Sociometrics of *Macaca mulatta*
I. Linkages and Cliques in Grooming Matrices

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Abstract. Grooming interactions among adult *Macaca mulatta* tabulated on matrices are analysed by sociometric techniques. Centricity in the grooming network correlates with dominance among females but not among males. Extreme-cliques, 2-cliques and 3-cliques show the diverse relations of the males to the central group. Methods are explained and an algorhithm given for detecting cliques.

Key Words
Social structure
Dominance
Sociometry
Cliques
Sampling techniques
Macaca mulatta

Introduction

Astute observers gain detailed personal knowledge about the complex workings of societies of non-human primates. However, comparisons of the structure of these societies suffer from a lack of adequate descriptive and analytical techniques. Without such techniques field workers must still rely more upon intuition than upon measurement. The description of social structure, defined as the network of attachments which coordinate a social unit, is especially difficult. Nevertheless, objective ways of comparing social structure are necessary in order to evaluate differences of possible evolutionary significance between species, the effects of different habitats on the organization of groups of the same species, naturally occurring changes in the structure of the same group in relation to demographic changes, and how experimental manipulations of individuals within a group, or of the entire group, affect the group's structure.

The purpose of this paper is to summarize briefly some ways in which social structure has been described in the literature, and to illustrate another method which may be of considerable use in primatology.

Review

Behavioral Studies

The first serious student of the social organization of groups of non-human primates, C. R. CARPENTER (whose collected papers are found in CARPENTER [1964]), clearly stated the problems of describing social structure, and indicated what direction research could take to find their solutions. CARPENTER [1942a; 1942b; 1952] emphasized that social groups were organized and coordinated by the interactions of individuals with each other. The network of mutual attractions and repulsions which comprise the structure (not CARPENTER's term) of the group is revealed by the characteristic interactions between individuals and between classes of individuals, and by the spacial relations of individuals. CARPENTER [1952] presents formulae which would express the characteristic spacial arrangements of individuals in groups of different species, when applied to measures of inter-individual distance. I have been unable to find a study in which these formulae were applied to actual data, however.

In practice, intuitive judgments about characteristic spatial relations have been used by nearly every field worker in determining the composition and structure of social groups, but spatial relations have proved difficult to measure.

YAMADA [1966, 1971] compared the social organization of five groups of *Macaca fuscata* on Shodoshima Island. His descriptions of the social structure of each group take the form of concentric, overlapping, and divided circles representing the nucleus, central part, and peripheral part of the group. Individuals are assigned membership in the appropriate part according to the observer's judgement of their spatial distribution on the provisioning ground. He also discovered sub-groups of mutually tolerant monkeys by observing which ones would feed together in a small enclosure. The five groups were also found to differ in the average number of individuals who would feed together in the enclosure. The differences between the groups were interpreted as being in part functions of the different personalities of males. These studies are representative of the many insightful investigations of Japanese primatologists. These studies are intuitively satisfying, but the methods are difficult to apply to groups of other species. One suspects that the observer's personal knowledge of the specific monkeys, rather than his measurement of social structure, plays a major role in producing the classifications.

In his unique study of *Papio hamadryas* KUMMER [1968] used both measures of spatial relations and a measure of interaction to reveal the network

of social attachments. He found that the relative distance between age-sex classes in a large sample show meaningful results, but that the estimated absolute distances were so variable as to be of little use. His measure of interaction was the number of observation minutes during which an exchange of any of a large number of specific gestures occurred between individuals. He constructed sociograms for specific one-male units. In these sociograms distances between nodes are proportional to the mean observed distance between individuals. The number of lines connecting the nodes represents the proportion of observation minutes during which an exchange of gestures occurred betwen the corresponding individuals. These sociograms surely contain close to the maximum amount of information which can be conveyed by a diagram.

SADE [1965] used sociograms to illustrate the progression through time of grooming relations in one of the six genealogies in group F of the Cayo Santiago colony of free-ranging *Macaca mulatta*. Genealogical relations are shown by one set of lines. Other lines between nodes indicate the direction of grooming and the proportion of each groomer's total episodes which was received by each recipient. The distances between nodes have no special meaning. These sociograms are so cluttered that little more information could be added to them.

Sociograms such as those used by KUMMER [1968] and by SADE [1965] can be used successfully only for small groups or sub-groups. Would not quantitative techniques which would accurately reveal the structure of groups of any size facilitate the study of societies of non-human primates?

Sociometric Studies

FORSYTH and KATZ [1946] showed that sociograms could be represented mathematically as N × N matrices, where N equals the number of interacting individuals. A value of one in a cell indicates that the individual represented in the row is in a relation to the individual represented in the column. What is meant by 'relation' varies according to what is being studied. In studies of human groups the relation might be: 'r sends a message to c', 'r prefers c', 'r chooses c', or 'r hates c'. In a group of monkeys the relation might be 'r grooms c'. The number of possible relations seems to be limited only by the ingenuity of the investigator. Since the presence of the relation is usually represented by 1, and the absence of the relation is usually represented by 0, matrices of this sort are often referred to as 'choice' or 'binary' matrices.

Considerable mathematical work in the late 1940s and the following decade (reviewed by GLANZER and GLASER [1959]) revealed that binary matri-

Table I. Illustrative hypothetical matrices

Table Ia
A (grooming episodes)

Groomer	Groomee				
	a	b	c	d	
a	0	4	2	0	6
b	1	0	2	0	3
c	4	3	0	1	8
d	1	0	0	0	1
	6	7	4	1	18

Table Ib
B (binary matrix on A)

Groomer	Groomee				
	a	b	c	d	
a	0	1	1	0	2
b	1	0	1	0	2
c	1	1	0	1	3
d	1	0	0	0	1
	3	2	2	1	8

Table Ic
W (row marginal % matrix on A)

Groomer	Groomee			
	a	b	c	d
a	0	0.667	0.333	0
b	0.333	0	0.667	0
c	0.500	0.375	0	0.125
d	1.00	0	0	0

Table Id
B (on W with DV = 0.25)

Groomer	Groomee				
	a	b	c	d	
a	0	1	1	0	2
b	1	0	1	0	2
c	1	1	0	0	2
d	1	0	0	0	1
	3	2	2	0	7

Table Ie
C (column marginal % matrix on A)

Groomer	Groomee			
	a	b	c	d
a	0	0.571	0.500	0
b	0.167	0	0.500	0
c	0.667	0.428	0	1.00
d	0.167	0	0	0

Table If
B (on C with DV = 0.25)

Groomer	Groomee				
	a	b	c	d	
a	0	1	1	0	2
b	0	0	1	0	1
c	1	1	0	1	3
d	0	0	0	0	0
	1	2	2	1	6

ces have some very interesting and important properties which seem particularly useful in describing the structure of groups of interacting individuals. To my knowledge these methods have not been applied to the study of groups of non-human primates. Two of these methods are illustrated below, and then applied to data from a study of free-ranging rhesus monkeys.

Grooming Matrices

Meaning of Values in Matrices

Consider of hypothetical grooming episodes (table Ia). Let a, b, c, and d be the individual members of the social group, and A be the matrix of grooming interactions within the group. Let N be the number of animals in the group. The value in cell A_{ij} of matrix A is the number of times the monkey in the ith row groomed the monkey in the jth column. Let the cells on the main diagonal equal zero ($A_{ii} = 0$), since the mathematical techniques require it, and since autogrooming is not being considered. The sum of the values in a row is the row marginal.

$$RM = \sum_{j=1}^{N} A_{ij}.$$

The sum of the values in a column is the column marginal:

$$CM = \sum_{i=1}^{N} A_{ij}.$$

RM_i therefore equals the total number of episodes of grooming done by the ith monkey, and CM_j equals the total number of episodes of grooming received by the jth monkey. The sum of the row marginals equals the sum of the column marginals, and is the total number of grooming episodes observed. This figure, however, is not as useful as are the individual marginal values.

Converting Matrices of Episodes into Binary Matrices

The sociometric techniques illustrated in this paper require that the matrix of grooming observations be converted to a binary matrix. There are several ways of performing the conversion, and each gives a binary matrix which differs slightly in content and meaning.

The matrix of observed grooming episodes, A, can be converted directly to a binary matrix, B, by changing all non-zero values in A to ones: if $A_{ij} = 0$, $B_{ij} = 0$; if $A_{ij} \neq 0$, $B_{ij} = 1$; $A_{ii} = 0 = B_{ii}$. The binary matrix produced by this method on matrix A (table Ia) is shown as matrix B (table Ib). The meaning of entries in the binary matrix (B) differ somewhat from the meaning of entries in the matrix of grooming episodes (A). A zero in cell B_{ij} means that the ith monkey did not groom the jth monkey, whereas a one in cell B_{ij} means that the ith monkey did groom the jth monkey, during the period of time over which observations were made. The RM_i equals the total number of individuals that were groomed by the ith monkey, and the CM_j equals the total number of monkeys who groomed the jth monkey. The binary matrix indicates the number of grooming partners

for each monkey and who they were, rather than the frequency with which any monkey groomed or was groomed.

Percent Matrices

Converting the matrix of grooming episodes directly into the binary matrix means that in the subsequent analysis all of the observed grooming relations will be treated as equally important. This is not necessarily desirable. Some individuals may show a strong preference for others by grooming them frequently, and yet may casually groom a number of other individuals. Frequent and persistent grooming relations reveal more about the structure of a group than do casual grooming relations [SADE, 1965]. On the other hand, some monkeys groom much less frequently than others. A low number of grooming episodes given by an infrequent groomer may be relatively more important in revealing his attachments than the same number of episodes would be for a more frequent groomer. One would like to be able to convert each value in the matrix of the observed grooming episodes into a value which would be equivalent to the others in indicating the relative importance of the grooming relation represented by that cell. Then one would like to be able to eliminate casual relations from further consideration.

A matrix, W (table Ic), containing cell values which indicate the relative importance of each grooming relation for the groomer is produced by dividing each cell value by its corresponding row marginal:

$$W_{ij} = \frac{A_{ij}}{RM_i}$$

This matrix can be called a 'row marginal percent matrix'. The value in the cell W_{ij} indicates the strength of the ith monkey's orientation toward the jth monkey as measured by the proportion of the ith monkey's total grooming that the jth monkey receives. RM_i of W equals 1.000. CM_j of W has no meaning.

A matrix, C (table Ie), containing cell values which indicate the relative importance of each grooming relation for the groomee is produced by dividing each cell value by its corresponding column marginal:

$$C_{ij} = \frac{A_{ij}}{CM_j.}$$

This matrix can be called a 'column marginal percent matrix'. The value in the cell C_{ij} indicates the importance of the ith monkey's grooming of the jth monkey for the jth monkey, as measured by the proportion of the number of total grooming episodes which the jth monkey received, which he received from the ith monkey. CM_j of C equals 1.000. RM_i of C has no meaning.

Discriminant Value

Either the row marginal percent matrix or the column marginal percent matrix can be converted into a binary matrix. In order to eliminate casual grooming relations from further consideration a discriminant value (DV) can be chosen. Any value in the percent matrix which equals or exceeds the DV is changed to one; all other values are changed to zero: if $W_{ij} \geqslant DV$, $B_{ij} = 1$; if $W_{ij} < DV$, $B_{ij} = 0$; $W_{ii} = 0 = B_{ii}$; if $C_{ij} \geqslant DV$, $B_{ij} = 1$; if $C_{ij} < DV$, $B_{ij} = 0$; $C_{ii} = 0 = B_{ii}$. Binary matrices produced on W (table Ic) and on C (table Ie) are shown in table Id and table If, respectively. Both were computed with DV = 0.25.

No algorithm for choosing the best DV is yet available. A series of increasing DVs applied to the same percent matrix allows the investigator to view the structure within the matrix at several levels of intensity.

The DV places limits on the maximum possible number of dyads in which an individual can be represented on the binary matrix. The maximum number of partners, for any individual, which can be represented on the binary matrix equals 1/DV, and that number can be achieved only if the individual's grooming is distributed exactly evenly among the potential partners. If $1/DV \geq N-1$, where N is the number of individuals in the group, then it is theoretically possible for each individual in the group to be in the specified relation with each other individual. The observed departure from this theoretically possible condition reflects the differentiation of structure within the group. A high DV restricts the possible structures which can be observed in the binary matrix. On the other hand, a structure observed in a binary matrix produced with a high DV is that which is produced by the most intense relationships.
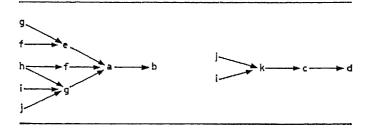
I have not yet sufficiently explored the utility of the binary matrices produced from column marginal percent matrices. All further discussion and examples in this paper will be based on binary matrices produced from row marginal percent matrices.

Status Based on Linkages

One-Step, Two-Step, and Three-Step Links

One measure of the importance of a monkey in the social group is the number of other monkeys who groom him. This number is given by the column marginal of his column in the binary matrix. The column marginals of the binary matrix therefore can be ranked to indicate the relative status of each monkey. Let an individual's rank be called his 'grooming status', and let the individual who has the highest column marginal be given rank 1. This measure could be used to determine animals who were central or peripheral in importance, as far as it could be measured by grooming status. However, KATZ [1953], JAMRICH [1960], and SCHIPPERT [1966] argue that a more meaningful measure of the status of an individual takes into account not only the number of individuals who choose him, but the statuses of those who choose him as well.

Table II. Illustrative hypothetical grooming networks:
arrows indicate direction of grooming episodes;
letters represent names of hypothetical monkeys

Consider the two hypothetical sociograms in table II. Using grooming statuses based on the one-step links, as indicated above, it would appear that monkeys b and d have equal status, since each is groomed by one individual. However, the monkey who grooms b is himself groomed by 3 monkeys, but the monkey who grooms d is only groomed by one monkey. Therefore monkey b should be assigned higher grooming status than monkey d because b is chosen by a monkey with higher status than the monkey who chooses d. The number of monkeys who are linked to b via one-step and two-step links is 4, but the corresponding number for monkey d is only 2; these sums differentiate the status of b and d better than do the sums of the one-step links alone.

The same argument can be extended to status based on 3-step links, and links of higher order. In the hypothetical sociograms in table II, the number of monkeys who are linked to b via one-step, two-step, and three-step links is 10, whereas monkey d's status is only 4.

The computation of n-steps is based on some simple rules of matrix algebra. These are given in appendix I, with an algorithm for computing one-, two-, and three-step linkages.

Behavioral Interpretation of n-Links for n > 1

The behavioral meaning of a one-step link is obvious: the groomer orients to the groomee, who accepts his presence and attention. Although the groomee may have initiated the episode by soliciting grooming from the groomer, the groomer had the choice of responding to the solicitation with grooming or not. Therefore it is still appropriate to use the episode as indicating a choice of the groomee by the groomer.

Can two-step links be interpreted behaviorally, or are they a mathematical artifact? There is really no difficulty with the concept of two-step or higher order linkages if one considers that a society is a group of individuals whose behavior is coordinated to some degree. Unless every individual in the group is linked directly to some common individual, there must be functional intermediate links, or the group would not in fact be a single coordinated society. A monkey central in the network of interactions may control or affect the behavior of individuals who do not interact directly with him, by controlling the behavior of individuals who are linked to the tertiary animals. It may be that grooming statuses in fact approximate the importance of an individual in a functional control network.

Cliques

Closely related to the concept of linkages is the concept of cliques. Intuitively a clique is a tightly integrated sub-group of individuals within a larger group. The larger group may or may not contain other cliques. The genealogical sub-groups described for *Macaca fuscata* by YAMADA [1963] and for *Macaca mulatta* by SADE [1965] are cliques in the intuitive sense, as are the one-male units of *Papio hamadryas* described by KUMMER [1968].

Extreme Cliques

FESTINGER [1949] and LUCE [1950] give a precise definition to cliques which are detectable in binary matrices. Cliques are maximal sub-groups of 3 or more individuals,

each of whom chooses all other members of the sub-group. Although by definition no clique can be a proper sub-set of another clique, one or more members of a clique can be members of one or more different cliques. In table Ib hypothetical monkeys a, b, and c form an extreme clique, because each grooms the other two. Monkey d is not a member of the clique, even though he grooms a, and is groomed by c. Note that the clique (a; b; c) persists in the binary matrix produced from the row marginal percent matrix with DV = 0.25, indicating that the clique is based on persistent or strong relations rather than on casual ones.

FESTINGER [1949] and LUCE [1950] discuss some of the mathematical properties of cliques in binary matrices. HARARY and ROSS [1957] extended their findings, and derived an algorithm for detecting the exact cliques contained in a group of any size. This method is given in appendix II.

n-Cliques

LUCE [1950] showed that the extreme clique, in which each individual is linked to each other individual by a 1-step relation, is a special case of the n-clique, in which each individual is linked in n or fewer steps to each other individual. LUCE [1950] supposes that n-cliques with n = 2 or n = 3 will have the greatest utility in practical application, because cliques of higher order than n = 3 are very diffuse structures. His supposition has not yet been tested on monkey groups.

In table Ib hypothetical monkey d is linked to monkey a by a 1-step link, and through a to b and c by 2-step links. Monkeys a and b are linked to d through c by 2-step links, while c is linked to d by a 1-step link. Therefore the entire group (a; b; c; d) forms a single 2-clique. Where DV equals 0.25, however (table Id), d is no longer co-cliqual with a, b, and c, because his grooming of c is not reciprocated, even in 2-steps.

The binary matrix, M, on which n-cliques are computed by the method of HARARY and ROSS [1957] is produced by (1) summing the matrices of 1-step, 2-step, ..., (n-1)-step, n-step links (which are computed by the method in appendix I); (2) converting each non-zero value in the resulting matrix to 1, and (3) replacing the main diagonal values to zero:

$$L = \sum_{p=1}^{n} B_p$$

where p = the number of links represented by the cell values of matrix B. $M_{ij} = 0$ if $L_{ij} = 0$; $M_{ij} = 1$ if $L_{ij} \neq 0$; $M_{ii} = 0$ by convention.

The concept of n-cliques is likely to prove extremely useful in describing social structure in monkey groups. It is unlikely that functional sub-groups would usually meet the very strict criteria of the extreme clique. The slightly more diffuse structures of 2-, 3-, or n-cliques might very well provide good approximations to the functional units in monkey groups.

Sociometrics of Rhesus Monkeys

In this section the methods described above are applied to observations on a group of free-ranging rhesus monkeys *(Macaca mulatta)*.

Table III. Genealogical profile of Cayo Santiago group F
during period 14th June to 31st July 1963

Older	Year of birth							
	1956	1957	1958	1959	1960	1961	1962	1963
065 ♀						JS ♂	TD ♂	WK ♂
004 ♀						JT ♂		
AC ♀				DL ♀	EC ♂	IU ♀	GW ♂	
							TK ♂	WO ♀
(073 ♀dead)		EK ♀	ER ♂	EZ ♂	K ♀	JJ ♀		
					HU ♂	JG ♂	TG ♂	YB ♀
076 ♀		CN ♂ (castrate)		KD ♀		JH ♀	NT ♂	YA ♂
								YL ♀
022 ♀				CY ♂	KE ♀	W ♀	JI ♀	NW ♂ inf. ♂

Non-natal males:

066 ♂   R006 ♂

Profile of the Group

This study is based on observations of group F on Cayo Santiago, Puerto Rico done between 14th June and 31st July 1963, just prior to the mating season on Cayo Santiago. The effects of the annual reproductive cycle on social structure will be considered in a later paper. The members of the group

Table IV. Demographic profile of Cayo Santiago group F during period 14th June to 31st July 1963, with year of birth indicated between solid lines, and non-natal males placed below dashed line

				♀ ♀				
								065
WO		JJ						AC
YB		JH	K	KD			004	076
YL		JI	W	KE	DL		EK	022
1963	1962	1961	1960	1959	1958	1957	1956	older
WK	TD	JS	HU	EC	CY	ER	CN	066
YA	TK	JT		EZ			R006	
GW	TG	IU						
inf-	NT	JG						
022								
	NW							
				♂ ♂				

are tattooed with identifying combinations of letters and numbers. The genealogical profile of the group for the period of observations is shown in table III. The 38 members comprise 6 genealogies and 2 non-natal males. The demographic profile of the group is shown in table IV. The non-natal males are shown below the dashed line. Male *CN* had been castrated in 1960. Male *066* had been dominant in group F since at least 1960. Male *R006* had been solitary in 1962, and joined group F in early 1963. *R006* replaced *066* as dominant male the fall of 1963, but detailed observations were not made at that time.

Dominance Relations

Dominance relations were determined by observing the direction of aggressive and submissive gestures in agonistic encounters. The relation between genealogy and dominance among the juveniles in group F was discussed earlier [SADE, 1967] along with a discussion of methods. This report is concerned only with adults and sub-adults. The winners and losers among all members who were 4 years old or older in 1963 are shown in the matrix of agonistic encounters (table V). Encounters with doubtful outcomes are enclosed in parentheses to indicate the probable winner and loser. The rows and columns are ordered so as to minimize reversals across the main diagonal.

Table V. Agonistic encounters among sub-adults and adults in Cayo Santiago group F during period 14th June to 31st July 1963, with probable winner of doubtful encounters indicated in parentheses

Winner \ Loser	066 ♂	065 ♀	004 ♀	AC ♀	ER ♂	DL ♀	R006 ♂	EZ ♂	EC ♂	EK ♂	076 ♀	CY ♂	CN ♂	KD ♂	022 ♀	KE ♀
066 ♂	–	2	7	3	4	2	(1)	1	1	1	1	1		3		1
065 ♀		–	7	3	6	9	(1)	1	1	6	4			3	2	1
004 ♀			–	6	10	7	(1)	3	2	13	1	1	7	1	(1)	2
AC ♀			1	–	4	1		5	3	5	5		–	3	2	2
ER ♂				(1)	–	2	10	4	3	5	7	3	9	2	1	1
DL ♀						–			2	12	6		1	2	1	2
R006 ♂						–	–		(1)	2		1	1	2	2	2
EZ ♂								–	1	2	2	6	1	2	1	2
EC ♂									–	4	2	1	3	3	2	2
EK ♀										–	1		1	5	2	1
076 ♀											–		2	6	6	2
CY ♂												–	6			2
CN ♂								1					–	1	1	
KD ♂														–		
022 ♀															–	
KE ♀															–	–

A linear hierarchy is apparent among the males if transitivity is assumed in one case (*066 : CN*), and if *R006* is assumed to be dominant to *EZ*, based on events which occurred outside the period of observations. A linear hierarchy is apparent among the females, except that one encounter between *AC* and *004* went contrary to the usual direction. Males and females are listed according to their dominance rank in table VI.

Observability

A sampling technique for estimating the observability of individuals [SADE, 1966] was used during this period of observation. During each hour of

Table VI. Males among males and females among females in aggressive dominance rank, observability and observability rank, and grooming status and grooming status rank at three discriminant levels, in Cayo Santiago group F during period 14th June to 31st July 1963

	Column-marginal grooming status			Obser-vability	Dominance rank
	direct conversion	0.0625	0.1250		
Males					
066	408 – 1	143 – 1	41 – 1	36 – 1	1
ER	205 – 4	12 – 4.5	5 – 2.5	31 – 3	2
R006	200 – 5	9 – 7	4 – 5.0	20 – 6	3
EZ	189 – 6	10 – 6	4 – 5.0	22 – 4	4
EC	235 – 3	87 – 2	0 – 7	32 – 2	5
CY	106 – 7	12 – 4.5	4 – 5.0	18 – 7	6
CN	300 – 2	24 – 3	5 – 2.5	21 – 5	7
Females					
065	627 – 1	221 – 1	59 – 1	37 – 6	1
004	550 – 3	215 – 2	33 – 3	48 – 1	2
AC	540 – 4	173 – 4	25 – 4	43 – 3	3
DL	564 – 2	186 – 3	41 – 2	40 – 5	4
EK	470 – 7	65 – 7	4 – 8.5	45 – 2	5
076	511 – 5	66 – 6	6 – 5	41 – 4	6
KD	430 – 8	51 – 8	5 – 6.5	34 – 7	7
022	477 – 6	116 – 5	4 – 8.5	27 – 8	8
KE	264 – 9	31 – 9	5 – 6.5	23 – 9	9

The rank of each male among males and of each female among females follows the hyphen.

observation a short interval was chosen at random for a time sample. During the sample each monkey which could be seen was recorded. Samples of various duration were tried, but 2-min intervals were the most practical under the current conditions of observation. Longer periods often left the observer with no further monkeys in sight to record. Often too many monkeys were visible to be recorded during shorter periods. 89 2-min samples were taken during this period of observation. The observability of any monkey is indicated by the number of samples in which it occurs. This figure is given for each monkey in table VI.

Grooming Status

SADE [1965] described motor patterns and their sequences within grooming episodes among rhesus monkeys, and discussed the multiple functions of grooming in inter-individual relations. It was argued that grooming was the best single class of interactions for revealing the network of social attachments within the group.

Of the 2,181 episodes of allo-grooming observed in group F during 1963, 647 occurred between the 16 sub-adults and adults considered in this paper (table VII). A binary matrix (table VIII) was produced directly from the matrix of grooming episodes. A second binary matrix (table IX) was produced from the matrix of grooming episodes via a row marginal percent matrix, with $DV = 0.0625$. A third binary matrix (table X) was produced from the matrix of grooming episodes via a row marginal percent matrix, with $DV = 0.1250$.

Matrices of 2-step and 3-step linkages were computed (appendix I) on each binary matrix. The column marginals of the matrices produced by summing each binary matrix with its corresponding matrices of 2-step and 3-step linkages are listed in table VI. The column marginal for each monkey is the sum of the 1-step, 2-step and 3-step links directed towards him, and is his grooming status. The rank of each male among males, and of each female among females, follows the hyphen.

Kendall's rank correlation coefficient, τ [SIEGEL, 1956], was computed between grooming status and dominance, and between grooming status and observability, at each discriminant level. The coefficients together with their one-tailed probabilities are given in table XI.

Relation Between Grooming Status and Dominance

Among females dominance and grooming status are clearly correlated (table XI), indicating that the higher ranking females are more central in the

Table VII. Matrix of grooming episodes among subadults and adults in Cayo Santiago group F during period 14th June to 31st July 1963

Groomer \ Groomee	066 ♂	R006 ♂	CN ♂	ER ♂	CY ♂	EC ♂	EZ ♂	004 ♂	065 ♀	022 ♀	076 ♀	AC ♀	EK ♀	DL ♀	KD ♀	KE ♀	
066 ♂	0	0	0	0	0	0	0	3	4	0	0	0	0	0	0	0	7
R006 ♂	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
CN ♂	0	0	0	15	8	2	2	0	2	1	9	3	1	0	4	2	47
ER ♂	17	0	5	0	0	8	0	0	1	0	4	0	3	1	0	0	39
CY ♂	0	0	5	0	0	2	1	0	0	2	0	0	0	0	0	11	21
EC ♂	0	0	0	0	0	0	0	0	2	1	0	3	1	3	0	0	12
EZ ♂	0	0	0	11	1	0	0	0	0	0	0	0	0	0	0	0	12
004 ♀	49	3	0	0	0	0	8	0	41	3	0	1	6	9	0	0	115
065 ♀	25	0	0	0	0	0	0	3	0	5	0	9	2	21	2	0	73
022 ♀	0	0	0	0	0	0	4	0	6	0	0	4	0	1	2	6	23
076 ♀	1	0	5	3	0	0	0	4	0	0	0	8	5	11	16	0	59
AC ♀	5	0	1	0	0	0	0	7	0	2	13	0	0	10	1	1	43
EK ♀	0	0	2	1	0	3	0	0	24	0	4	5	0	25	2	1	70
DL ♀	0	1	0	0	0	3	0	6	23	0	0	13	2	0	5	1	54
KD ♀	1	0	2	0	0	0	0	9	9	2	21	3	4	5	0	0	47
KE ♀	0	3	0	0	1	0	1	1	8	8	1	0	5	2	1	0	24
	98	7	20	30	10	10	16	42	124	28	47	49	29	88	28	21	647

Table VIII. Binary matrix produced on table VII by direct conversion

Groomer	Groomee																Total
	066 ♂	R006 ♂	CN ♂	ER ♂	CY ♂	EC ♂	EZ ♂	004 ♀	065 ♀	022 ♀	076 ♀	AC ♀	EK ♀	DL ♀	KD ♀	KE ♀	
066 ♂	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
R006 ♂	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
CN ♂	0	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	10
ER ♂	1	0	1	0	0	0	1	0	1	0	1	0	1	1	0	0	7
CY ♂	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	1	5
EC ♂	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	6
EZ ♂	0	1	0	1	1	1	0	0	0	0	0	0	0	0	1	0	2
004 ♀	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	9
065 ♀	1	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	8
022 ♀	0	0	1	1	0	0	0	1	1	0	0	1	1	1	1	0	6
076 ♀	1	0	1	0	0	1	0	1	1	1	0	1	1	1	1	0	10
AC ♀	1	0	1	1	0	0	1	1	1	0	1	0	0	1	0	1	9
EK ♀	0	0	0	0	0	1	0	1	1	1	1	1	0	0	1	1	10
DL ♀	0	1	1	0	0	0	0	1	1	1	1	1	1	0	0	0	8
KD ♀	1	0	0	0	0	0	0	0	1	1	1	0	1	1	0	0	8
KE ♀	0	1	0	0	1	0	1	1	1	0	1	1	1	1	0	0	10
	6	3	6	4	3	3	5	11	12	9	9	9	9	10	7	5	111

Table IX. Binary matrix produced on table VII via row marginal percent matrix, with discriminant value 0.0625

Groomer \ Groomee	066 ♂	R006 ♂	CN ♂	ER ♂	CY ♂	EC ♂	EZ ♂	004 ♀	065 ♀	022 ♀	076 ♀	AC ♀	EK ♀	DL ♀	KD ♀	KE ♀	
066 ♂	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
R006 ♂	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
CN ♂	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1	0	5
ER ♂	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	1	5
CY ♂	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	4
EC ♂	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	6
EZ ♂	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2
004 ♀	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	3
065 ♀	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	1	5
022 ♀	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	0	5
076 ♀	1	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	7
AC ♀	0	0	0	0	1	0	0	0	1	1	0	1	0	1	0	0	6
EK ♀	0	0	0	1	0	0	0	0	1	0	1	1	0	1	0	0	3
DL ♀	0	0	0	1	1	1	0	0	1	0	1	1	1	0	0	0	5
KD ♀	0	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	5
KE ♀	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	4
	4	1	3	2	2	2	2	8	9	5	4	8	5	8	3	2	68

grooming network. No relation between grooming status and observability is shown, indicating that differential observability of the females has not biased the measures of their grooming statuses.

Among males the dominant male, 066, clearly has the highest grooming status (table VI), but dominance rank and grooming status do not correlate (table XI) in the series of males as a whole at any discriminant level. A significant correlation between observability and grooming status determined from the binary matrix produced directly from the matrix of grooming episodes suggests that a significant correlation between dominance and grooming status might be obscured by differential observability. However, Kendall's partial rank correlation coefficient computed between dominance and grooming status partialling out observability was very low (partial $\tau = 0.03$), indicating that differential observability did not mask a significant correlation between dominance and grooming status.

The observation that grooming status among males does not correlate with dominance rank suggests that the males are less homogeneous in relation to the social group than are the females. An examination of the clique structure of the group shows this to be true.

Cliques in Group F

The binary matrix (table IX) produced at the intermediate DV (0.0625) was examined for 1-cliques, 2-cliques, and 3-cliques by a combination of the methods of LUCE [1950] and HARARY and Ross [1957], which is described in appendix II. The relative amount of overlap of each pair of cliques within each set of cliques was estimated by the similarity index:

$$SI_{ab} = \frac{n_{ab}}{n_a + n_b - n_{ab}}$$

where n_{ab} = the number of members shared by cliques a and b, n_a = the number of members in clique a, and n_b = the number of members in clique b [STERLING and POLLACK, 1968]. Although no unique clustering within each set of cliques was found, the cliques were arranged as rows in tables XII, XIV, and XVI so that cliques with high similarity indices would be close together. Matrices of similarity indices for each set of cliques are given in tables XIII, XV, and XVII. Individuals are ordered so that each has a unique column.

Table X. Binary matrix produced on table VII via row marginal percent matrix, with discriminant value 0.1250

Groomer	Groomee																
	066 ♂	R006 ♂	CN ♂	ER ♂	CY ♂	EC ♂	EZ ♂	004 ♀	065 ♀	022 ♀	076 ♀	AC ♀	EK ♀	DL ♀	KD ♀	KE ♀	
066 ♂	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
R006 ♂	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
CN ♂	0	0	0	1	1	0	0	0	0	0	1	0	0	0	0	0	3
ER ♂	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3
CY ♂	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	2
EC ♂	0	0	0	1	0	0	0	0	0	0	0	1	0	1	0	1	4
EZ ♂	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
004 ♀	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2
065 ♀	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	2
022 ♀	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	4
076 ♀	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	3
AC ♀	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	3
EK ♀	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	2
DL ♀	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2
KD ♀	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2
KE ♀	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	3
	3	1	2	2	1	0	1	5	8	1	2	4	1	5	1	2	39

Table XI. Matrices of Kendall's τ with onetailed probabilities for dominance and grooming status and observability and grooming status, for males among males and females among females, at three discriminant levels

	Grooming status	
DV	Dominance	Observability
Males		
Direct	$\tau = 0.28$	$\tau = 0.61$
conversion	$0.27 > p > 0.12$	$p = 0.035$
0.0625	$\tau = 0.00$	$\tau = 0.29$
	$0.59 > p > 0.55$	$0.068 > p > 0.035$
0.1250	$\tau = 0.42$	$\tau = 0.30$
	$p = 0.19$	$p = 0.28$
Females		
Direct	$\tau = 0.72$	$\tau = 0.27$
conversion	$p = 0.003$	$p = 0.18$
0.0625	$\tau = 0.72$	$\tau = 0.16$
	$p = 0.003$	$p = 0.18$
0.1250	$\tau = 0.64$	$\tau = 0.17$
	$p = 0.012$	$p = 0.31$

Table XII. Grooming 1-cliques among Cayo Santiago group F adults during period 14th June to 31st July 1963, computed on table IX

1					065 ♀	004 ♀	066 ♂
2				DL ♀	065 ♀	004 ♀	
3			AC ♀	DL ♀	065 ♀		
4	022 ♀		AC ♀		065 ♀		
5		EC ♂	AC ♀	DL ♀			

Table XIII. Matrix of similarity indices among 1-cliques of table XII

1	–				
2	0.5000	–			
3	0.2000	0.5000	–		
4	0.2000	0.2000	0.5000	–	
5	0.0000	0.2000	0.5000	0.2000	–
	1	2	3	4	5

1-Cliques (Extreme Cliques)

Only 7 animals form 1-cliques; the rest are non-cliqual. Of the 5 1-cliques (table XII) only 2 contain males. The dominant male, *066*, is co-cliqual with the first and second dominant females. *EC*, a 4-year-old male, is co-cliqual with his mother and sister. The 4 multi-cliqual monkeys, *065*, *004*, *AC* and *DL*, are the 4 highest ranking females, both in dominance and grooming status (table VI), although the latter measure is not completely independent of their cliquishness. These 4 females form the core of the grooming network.

2-Cliques

These slightly more diffuse structures (table XIV) include 15 of the 16 monkeys. Only *R006*, the non-natal male who recently joined the group, remains non-cliqual.

One-cliques number 1, 2, 3, and 4 merge into 2-clique number 1, affirming the dominant male's integration with the female core of the group. *EC*, one of the two 4-year-old males, is found only in his mother's cliques, except where she is co-cliqual with the dominant male. The other 4-year-old male, *EZ*, occurs only in his brother *ER*'s clique with the other natal males. *CN*, the adult male castrate, is co-cliqual with his mother and sister, as well as with the 3 males, and may link their clique to the main group.

3-Cliques

The structure of group F revealed by the set of 2-cliques (table XIV) is still apparent in the set of 3-cliques (table XVI). The core of females is represented by 3-cliques number 4 and 5. The dominant male is clearly integrated with the female core. Male *EC* still occurs only in his mother's cliques. The genealogy of *CN*, the adult male castrate, overlaps more extensively with the cliques containing the other natal males. *R006*, the new non-natal male, at last be-

Table XIV. Grooming 2-cliques among Cayo Santiago group F adults during period 14th June to 31st July 1963, computed on table IX

	Members
2	EZ ♂ ER ♂ CY ♂ CN ♂ 076 ♀ DL ♀ EC ♂ AC ♀ 022 ♀ 065 ♀
3	ER ♂ CY ♂ CN ♂ 076 ♀ DL ♀ EC ♂ AC ♀ 022 ♀ 065 ♀
1	CY ♂ CN ♂ 076 ♀ DL ♀ EC ♂ AC ♀ 022 ♀ 065 ♀ EK ♀
4	076 ♀ KD ♀ DL ♀ EC ♂ AC ♀ 022 ♀ 065 ♀ 004 ♀
5	076 ♀ KD ♀ DL ♀ EC ♂ AC ♀ 022 ♀ 065 ♀ 004 ♀
6	076 ♀ DL ♀ EC ♂ AC ♀ 022 ♀
7	AC ♀ 022 ♀ EK ♀ KE ♀
8	066 ♂

Table XV. Matrix of similarity indices among 2-cliques of table XIV

	1	2	3	4	5	6	7	8
1	—							
2	0.3750	—						
3	0.3333	0.3750	—					
4	0.6250	0.5000	0.6250	—				
5	0.4444	0.5000	0.6250	0.7500	—			
6	0.1111	0.0000	0.2500	0.2222	0.3750	—		
7	0.0000	0.0000	0.1111	0.1000	0.1000	0.3333	—	
8	0.0000	0.0000	0.0000	0.0000	0.0000	0.1428	0.6000	—

Table XVI. Grooming 3-cliques among Cayo Santiago group F adults during period 14th June to 31st July 1963, computed on table IX

	Members
1	EZ ♂ CY ♂ ER ♂ CN ♂ 076 ♀ KD ♀ DL ♀ EC ♂ AC ♀ 065 ♀ 022 ♀ KE ♀ 004 ♀
2	CY ♂ ER ♂ CN ♂ 076 ♀ KD ♀ DL ♀ EC ♂ AC ♀ 065 ♀ 022 ♀ KE ♀ 004 ♀ 066 ♂
3	EK ♀ CN ♂ 076 ♀ KD ♀ DL ♀ EC ♂ AC ♀ 065 ♀ 022 ♀ R006 ♂
4	DL ♀ EC ♂ AC ♀ 065 ♀ 022 ♀
5	DL ♀ EC ♂ AC ♀ 065 ♀ 022 ♀

Table XVII. Matrix of similary indices among 3-cliques of table XVI

	1	2	3	4	5
1	–				
2	0.5714	–			
3	0.1428	0.3076	–		
4	0.0714	0.2307	0.7500	–	
5	0.0000	0.0000	0.3333	0.3636	–

comes unicliqual with the dominant and third ranking females, *065* and *AC*, and *AC*'s son. This shows that *R006*'s attachment to the group is not to the clique of males, as might have been predicted, but rather directly, although distantly, to the core of females. This is especially interesting when his later history is considered. *R006* became the dominant male in group F late in 1963 [SADE, 1966] and continued in that status until late 1967 [LOY, 1971].

Relation of males to the Group

Consideration of the 1-, 2-, and 3-cliques shows clearly that the males are not homogeneous in their relations to the group. The dominant male *066*, is integrated into the core with the females. The new male, *R006*, is distantly attached to the core of females. One sub-adult male, *EC*, is still integrated into his genealogy. The other natal males form a distinct sub-group. *CN*, the castrate, is intermediate in his position, which overlaps that of the natal males and the female core.

Orientations away from the Cliques

Examination of the matrix of grooming episodes (table VII) is conjunction with the tables of cliques (tables XII, XIV, and XVI) reveals that some individuals may orient strongly towards monkeys outside their cliques. The dominant male, *066*, received the largest share (77 %) of male *ER*'s grooming episodes. *ER*'s cautious approaches from behind to groom sleeping *066* suggested that he was reorganizing his patterns of orientation as he reached full adulthood. The largest share (52 %) of *CY*'s grooming was received by his younger sister, *KE*, perhaps indicating a reverberance of an earlier sibling relation. If *CY* had had an elder brother, would his orientation in the grooming network have been more like *EZ*'s, who groomed his elder brother almost exclusively? The relation between the cliqual structure of the group and the

strong orientations of certain individuals away from the cliques remains to be investigated.

Conclusions

The sociometric techniques illustrated in this paper produce results which are intuitively satisfying and yet which are strictly objective and quantitative. The utility of these techniques has yet to be explored sufficiently. Certain comments about further developments are appropriate at this time.

The use of the relation '*a* grooms *b*' in this paper should not be taken to mean that the techniques are only suitable for analysing grooming networks. Any definable relation or combination of relations can be used but, of course, the choice should make biological sense.

Differential observability of the individual monkeys was not a major problem in this study but could be in a larger, less homogeneous group. When observability becomes a serious problem better techniques will be needed to (1) estimate the amount of bias due to differential observability; (2) estimate the effect of the bias upon the problem being studied, and (3) adjust the raw data to correct the bias. The problem of correcting bias in an interaction matrix seems to be especially great, since observability may differ at each node in a chain of interactions.

As yet there is no method for deciding what number of observations is necessary to reveal the structure of a group. This problem is closely related to the problem of choosing the best discriminant value in the current study.

Finally, it must be pointed out that there are other techniques in the sociometric literature which have yet to be applied to the study of societies of non-human primates.

Summary

Social structure is defined as the network of attachments which coordinate a social unit. Quantitative techniques for describing social structure are available and are described in the literature on sociometry. Sociograms can be expressed as matrices. Two methods for analysing sociomatrices are described and used to analyse grooming interactions among adult *Macaca mulatta* in group F of the Cayo Santiago colony during the late non-mating season. The column marginals of matrices containing the sums of 1-step, 2-step, and 3-step linkages indicate the status of individuals in the network of grooming relations. These statuses correlate with dominance among females, but not

SADE

among males. Differential observability is controlled by a sampling technique. Analysis of 1-cliques, 2-cliques, and 3-cliques show that the males are not homogeneous in their relations to the group. Algorhithms are given for computing status based on linkages and for determining cliques.

Appendices

All derivations of formulae and proofs of theorems are found in the references cited in the text. The following conventions and notations are used in appendices I and II.

Given matrices A and B, $A \cdot B = C$ means ordinary matrix multiplication. $A^n = A^{(n-1)} \cdot A$. $A \times B = C$ means elementwise matrix multiplication with $C_{ij} = A_{ij} \cdot B_{ij}$. A' means the transpose of matrix A. The diagonal operator $d(A)$ is the matrix found by changing to zero all entries in A except those on the main diagonal.

Appendix I: Computation of n-Steps

Given a binary matrix B with $B_{ii} = 0$ by convention, the number of n-steps which lead from the ith monkey to the jth monkey is found in B^n_{ij}. Entries on the main diagonal, B^n_{ii} are the number of chains of n-steps which lead from the ith monkey back to himself.

Matrix B^n for ≥ 3 contains redundant chains. Let R_n be the matrix of all redundant chains found in B^n. The matrix of pure n-step paths found in $B^n = P_n = B^n - R_n$. Ross and HARARY [1952] give formulae for computing R_n for $n \leq 6$. For $n = 3$, $R_3 = B \cdot d(B^2) + d(B^2) \cdot B - B \times B'$. E_{ij}, where $E = B + B^2 + P_3$, equals the number of 1-step $+$ 2-step $+$ non-redundant 3-step chains which lead from the ith monkey to the jth monkey. Grooming statuses as used in table VI are the column marginals of E.

Appendix II: Detection of Cliques

Let B be the initial binary matrix of relations. To detect the n-cliques in B:

1. Find the matrix $D = \sum_{i=1}^{n} B^i$. It is not necessary to remove redundant chains.

2. Convert D to a new binary matrix M so that $M_{ij} = 1$ if $D_{ij} \neq 0$, $M_{ij} = 0$ if $D_{ij} = 0$, $M_{ii} = 0$ by convention.

3. Compute the symmetric matrix S on M where $S = M \times M'$.

4. Compute the intermediate matrix I, where $I = S^2 \times S$. Non-cliqual monkeys have zero row marginals in I.

5. Compute the matrix G by deleting the rows and columns of non-cliqual monkeys from I. Let sG be the set of all monkeys in G.

6. All monkeys in G who are co-cliqual with monkey m in G are those whose entries in row m are not zero. If $RM_m = n(n-1)$, where n equals the number of monkeys cocliqual with m, then monkey m is unicliqual.

7. Find monkey m in G where RM_m is minimal. If monkey m is unicliqual, go to step 8. If monkey m is not unicliqual, go to step 13.

8. Find clique C_m. C_m equals unicliqual monkey m and all monkeys co-cliqual with m.

9. All monkeys in C_m whose row marginals $= RM_m$ are unicliqual in C_m. Let the set of all unicliqual monkeys in C_m be sC_m. Find sC_m. If $sC_m = sG$, go to step 10. If $sC_m \neq sG$, go to step 11.

10. Are there any sets in storage? If yes, go to step 16. If there are no sets in storage all cliques have been detected. STOP.

11. Find the set sM, where $sG-sC_m = sM$.

12. From matrix M (step 2) create a submatrix containing only monkeys in sM. Send this new sub-matrix M to step 2 and recycle.

13. Arriving at step 13 from step 7 we must construct two sub-groups, which may have members in common: find monkey m in G, where RM_m is minimal. Let mG be the set including only m and all monkeys co-cliqual with m. Find another set pG which includes all monkeys not co-cliqual with m. Find another set qG which contains all monkeys co-cliqual with monkeys in set pG. Sets qG and mG may intersect, but sets pG and mG are disjoint.

14. Find the union of sets pG and qG. Send the new set (pG U qG) to storage. It may be necessary to store further sets before processing set (pG U qG).

15. From matrix M (step 2) create a sub-matrix containing only the monkeys in mG. Send this new sub-matrix M to step 2, and recycle.

16. Arriving at step 16 from step 10, retrieve a set from storage. From matrix M (step 2) create a sub-matrix containing only the monkeys in the retrieved set. Send this new sub-matrix to step 2, and recycle.

Note to step 9. At this point unicliqual monkeys who are not co-cliqual with each other may be found. If all of these are removed, one may be left with a set of monkeys co-cliqual with exactly the unicliqual monkeys deleted in step 11. These residual monkeys therefore will from a proper sub-set of more than one clique, but do not themselves constitute a clique, although continued processing will erroneously identify them as a clique.

Acknowledgements

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