate	-.60	-.84		+.89	+.87	+.81	+.75	+.46	+.77	-.30
4. Grooming Rate	-.24	-.48	+.20		+.93	+.84	+.58	+.16	+.75	-.59
5. Grooming Present Rate	+.00	+.00	+.34	-.85		+.65	+.74	+.04	+.74	-.70
6. Present Rate	-.60	-.84	+.77	+.77	-.34		+.37	+.47	+.53	-.06
7. Mount Rate	-.61	-.85	+.99	+.17	+.34	+.75		+.46	+.44	+.02

The coefficient of concordance was stronger in thereproductive group (W=.84, $p<.001$) than in the sexually active group (W=.51, P=.003). There were stronger mean squared correlations in the reproductive group for all variables except mount rate. The correlation between grooming and grooming present rates differed most between groups. Grooming and grooming presents were complementary in the sexually active group ($r=-.34$) whereas they were reciprocal in the reproductive group ($r=+.65$).

Intrasexual competition (Wilson, 1975) between males in the sexually active group over access to the females seems likely to have been expressed by their less reciprocal affiliative interactions. For example, the more a male solicited grooming from another the less likely he was to groom the other male. Analyses were not conducted solely on the dyads composed of sexually mature males since there were only two of these directional dyads in each group.

Female => Female Dyads

There were 56 directional female => female dyads in each group. The matrix correlation for these was positive and significant (+.90, $p<.001$). Nineteen of the 21 correlations in the sexually active group were in the expected reciprocal direction; in the reproductive group all correlations were reciprocal (Table 5). The coefficients of concordance were nearly identical in the two groups (sexually active W=.48, $p<.001$; reproductive W=.49, $p<.001$).

Nearest neighbor distance, close neighbor distance, ALF rate, and

Table 5. Female => Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.64	-.76	-.66	-.43	-.26	-.07	+.35	+.28	+.07
2. Close Neighbor	+.85		-.47	-.52	-.47	-.26	-.13	+.33	+.20	+.12
3. ALF Rate	-.73	-.72		+.64	+.42	+.44	+.32	+.30	+.28	+.02
4. Grooming Rate	-.78	-.71	+.64		+.10	+.39	+.12	+.29	+.22	+.07
5. Grooming Present Rate	-.17	-.14	+.22	+.00		+.30	+.32	+.07	+.13	-.06
6. Present Rate	-.44	-.42	+.46	+.45	-.01		+.79	+.14	+.20	-.06
7. Mount Rate	-.15	-.15	+.28	-.00	+.58	+.21		+.08	+.15	-.06

grooming rate had stronger mean squared correlations in the sexually active group; the opposite was true for grooming present, present, and mount rates. The correlation between present and mount rates differed most between groups. In the reproductive group presents and mounts were more strongly reciprocal.

In the sexually active group there was less reciprocity in some affiliative behavioral patterns. This may be the result of their more frequent use in complementary and status-related interactions.

Mature Female => Mature Female Dyads

Separate analyses could be conducted on mature female => mature female interactions since there were 20 of these directional dyads in each group. The matrix correlation was +.75 ($p<.001$). Fifteen of 21 correlations in the sexually active group were in the expected reciprocal direction; all correlations in the reproductive group were reciprocal (Table 6). The coefficient of concordance between dyadic values of variables in the sexually active group was .36 ($p<.001$), and coefficient in the reproductive group was a stronger .55 ($p<.001$).

All variables, except close neighbor distance, had larger mean squared correlations in the reproductive group. The correlation between present and mount rates again differed most between groups. In the reproductive group presents and mounts were reciprocal ($r=+.44$). In the sexually active group they were complementary ($r=-.42$).

The matrix correlation was smaller in magnitude than it was for all female => female dyads. The coefficient of concordance of the variables

Table 6. Mature Female => Mature Female Affiliation. Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.54	-.94	-.70	-.34	-.73	-.44	+.30	+.42	-.12
2. Close Neighbor	+.79		-.42	-.67	-.61	-.28	-.24	+.32	+.24	+.08
3. ALF Rate	-.74	-.76		+.61	+.33	+.61	+.34	+.23	+.34	-.11
4. Grooming Rate	-.64	-.76	+.49		+.20	+.66	+.19	+.24	+.30	-.07
5. Grooming Present Rate	-.30	-.26	+.06	+.09		+.09	+.47	+.05	+.15	-.10
6. Present Rate	-.33	-.29	+.14	+.46	-.52		+.44	+.07	+.27	-.20
7. Mount Rate	+.05	+.03	-.05	-.12	+.36	-.42		+.02	+.14	-.11

variables in the sexually active group was considerably less than between all female => female dyads in that group. Competition between adult females in the in the sexually active group (Michael & Zumpe, 1984) seems a probable cause of the lower concordance of variables and the smaller mean squared correlations for six of the seven variables.

There were negative correlations between several affiliative variables for the females in the sexually active group. In this group, for example, the more mature female "A" mounted mature female "B", the less she tended to groom, present, approach, leave or follow "B". The complementary relationships between the variables may be due to their differential use as a function of status.

Male <=> Female Dyads

There were 48 directional dyads composed of male => female and female => male interactions in each group. The matrix correlation for these interactions was +.97 ($p<.001$). In both groups all correlations were in the expected reciprocal direction (Table 7). The coefficients of concordance in the groups were nearly identical (sexually active group W=.53, $p<.001$; reproductive group W=.55, $p<.001$).

Four of the mean squared correlations were larger in the reproductive group, 2 were larger in the sexually active group, and the mean squared correlation for grooming present rate was the same in both groups. The correlation between grooming present and present rates differed most between groups; grooming presents and presents were more strongly reciprocal in the reproductive group.

Table 7. Male <=> Female Affiliation. Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.72	-.93	-.83	-.39	-.39	-.33	+.36	+.41	-.05
2. Close Neighbor	+.83		-.65	-.57	-.21	-.21	-.15	+.27	+.23	+.04
3. ALF Rate	-.81	-.66		+.84	+.46	+.49	+.39	+.38	+.43	-.05
4. Grooming Rate	-.60	-.57	+.67		+.36	+.49	+.32	+.26	+.37	-.11
5. Grooming Present Rate	-.38	-.17	+.58	+.42		+.62	+.42	+.18	+.18	+.00
6. Present Rate	-.45	-.33	+.39	+.48	+.35		+.29	+.14	+.19	-.05
7. Mount Rate	-.36	-.22	+.49	+.09	+.56	+.14		+.13	+.11	+.02

There was little difference between groups for male <=> female interactions: The matrix correlation was strong, the coefficients of concordance were nearly identical, and there was no strong trend in the differences of the mean squared correlations.

Male => Female Dyads

There was a positive and significant matrix correlation for the 24 male => female directional dyads (r=+.93; p<.001). In both groups all correlations were in the expected reciprocal direction (Table 8). The coefficients of concordance in the groups were significant and nearly identical (sexually active W=.56, p<.001; reproductive W=.55, p<.001).

Five of the seven variables had larger mean squared correlations in the sexually active than in the reproductive group. The mean squared correlation for present rate differed most between groups: it was stronger in the reproductive group. The correlation between nearest neighbor distance and grooming presents differed most between groups: in the sexually active group it was -.59; whereas in the reproductive group it was -.19.

Male => female interactions also differed little between groups: The matrices were strongly and positively correlated and the coefficients of concordance were nearly identical. There was, however, a tendency toward greater reciprocity of male => female affiliative interactions in the sexually active group.

Table 8. Male => Female Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.64	-.85	-.52	-.19	-.19	-.50	+.36	+.29	+.08
2. Close Neighbor	+.70		-.66	-.56	-.17	-.13	-.14	+.22	+.20	+.02
3. ALF Rate	-.82	-.67		+.78	+.39	+.35	+.58	+.43	+.40	+.03
4. Grooming Rate	-.49	-.41	+.65		+.26	+.40	+.47	+.22	+.27	-.05
5. Grooming Present Rate	-.59	-.13	+.63	+.55		+.71	+.27	+.27	+.14	+.13
6. Present Rate	-.32	-.14	+.26	+.08	+.47		+.57	+.10	+.19	-.10
7. Mount Rate	-.57	-.43	+.75	+.46	+.58	+.40		+.29	+.20	+.09

Mature Male => Mature Female Dyads

The matrix correlation for the 10 mature male => mature female directional dyads in each group was +.78 ($p<.001$). In the sexually active group all 21 correlations were in the expected reciprocal direction; whereas 18 were in this direction in the reproductive group. There was a strong coefficient of concordance in the sexually active group (W=.71, $p<.001$) and a weaker coefficient of concordance in the reproductive group (W=.49, $p<.003$).

Every variable in the sexually active group had a larger mean squared correlation. The correlation between grooming and grooming present rates differed most between groups: Sexually active males had a strong tendency to grooming present most frequently to the females who they also groomed most frequently (r=+.82). There was a faint tendency in the opposite direction in the reproductive group (r=-.15).

Greater differences appear between groups for adult male => female interactions. The matrix correlation was lower in magnitude. There were more reciprocal correlations in the sexually active group. The concordance of variables was much stronger in the sexually active group. And every variable in the sexually active group had a stronger mean squared correlation than in the reproductive group.

The greater reciprocity and consistency of affiliative interactions directed by mature males to mature females in the sexually active group may be due to the affiliative interactions between consort pairs. There was, for example, a strong positive tendency for the sexually active

Table 9. Mature Male => Mature Female Affiliation. Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.69	-.79	-.62	+.12	-.33	-.68	+.53	+.34	+.18
2. Close Neighbor	+.74		-.61	-.46	+.20	-.13	-.34	+.32	+.20	+.12
3. ALF Rate	-.90	-.57		+.87	+.05	+.52	+.79	+.63	+.44	+.19
4. Grooming Rate	-.73	-.62	+.78		-.15	+.38	+.90	+.51	+.39	+.13
5. Grooming Present Rate	-.81	-.38	+.95	+.82		+.48	+.02	+.55	+.05	+.50
6. Present Rate	-.41	-.39	+.66	+.69	+.62		+.61	+.34	+.19	+.15
7. Mount Rate	-.69	-.60	+.85	+.64	+.73	+.64		+.49	+.40	+.09

males to grooming present at higher rates to the females they groomed at highest rates. There was a faint tendency for these behavioral patterns to be complementary in the reproductive group.

Female => Male Dyads

The matrix correlation for the 24 female => male directional dyads was +.97 ($p<.001$). In the sexually active group, 20 of the 21 correlations were in the expected reciprocal direction; in the reproductive group all correlations were in this direction (Table 10). The coefficients of concordance were similar in the two groups (sexually active group W=.54, $p<.001$; reproductive group W=.58, $p<.001$).

Four of the 7 mean squared correlations were larger in the reproductive group. The correlation between grooming and mount rates differed most between groups. There was a weak tendency for reproductive females to have higher rates of grooming with the males who they mounted at higher rates whereas there was no tendency in this direction in the sexually active group.

The interrelationships between the variables in the two groups were nearly identical for female => male interactions since the matrix correlation approached +1.0.

Mature Female => Mature Male

The matrix correlation of mature female => mature male interactions among the 10 directional dyads was +.93 ($p<.001$). In both groups all 21

Table 10. Female => Male Affiliation.
Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.64	-.86	-.85	-.25	-.60	-.11	+.39	+.38	+.01
2. Close Neighbor	+.70		-.60	-.60	-.28	-.31	-.14	+.24	+.22	+.02
3. ALF Rate	-.88	-.55		+.93	+.49	+.64	+.25	+.36	+.44	-.08
4. Grooming Rate	-.74	-.54	+.73		+.44	+.61	+.24	+.34	+.43	-.09
5. Grooming Present Rate	-.34	-.02	+.45	+.27		+.47	+.65	+.13	+.20	-.07
6. Present Rate	-.64	-.57	+.52	+.78	+.32		+.26	+.29	+.26	+.04
7. Mount Rate	-.18	-.11	+.33	-.03	+.53	+.15		+.08	+.11	-.03

correlations were in the expected reciprocal direction (Table 11). The coefficient of concordance was larger in the sexually active group (W=.67, $p<.001$) than in the reproductive group (W=.60, $p<.001$).

The mean squared correlations were larger for 4 of the 7 variables in the sexually active group, and the mean squared correlation for grooming rate was identical in the two groups. The mean squared correlation for females' rate of mounting males was much larger in the sexually active group. The correlation between present and mount rates differed most between groups: There was a stronger tendency for sexually active females to have higher rates of mounting of the males to whom they presented at highest rates.

Although of lesser magnitude, the differences between groups in mature female => mature male affiliative behavior were in the same direction as those for mature male => mature female affiliative behavior. The variables were more concordant in the sexually active group and 4 of the mean squared correlations were larger in the sexually active group. Mature female => mature male affiliative interactions were therefore more reciprocal in the sexually active group.

The greatest difference between groups was the stronger tendency for sexually active females to mount the males at higher rates to whom they presented at higher rates. Female mounts of males have seldom been analyzed in the literature, yet this infrequent behavioral pattern may be an important component of sexual interactions in rhesus. While further research is necessary, female mounts of males, like threatening away (Zumpe & Michael, 1970), appear to be strong indicators of female proception. The stronger association between sexually active females'

Table 11. Mature Female => Mature Male Affiliation. Abbreviations as in Table 2.

	NN	CN	ALF	GR	GP	PR	MT	Sr^2	Rr^2	Diff
1. Nearest Neighbor		+.69	-.77	-.78	-.31	-.74	-.01	+.44	+.39	+.05
2. Close Neighbor	+.74		-.48	-.55	-.41	-.51	-.01	+.33	+.24	+.09
3. ALF Rate	-.94	-.66		+.96	+.60	+.76	+.18	+.52	+.45	+.07
4. Grooming Rate	-.89	-.64	+.84		+.73	+.88	+.31	+.54	+.54	+.00
5. Grooming Present Rate	-.40	-.27	+.51	+.54		+.76	+.45	+.28	+.32	-.05
6. Present Rate	-.69	-.56	+.62	+.88	+.51		+.33	+.42	+.47	-.05
7. Mount Rate	-.57	-.44	+.65	+.55	+.78	+.54		+.36	+.07	+.28

mounts of males, and their presents to those males, may therefore be the result of the greater use of both behavioral patterns in sexual interactions.

DISCUSSION

The positive and significant matrix correlations and coefficients of concordance for every dyad type in both groups were striking results (Table 12). The significant matrix correlations show the measures of affiliation were related in similar ways across the social contexts of the two groups. The significant coefficients of concordance indicate the measures of affiliation tend to assess similar aspects of behavior within groups across the 10 dyad types. These results suggest (1) that affiliation is a useful intervening variable and (2) that the measures used here do assess affiliation.

The matrix correlations, the number of correlations in the expected reciprocal direction, the coefficients of concordance, and differences between groups varied with social context. The utility of measures for the assessment of affiliation was thus partially contingent on who was interacting with whom and the group in which the interactions occurred.

Matrix Correlations

There were three dyad categories for which the matrix correlations were less than +.90 (Table 13). The smallest matrix correlation was for

Table 12. Summary of Variables Used to Describe the Interrelationships between Affiliative Measures for each Dyad Type.

Reciprocal shows the number of correlation coefficients in the expected reciprocal direction; S, Sexually Active Group; R, Reproductive Group; * indicates statistical significance at $p<.05$.

Dyad Type	N of Dyads per group	Matrix Correlation	W Concordance			# Reciprocal	
			R	S	R-S	R	S
all	110	+.95*	+.55*	+.50*	.05	21	21
all sexually mature	42	+.92*	+.55*	+.45*	.10	21	19
all male => male	6	+.65*	+.84*	+.51*	.33	21	17
all female => female	56	+.90*	+.49*	+.48*	.01	21	19
mature female =>female	20	+.75*	+.55*	+.36*	.19	21	16
male <=> female	48	+.97*	+.55*	+.53*	.02	21	21
male => female	24	+.93*	+.55*	+.56*	-.01	21	21
mature male => female	10	+.78*	+.49*	+.71*	-.22	18	21
female => male	24	+.97*	+.58*	+.54*	.04	21	20
mature female => male	10	+.93*	+.60*	+.67*	-.07	21	21

male => male dyads, the next smallest was for mature female => mature female dyads, and the third smallest was for mature male => mature female dyads. Contextual differences between groups therefore had the greatest influence on the variables' interrelationships for intrasexual interactions and on interactions directed by mature males to females.

Greater intrasexual competition in the sexually active group seems a probable cause of the smaller matrix correlations for male => male and mature female => mature female interactions. The measures of affiliation were less reciprocal and more complementary in the sexually active group. For example, the greater use of presents between males for appeasement in the sexually active group appeared responsible for the complementary relationship between male => male grooming presents and presents. Males of higher rank solicited grooming with grooming presents and were presented to by the males from whom they solicited grooming. In contrast, male => male grooming presents and presents were strongly reciprocal in the reproductive group.

Mature male => mature female interactions had the third lowest

Table 13. Matrices of the Coefficients of Variation of the Correlation Coefficients across the Interaction Categories Listed in Tables 3-12. Upper Half Matrix: Reproductive Group (R); Lower Half Matrix: Sexually Active Group (S); SCV RCV: The mean squared coefficient of variation for all correlations with the variable in each row for the Sexually Active (S) and the Reproductive Groups (R).

	NN	CN	ALF	GR	GP	PR	MT	SCV	RCV*
1. Nearest Neighbor		+.17	-.08	-.17	-.76	-.43	-.73	+.17	+.23
2. Close Neighbor	+.14		-.24	-.22	-.80	-.62	-.92	+.28	+.34
3. ALF Rate	-.12	-.14		+.14	+.46	+.25	+.52	+.16	+.10
4. Grooming Rate	-.28	-.18	+.28		+.88	+.32	+.68	+1.05	+.24
5. Grooming Present Rate	-.61	-.71	+.54	1.96		+.43	+.56	+2.12	+.45
6. Present Rate	-.27	-.47	+.42	+.41	2.76		+.38	+1.74	+.18
7. Mount Rate	-.68	-.93	+.62	1.44	+.26	1.48		+1.01	+.43

matrix correlation. This was the result of the greater reciprocity of these interactions in the sexually active group. Sexually active adult males had, for example, a strong tendency to groom most with the adult females to whom they also most frequently grooming presented. There was a faint tendency in the opposite direction in the reproductive group. The greater reciprocity of mature male => mature female interactions in the sexually active group seems likely to be the result of the affiliative interactions occurring between sexually interacting pairs and the more solicitous and tolerant behavior (Carpenter, 1942b) of the males in those pairs.

Coefficients of Concordance

Male => male interactions had the greatest difference in coefficients of concordance, mature male => mature female interactions had the second greatest, and the third greatest difference was in mature female => mature female interactions. These are the three dyad types that had the smallest matrix correlations.

Two of the three greatest differences in the coefficient of concordance arose for intrasexual interactions. Intrasexual competition associated with higher rates of sexual behavior is, again, the probable cause of the lower concordance between affiliative variables in the sexually active group. Decreased reciprocity of intrasexual interactions

in the sexually active group may be a form of intrasexual competition: One individual in the dyad receives decreased social resources compared to the other. If, for example, a male in the sexually active group more frequently presented for grooming to another male he was less likely to groom that male.

Discordance between measures of affiliation suggests social signals might sometimes be inconsistent, an inconsistency that could be an indirect measure of deception (Byrne & Whiten, 1988). For intrasexual interactions in the sexually active group, patterns of affiliation as assessed by one variable tended to be much less predictive of affiliation as measured by the other variables. In the sexually active group, for example, a strong tendency for male "A" to be a close neighbor to "B" had no covariation with rate at which male "A" grooming presented to "B" (r=0). In the reproductive group these two variables were almost perfectly related (r=-.97).

The second greatest difference in the coefficients of concordance between groups was for mature male => mature female interactions. There was a much stronger coefficient of concordance in the sexually active group. The greater reciprocity of mature male => mature female interactions in the sexually active group appeared to cause the difference in the coefficients of concordance between the two groups.

Number of Correlations in the Expected Reciprocal Direction

The number of correlations in the expected reciprocal direction differed across groups and interaction categories (Table 12). In the reproductive group 9 of the 10 interaction categories had all 21 correlations between the measures of affiliation in the expected reciprocal direction. In the sexually active group only half the interaction categories had all correlations in this direction. Interactions were therefore more consistently reciprocal in the reproductive group than in the sexually active group. The only deviation from the trend was for mature male => mature female interactions. For these, all correlations were in the expected reciprocal direction in the sexually active group whereas 18 of 21 were in this direction in the reproductive group.

Variability of the Correlations between Affiliative Variables

There was variation in the sign and magnitude of the correlations between measures of affiliation across interaction categories. This variation between groups and across the 10 dyad categories was measured with coefficients of variation. These were calculated for each of the 21 correlation coefficients across the 10 dyad types (Table 13).

The coefficients of variation were larger and more varied in the sexually active group (mean =+.28, SD=.95) than in the reproductive group (mean =-.01, SD =.54). Correlations with grooming presents had the largest mean squared coefficient of variation across dyad types in both groups. Grooming presents were therefore the measure of affiliation most sensitive to dyad type.

In the sexually active group the correlation between grooming presents and presents varied most across dyad types (CV=2.76). This correlation was large and negative for the mature female => mature female and male => male interactions. The correlation was large and positive for the mature female => mature male and the mature male => mature female interactions. The magnitude of variation in this correlation across dyad categories was the result of the complementary use of grooming presents and presents in intrasexual interactions and their reciprocal use in the heterosexual interactions.

In the reproductive group the correlation between grooming and grooming presents was also most varied across dyad types. Exactly opposite to the sexually active group, this correlation was smallest and negative for mature male => mature female interactions and reached its largest positive value for male => male interactions. This contrast between groups may be the result of more status related, and less sexual, heterosexual affiliative interactions between adults and the less competitive interactions between males in the reproductive group.

CONCLUSION

Nearest and close neighbor distances and ALF rate tended to be most strongly correlated with the other measures of affiliation; these might therefore be considered the most general measures of affiliation. These measures also varied least across dyad types and differed least between groups. These measures might therefore be those most appropriate for comparisons of affiliative tendencies across dyad types and social contexts. This result supports Carpenter's belief (1942a) that the strength of attachment between two individuals could be measured by the average distance separating the two animals.

There was variation in the relationships between the measures of affiliation within and between groups across dyad types. If the variables are "measuring sticks" of affiliation their length is not constant. The social context and the dyad types must therefore be considered for an accurate assessment of the affiliative relationships between individuals and the meaning of these affiliative relationships.

The differential concordance of the measures of affiliation suggests

that overlapping sources of information could be used by monkeys to both signal their affiliative tendencies toward each other and interpret the affiliative interactions that they receive. We tend to feel more confident say, that another person means yes when they nod yes, say yes and write yes. When a person nods yes, says yes and writes no, then meaning becomes more difficult to interpret and we may suspect deception.

The analyses presented here only provide an initial step toward the assessment of the utility of affiliation as an intervening variable. Further analyses are necessary to determine how these measures are associated with unambiguously sexual or agonistic interactions. Analyses are also necessary on the use of affiliative interactions, such as grooming presents, in status interactions. When affiliative interactions are used in status interactions they may simultaneously convey both agonistic and affiliative information.

Evolutionary theory is the unifying theory by which we determine the functional significance of behavior, the way in which the behavior is associated with fitness (Tinbergen, 1965; Wilson, 1975; Rasmussen, 1988). Intervening variables used in studies of behavior should therefore be useful for understanding fitness (Brown, 1983). There has, for example, been considerable attention devoted to the links between dominance and aspects of fitness (Cowlishaw & Dunbar, 1991). Analyses must also be made of the relationships between affiliative interactions and increments or decrements in fitness.

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APPENDIX

Neighbor Distances

The coded distance of the focal subject to the nearest male and the nearest female was instantaneously sampled at the beginning of each 2 min interval (codes: contact=0, not touching to 1/3 m=1, 1/3-2/3 m=2, 2/3-1 m=3, 1-4/3 m=4, 4/3-5/3 m=5, 5/3-2m=6, greater than 2 m=7). When individuals were engaged in agonistic behavior with the focal subject they were excluded as nearest neighbors since neighbor distances were used to assess affiliation (Rasmussen, 1984). On the rare occasions when two or more individuals of the same sex were exactly the same distance to the focal subject, the individual chosen as the nearest neighbor was determined by application of 3 successive decision rules: First, the neighbor who was near the focal subject for the longest duration of time was scored as the nearest neighbor. Second, if the neighbors had been close to the focal subject for an equal amount of time, the one who was either grooming, or who was being groomed, by the focal subject was scored as the nearest neighbor. Third, if the neighbors were close to the focal subject for an equal time and engaged in grooming

with the focal subject, the individual chosen as the nearest neighbor was the one who had the greatest amount of body contact with the focal subject.

Two types of mean distance between dyads were calculated: First, the mean ordinal distance across all focal samples, nearest neighbor distance. Second, the mean distance during only those intervals when dyad members were separated by 2 m or less, close neighbor distance (Rasmussen, 1983). Nearest neighbor (NN) distance was the sum of coded distances between dyad members divided by all focal two min intervals collected on the dyad. When the focal subject had a nearest neighbor all other group members of the same gender as the nearest neighbor were given a coded distance of 7 from the focal subject for that 2 min interval. Close distance (CD) was sum of coded distances between a dyad, excluding code 7, divided by all 2 min samples on the dyad when they were nearest neighbors and within 2 m.

ALF - Approach, Leave and Follow

"A" was scored as approaching another "B" when it approached within 1 m of "B", and remained within 1 m for at least 15 sec. When several animals were approached, the approach was scored only for the animal most closely approached. A leave was scored when "A" walked at least 1 m away from "B" who had been its nearest neighbor and separated by no more than 1 m for at least 15 sec. "A" was scored as following "B" when it walked at 1 m or less behind "B" over a distance of at least 1 m. Since approaches, leaves and follows were used to assess affiliation, these variables were not scored if they were part of an agonistic interaction with the focal subject. Approach, leave and follow rates were calculated as the sum frequency of each variable divided by all 2 min samples collected on the dyad members. The rate at which the oldest male approached the oldest female was, for example, the number of times the male approached the female divided by all 2 min samples collected on the male and female.

The Pearson correlation between approach and follow rates across all directional dyads in both groups (N=220) was +.80; the correlation between approach and leave rate was +.87; and the correlation between leave and follow rate was +.66. Because of their strong correlations, the three variables were combined in a composite variable called ALF rate: the sum frequency of the variables divided by all 2 min focal sample intervals collected on both dyad members.

Grooming

Picking through the hair or skin of another with fingers or teeth was defined as grooming (e.g. Cullen 1963; Sade, 1965; Sparks, 1969; Rasmussen, 1984). The beginning and end of grooming bouts were difficult to accurately record because many variables were used to assess group social organization. Grooming was therefore assessed with 1/0 sampling. 1/0 grooming rate per 2 min interval was calculated as the sum of intervals one group member was observed to groom another divided by all 2 min intervals collected on the group.

Grooming Presents

"A" grooming presented (Boccia et al., 1982) to "B" when it approached and exposed a body part at 1/3 m or less to "B's" hands or mouth. Sometimes an individual presented the genital area for grooming. When this happened a grooming present was distinguished from a present by (1) the lowering of the head and shoulders below

horizontal, often so that the head touched the floor, and (2) by the animal who received the grooming present responding by grooming. "A" => "B" grooming present rate was calculated by dividing all grooming presents of "A" => "B" by the sum of focal 2 min intervals on "A" and "B".

Presents

"A" presented to "B when it was within 2 m of "B" and oriented its anogenital region to "B's" face. Present rate was calculated by dividing all"A" => "B" presents by the sum of focal 2 min intervals collected on "A" and "B".

Mounts

"A" mounted "B" when it placed both hands on "B's" back and the anogenital regions of the two were aligned in a copulatory posture. Mount rate was calculated by dividing the sum of "A" => "B" mounts by the sum of all 2 min intervals collected on their group.