J. theor. Biol. (1977) **65**, 671–698

A Model of Social Grooming Among Adult Female Monkeys

ROBERT M. SEYFARTH†

Sub-Department of Animal Behaviour, University of Cambridge, Madingley, Cambridge, England

(*Received* 18 *June* 1976)

Grooming networks among adult female monkeys exhibit two similar features across a number of different species. High-ranking animals receive more grooming than others, and the majority of grooming occurs between females of adjacent rank. A theoretical model which duplicates these features is presented, and the properties of the model are used to explain the possible causation and function of female grooming behaviour. The model illustrates how relatively simple principles governing the behaviour of individuals may be used to explain more complex aspects of the social structure of non-human primate groups.

1. Introduction

The aim of this paper is to provide a simple explanation of one aspect of the social structure of non-human primate groups. I hope to show how available data from a number of different species can be used to generate models of social interaction, and to illustrate some of the ways in which these models contribute to an understanding of individual variation, social structure, and the causal factors underlying behaviour.

Grooming among adult female monkeys has been chosen not because it is the only behaviour suitable for this purpose, but because it provides an ideal starting point from which to generate more complex models of social interaction and social structure. Grooming is the friendly behaviour most frequently exchanged between adult primates, and adult females are generally thought to comprise the stable "core" of most Old World Monkey groups (e.g. Bernstein & Sharpe, 1966; Crook, 1970; Gartlan, 1975). Grooming among adult female monkeys is also slightly less complex than grooming among some other primates, since female monkey grooming is primarily

---

†Present address: Rockefeller University, Field Research Center, Tyrrel Road, Millbrook, New York 12545, U.S.A.

dyadic, while that among male chimpanzees, for example, may involv three or more individuals simultaneously (Simpson, 1973).

I shall begin by adopting Hinde's (1976) definition of social structur as "those aspects of the content, quality, and patterning of relationship which show regularities across individuals and across societies . . .". Thi definition has a number of advantages over others (e.g. Eisenberg *et al* 1972), the most important of which, I believe, is that it provides a framewor within which primatologists can progress from simple descriptions of socia interaction to more complete explanations of behaviour and social structur in terms of general causal and functional principles.

By defining social structure in terms of the patterning of relationship (see above), Hinde implies that one important factor affecting social structur is the amount of attraction between individuals. An understanding of th bases for such attraction, and of the ways in which it is expressed, is therefor an important part of any explanation of principles governing the structur of primate groups. Primatologists have thus far studied the attractio between individuals in two ways.

Most commonly, observers have simply recorded the frequency c proximity or non-agonistic behaviour, and have assumed that these measure directly reflected the degree of attraction between individuals. Kummer (1968) study of hamadryas baboons and Dunbar & Dunbar's (1975) monc graph on geladas are examples of this approach, and they illustrate ho simple observation can reveal differences between species whose soci structures appear at first to be similar. Despite the advantages of this tech nique, however, its basic assumptions may be incorrect (Vaitl, 1977). Fo example, in both hamadryas and gelada one-male units, leader male interact with only a few of the available females. Does this mean that onl a few of the females are attracted to the male, or vice versa? Or are ther other social factors, such as competition, which might prevent the complet *expression* of attraction between certain individuals?

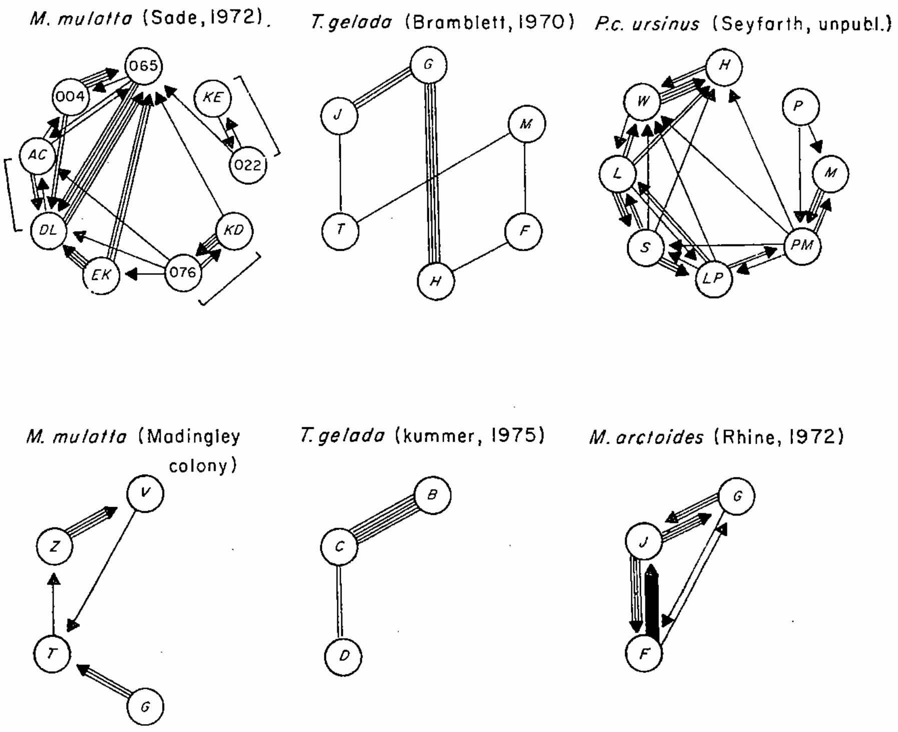
In an effort to overcome the limits of simple observation, both Kumm (1975) and Vaitl (1977) have conducted experiments involving the recordin of individual behaviour both in groups and in isolated dyads. Their studi have shown that the magnitude of attraction expressed between individua may differ in these two situations, and their results indicate clearly that on cause of this difference lies in the fact that some individuals in social grou may inhibit social interaction between others.

This paper presents a third technique for studying the relation betwee inter-individual attraction, competition, and social structure. It relies o simple mathematical models of social interaction presented in the for of social networks. The paper is organized into two parts. In the first, dat are presented on the distribution of grooming among adult females in four primate species. From this information a few essential features are abstracted which describe aspects of grooming common to all cases. Causal factors which might lead to such uniformity are discussed. In the second part of the paper a theoretical model is presented which accurately reproduces all the features of grooming described earlier. The model is introduced because it shows how relatively complex features of social structure can be explained in terms of simple principles governing individual behaviour, and because it offers one theoretical solution to a more general problem in behavioural analysis, namely, how can we measure aspects of social behaviour—such as the degree of attraction between individuals—which may not be fully expressed under natural conditions?

2. Observations to be Explained and the Causal Factors Known to Affect the Distribution of Grooming Among Individuals

Figure 1 illustrates networks of grooming relations among adult females in four different primate species. Despite both species and environmental differences, as well as wide variation in the number of genetically related individuals within each group, the networks nevertheless exhibit a number of similar features. These are listed in Table 1. In most cases there is a highly positive correlation between a female's rank (see below) and the total amount of time she spends engaged in grooming interactions. In all cases there is a positive correlation between a female's rank and both the number of females who groom her and the total amount of grooming she receives; there is no consistent relation between rank and the amount of grooming a female gives to others; and females with adjacent ranks always account for more grooming than expected if grooming were distributed randomly among all individuals. The relation between rank, total grooming received (R), and total grooming given (G) may be specified further by stating that in at least two cases there is a significant positive correlation between individual rank and the value R/G, i.e. high-ranking females receive more total grooming relative to the amount they give (Fig. 2).

As Levi-Strauss (1953) points out, one of the requirements for models of social structure is that they "be constituted so as to make immediately intelligible all the observable facts". Any model of grooming relations among adult female primates must therefore not only explain the similarities across species listed above but also incorporate all of the causal factors which previous studies have shown to affect the distribution of grooming among individuals. These causal factors are discussed below.


M. mulatta (Sade, 1972). *T. gelada* (Bramblett, 1970) *P.c. ursinus* (Seyfarth, unpubl.)

M. mulatta (Madingley colony) *T. gelada* (kummer, 1975) *M. arctoides* (Rhine, 1972)

FIG. 1. Networks of grooming among adult females in four species of Old World Monkeys. In each case females are shown in decreasing rank order reading counter-clockwise from the top. The study by Sade (1972) was carried out in the field among individuals of known blood relation (close genetic relatives, in this case mothers and their adul daughters, are indicated by brackets—see Breuggeman, 1973). The study by Seyfarth (unpublished) was carried out in the field where some individuals were presumably blood relations but this could not be determined; all other studies were carried out in captivity among individuals who were presumably unrelated. *M. mulatta* (Madingley colony) refers to one group of rhesus monkeys housed at the Sub-Department of Animal Behaviour University of Cambridge. Scale: *M. mulatta* (Sade, 1972) and Madingley colony ——— = 6–10 units; ═══ = 11–15 units, etc.

T. gelada (Bramblett, 1970) ——— = 5% of all grooming.
T. gelada (Kummer, 1975) = schematic drawing.
P.c. ursinus (Seyfarth, unpublished) ——— = 1–3 units; ═══ = 4–6, etc.
M. arctoides (Rhine, 1972) ——— = 10–19 units; ═══ = 20–29, etc.

TABLE 1

The essential features of adult female grooming in four species of Old World Monkeys. Individual rank is defined in the text
† = $P < 0·05$, ‡ = $P < 0·01$. *N/A = not assessed*

	M. mulatta		*M. arctiodes*	*P. ursinus*		*T. gelada*
	Sade (1972)	Madingley Colony	Rhine (1972)	Seyfarth (unpublished)	Bramblett (1970)	Kummer (1975)
1. Correlation between rank and the amount of time spent interacting by each individual (*T*).	$r_s = 0·87$	0·40	−0·50	0·6†	0·67	N/A
2. Correlation between rank and the total amount of grooming received by each indivdual (*R*).	0·85†	0·15	0·50	0·85†	N/A	N/A
3. Correlation between rank and the total number of animals who groom each individual.	0·83†	0·15	0·50	0·76†	N/A	N/A
4. Correlation between rank and the total amount of grooming given by each individual (*G*).	0·05	0·40	−1·00	0·43	N/A	N/A
5. Proportion of all grooming accounted for by females of adjacent rank.						
No. of dyads composed of adjacent-ranked individuals / Total no. of dyads	22%	50%	66%	25%	33%	66%
Amount of grooming between adjacent-ranked individuals / Total amount of grooming	44%	75%	89%	73%	50%	100%

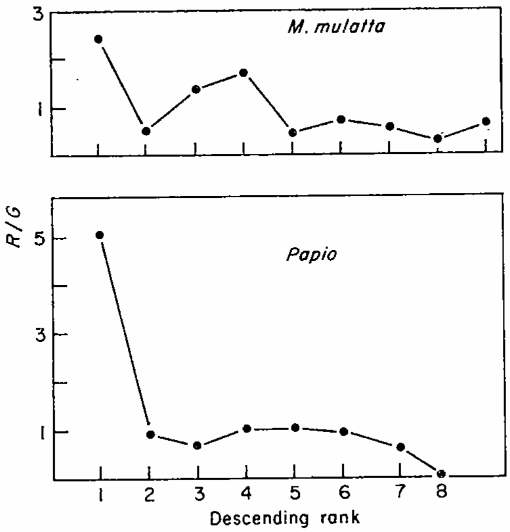


FIG. 2. The relation between individual rank (see text) and total grooming receiv divided by total grooming given (*R*/*G*) in two groups of Old World Monkeys. For *M mulatta* (Sade, 1972) $r_s = 0{\cdot}93$; for *Papio* (Seyfarth, unpublished) $r_s = 0{\cdot}69$ (both $P < 0{\cdot}0$

(A) DOMINANCE

The females whose grooming networks are illustrated in Fig. 1 can i all cases be ranked in a linear dominance hierarchy, where each individual rank is defined in terms of the direction of her agonistic interactions wit others (see references in Fig. 1). Since females are known to compete f access to each other (e.g. Hall, 1967; Kummer, 1975; Seyfarth, 197 dominance will clearly affect the distribution of grooming among individual High-ranking females should be able to groom whomever they choo whenever they like, while the grooming of low-ranking females should b constrained through competition.

(B) INDIVIDUAL DIFFERENCES IN ATTRACTIVENESS

Research on social behaviour other than grooming has shown that the may be individual differences in "attractiveness" within primate group For example, adult female baboons frequently show marked preference f one male over all others as a sexual consort (e.g. Saayman, 1971; Seyfart in prep.), and immature baboons and macaques are known to give mo friendly gestures to the infants of high-ranking, as opposed to low-rankin adult females (e.g. Gouzoules, 1975; Cheney Seyfarth, 1976). It seer reasonable to assume that the distribution of grooming among adult femal will also be affected by individual differences in attractiveness.

(C) THE TIME AVAILABLE FOR GROOMING, AND THE TEMPORAL DISTRIBUTION OF INDIVIDUAL GROOMING TIMES

A female's time for grooming with other adult females should be affected by both ecological and social factors. The demands of food-gathering, for example, should set an upper limit on the time available for grooming interactions, and grooming time should also be affected by both the number, ages, and sex of a female's offspring (e.g. Oki & Maeda, 1973) and the nature of her relations with adult males (e.g. Seyfarth, in prep.).

Despite wide variation in all of these factors, however (and thus wide individual variation in the time available for grooming interactions), the individuals shown in Fig. 1 nevertheless produced grooming networks with *similar* features. An accurate model of female grooming must therefore not only incorporate time as a finite, limiting variable (see above), but must also explain why individual variations in time available appear to have a relatively unimportant effect on the distribution of grooming among females.

Grooming relations should also be affected by the temporal distribution of individual grooming times. If two individuals are the only troop members who choose to groom early in the morning, each will of necessity be the other's grooming partner. In most primate species, however, observers have reported a high degree of "co-ordination", or inter-individual synchrony, in the temporal distribution of both food-gathering and social behaviour (e.g. Hall, 1962; Kummer, 1968; Altmann & Altmann, 1970; Clutton-Brock, 1974; Bernstein, 1975). This point is discussed further below. However, it should be emphasized that, whenever the social interactions of more than two individuals are even roughly synchronized, competition will be an important factor affecting the distribution of interactions among individuals.

(D) PREFERENCE AMONG CLOSE GENETIC RELATIVES

One of the most interesting features of primate social structure concerns the relation between grooming, rank, and the degree of genetic relatedness among adult females. For example, among female rhesus macaques Sade (1965, 1967, 1972) has shown that the close grooming relations formed between mothers and offspring and between siblings persist throughout the offsprings' adult lives, and that such closely related females also occupy similar ranks within each group. Females may therefore be arranged in a "hierarchy of families", where preference among close genetic relatives should be an important causal factor affecting the distribution of grooming among individuals.

The networks in Fig. 1, however, suggest a somewhat different conclusion Despite the fact that one group contained known blood relatives, anothe contained blood relatives who were unknown to the observers, and fou others contained individuals who were presumably unrelated, all group produced grooming networks with similar basic features. An accurate mode of female grooming must therefore not only allow for the possibility o preference among relatives but also explain why these preferences produc only minor variations in the distribution of grooming among individuals.

(E) CHANGES IN REPRODUCTIVE STATE

The networks illustrated in Fig. 1 all involve females without youn infants. As a result they give no indication of the marked changes in groomin behaviour which are known to occur whenever a female gives birth. Female with young infants receive more grooming, are groomed by a greate number of individuals, and may have an entirely different set of groomin partners than at other times during their reproductive cycles (Rowell, 1968 1969; Kaufmann, 1966; Struhsaker, 1971; Seyfarth, 1976; Hinde & Powe Proctor, 1977). Thus if a theoretical model is to offer a complete explanatio of female grooming it must not only deal with grooming when infants ar absent but also explain changes in the network of relations whenever on or more individuals gives birth.

(F) SUMMARY

The preceding section has considered five causal factors known to affec the distribution of grooming among females, and I have argued that an theoretical model which purports to explain female grooming must tak these factors into account. Specifically, an accurate model must

(1) Incorporate dominance among individuals. Or, if female dominanc relations are not apparent (e.g. Jay, 1965), make some explicit assumption about the ways in which the distribution of one animal's grooming migh limit the distribution of another's, particularly if animals engage in groomin during roughly the same time periods.

(2) Allow for possible individual differences in attractiveness [see als Section (4), below].

(3) Incorporate time available for grooming interactions as a finite limiting variable; but also explain why individual variations in time appea to have a relatively unimportant effect on the distribution of groomin among females.

(4) Allow for the possibility of strong attraction between close geneti relatives; but also explain why variation in the number of genetic relative

present appears to have only a minor effect on the distribution of grooming among females.

(5) Deal not only with grooming relations among females without infants but also with changes in grooming relations whenever infants are born.

3. A Model of Female Grooming

(A) INTRODUCTION

As a first step in the development of a model of female grooming, the following paragraphs specify assumptions about the function of grooming behaviour, and the evidence which exists to support these assumptions.

First, assume that the biological function of engaging in grooming has two aspects. Animals benefit when they receive grooming because of the removal of their ectoparasites; and animals benefit when they engage in grooming—regardless of who gives or receives—because there is a causal relation between X's interaction with Y and Y's subsequent support of X, for example in an aggressive coalition. At present there is some evidence to support the first point (Sparks, 1967; Rosenblum, Kaufman & Stynes, 1966), and although the second is hypothetical it is known that adult male baboons give the most support (through aggressive intervention in disputes) to those females with whom they groom most often (Kummer, 1968; Seyfarth, in prep.), and that adult female monkeys also support their most frequent grooming partners most often (Bramblett, 1970; Seyfarth, 1976). Close correlations between amount of grooming and support are known to exist even in the case of highest-ranking females (e.g. Bramblett, 1970; Seyfarth, 1976), suggesting that possible causal relations between grooming and support (see above) may be important even for those females who win the majority of their agonistic interactions. This may be due either to the need for support against males or to the maintenance of a female's rank during her adult life.

Second, assume that whereas all individuals are equally skilled at removing each other's ectoparasites, the likelihood of any individual successfully supporting another in an aggressive coalition is directly related to the supporting individual's rank (i.e. high-ranking animals are more successful than others). There is no evidence to support the former point, but the latter is a reasonable assumption because an animal's rank is generally defined in terms of the direction of her agonistic interactions with others (see also Weisbard & Goy, 1976).

Third, assume that females will be selected to maximize the total amount of benefit received from all others over a finite period. This assumption, together with those above, suggests a number of additional points concerning both the distribution of grooming partners within any group and the distribution of grooming given and received between any two individuals.

Concerning the distribution of grooming partners, the assumptions sugges the following.

(1) An individual's attractiveness will be derived from the potentia benefit she can offer others, making females attractive in direct relation t their ranks. This contrasts with behaviour among adult male chimpanzees where age as well as rank appears to be an important factor affectin individual attractiveness (Simpson, 1973; Bygott, 1976).

(2) Females will be selected to maximize the time they spend interactin with high-ranking individuals. For some this may involve simply synchronizing one's social activity to coincide with that of high-ranking females while for others it may entail a "waiting game" until high-ranking female become available. This point relates directly to an issue raised earlier concerning the temporal distribution of individual grooming times an observations of inter-individual synchrony in food-gathering and socia behaviour.

(3) Since all females have the same goal, however, and since the fulfillmen of one individual's goal necessarily precludes the fulfillment of another's competition will eventually force some animals to compromise. The exac nature of these compromises will be a major factor determining the distribution of grooming partners among females.

Concerning the distribution of grooming given and received between an two individuals, the assumptions suggest the following.

(1) For all individuals, giving grooming will bring benefit according t the rank of one's partner, while receiving grooming will bring benef according to the rank of one's partner plus the removal of ectoparasite Thus receiving grooming will always bring benefit at a higher rate than giving but giving grooming will become an increasingly acceptable alternative t receiving as the rank of one's partners increases.

(2) In any interaction the higher-ranking female will be more attractiv to her partner than vice versa.

(3) The lower-ranking female will therefore have to give more groomin if the interaction is to continue.

(4) The difference between the females' attraction to each other, and henc the amount of imbalance in their grooming, will be *least* when the individual ranks are most alike. Grooming will therefore tend to be most recipro when individuals occupy adjacent ranks.

(5) Since competition will affect who grooms whom within any group (s above), and since the relative ranks of individuals will affect the extent t which their grooming is reciprocal, competition will also affect the relati

amounts of total grooming received and total grooming given (or R/G) for each female with all her grooming partners.

Thus a few basic assumptions concerning the function of grooming behaviour suggest a number of additional conclusions concerning the characteristics of grooming relations among individuals. In the following section I use the assumptions above to develop a model of female grooming. The model illustrates explicitly how attractiveness and competition interact over time under a variety of hypothetical conditions, and it offers an explanation of observed grooming behaviour in terms of the compromises made by individuals in their attempts to maximize benefit.

(B) THE BASIC MODEL

First, assume that the adult females in a hypothetical group of monkeys can be ranked in a stable, linear dominance hierarchy where each female's rank is defined in terms of the direction of her agonistic interactions with others (female A is highest-ranking, female B is second-highest-ranking, etc.). Second, assume (as above) that each female is attractive to others in direct relation to her rank (A is most attractive, B is second-most-attractive, etc.), and hence that all individuals have goals reflecting which grooming partners are most attractive. Third, assume that all individuals *attempt* to devote an equal amount of total time (A_t) to grooming interactions with other adult females. Assume that this goal will be divided in some way between the total time an individual attempts to spend giving grooming to others (A_g), and the total time she attempts to spend receiving grooming from others (A_r). (These goals describing the time individuals attempt to spend in grooming interactions are distinguished from the total times which they *actually* spend: total times actually spent giving grooming (G), receiving grooming (R), and engaging in any grooming interaction (T) are discussed above, Table 1, Fig. 2.)

The outcome of these assumptions *over any relatively long period of time* (see below) can be simulated by a computer program which executes the following steps.

(1) The distribution of female A's grooming is calculated first. By beginning with female A the computer simulates the fact that over any relatively long period of time A will be unaffected by competition, and will distribute her grooming solely according to the attractiveness of others. A selects female B first, and grooms B until either A's time for giving grooming or B's time for receiving grooming has run out. If A still has time for giving grooming left after grooming B, then A moves on to C, D, E, etc., grooming each until either the recipient's time for receiving grooming or A's time for giving grooming runs out. (The order in which A selects other females

reflects their relative attractiveness to her.) A grooms others until her tim for grooming has been fully depleted.

(2) The distribution of female B's grooming is then calculated. By calculating B's grooming second the computer simulates the fact that over an relatively long period of time B's grooming will be constrained *only* b competition from female A. Otherwise, B will distribute her groomin solely according to the attractiveness of others. B selects others for groomin following the order A, C, D, E, etc.

(3) The distribution of each other female's grooming is then calculated following the same rules of access and attractiveness over any relativel long period of time illustrated above. (Note that within this system it i entirely possible that very low-ranking females will either receive no groomin or be unable to groom others, or both—see below.)

It is important to emphasize that this model does not attempt to describ the distribution of grooming which might be observed at any given moment Instead, the model attempts to illustrate the cumulative results of behaviou occurring over relatively long periods, giving the assumption that female are behaving according to the model's basic principles. Data from actua observation (see above)—against which the model will be compared (se below)—are based on observation over periods ranging from 1 to months.

Figure 3 presents a series of hypothetical grooming networks based on th computer program outlined above. In all networks all females attempt t devote 100 units of time to grooming interactions with others (i.e. $A_t = 100$) while in different networks females attempt to achieve different overal values of A_r/A_g. Computer simulation thus assumes that over a finite perio of time females have goals, in terms of both particular grooming partner (see above) and particular overall values of receiving and giving. Th simulations illustrate three points.

First, competition limits the ability of individuals to achieve their desire goals. Many females are prevented from interacting with the highest-rankin individual, many are unable to achieve the desired overall value of A_r/A_g and many are unable to devote 100 units of time to grooming interactions

Second, high-ranking females are always more able than low-rankin females to achieve their objectives. The higher an individual's rank the mor likely her partners will include others of high rank, and—as shown i Fig. 4—the more likely she will be to achieve the desired overall values o A_r, A_g, and A_t.

Third, hypothetical networks come closest to duplicating the feature of observed networks as individual goals for A_r/A_g approach one. Usin two features of observed networks as "tests" (see above, Table 1, Figs

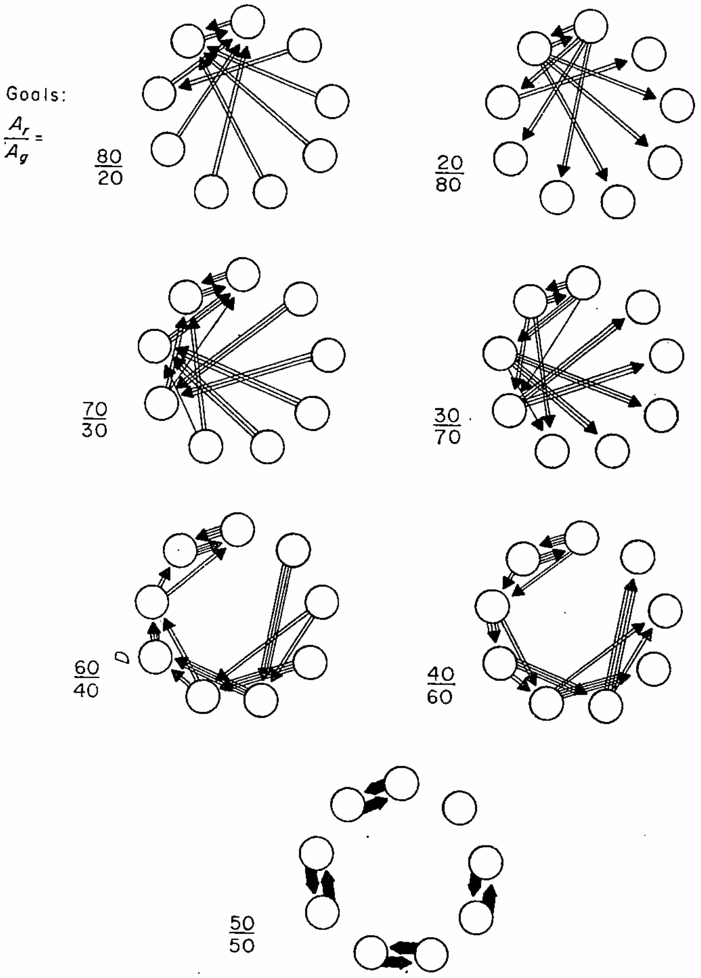


FIG. 3. Hypothetical grooming networks among nine adult females when individuals are assigned varying goals for receiving (A_r) and giving (A_g) grooming. Each line represents ten units of grooming. Solid bars (bottom sociogram) represent 50 units.

and 2), Fig. 5 illustrates this point more precisely. Hypothetical networks are characterized by a significantly positive correlation between rank and achieved overall values of R/G only when individual goals for A_r/A_g are greater than one; hypothetical networks show a greater-than-expected proportion of total grooming between females of adjacent rank only as individual goals for A_r/A_g approach one; and *both* features of observed networks are reproduced by the model only when individual goals for receiving and giving fall within the range $1 < A_r/A_g < 1{\cdot}9$.

Moving to a model which takes slightly more account of possible individu variation in goals for receiving and giving, Fig. 6 illustrates the extent t which the model above duplicates the essential features of observed network when individual values for A_r/A_g are chosen at random from within increa ingly wide limits. The features of observed networks are accurately duplicate in a high proportion of all simulations when goals for receiving and givin fall within the limits $1 < A_r/A_g < 3$. Hereafter the theoretical mode defined as above and with goals for receiving and giving falling within the limits, will be referred to as the "basic model".

The basic model's ability to reproduce the features of observed groomin networks strongly suggests that grooming relations among adult femal monkeys can be explained in terms of competition and the attractivene of high-ranking individuals (see also below). But why does the model *on* reproduce the features of observed networks when individual goals f A_r/A_g are set close to one? The answer, I believe, lies in a closer examinatio of the factors governing grooming within each bout in light of the principl of benefit maximization presented earlier.

In discussing the possible biological function of grooming behaviour (s above), I suggested that in any interaction each individual will "assess" t relative benefits of receiving and giving grooming with her particular partn at hand. The difference in the two females' assessments will reflect t difference in their attraction to each other, and these differences in attractiv ness will in turn be derived ultimately from the difference in the female ranks. Grooming will show the greatest imbalance when partners' ranks a most disparate, and will be most reciprocal when partners' ranks are mo alike.

From this it follows that, in any system where competition causes mo grooming to occur between females of adjacent rank, grooming interactio will generally be reciprocal, and most females will achieve overall valu of *R/G* approximately equal to one. This is characteristic of both observ grooming networks (see Fig. 2), and those hypothetical grooming networ which reproduce the features of observation (see Fig. 3).

Thus the model presented above, where individual goals for A_r/A_g a set close to one, succeeds in reproducing the features of observed networ because it assigns females goals for giving and receiving which are consiste with the model's assumptions concerning competition and the caus principles governing individual behaviour. The model offers a simpl straightforward explanation of *all* the features of observed grooming n works because it illustrates how the limits imposed on giving and receivin like the limits imposed on grooming partners, follow logically from t interaction between competition and individual attempts to maximize benef

(C) SUMMARY

The essential features of observed grooming networks are duplicated—and may be explained—by a model which assumes that females attempt to maximize benefit in their interactions with others. Attempts to maximize benefit cause individuals to be attractive in direct relation to their ranks, and these individual differences in attractiveness, combined with competition, produce the distribution of grooming observed. High-ranking females, who meet little or no competition, interact with others of high rank; middle-ranking females, who meet competition for those of high rank, compromise by interacting with others of middle rank; and low-ranking females, who meet competition for all individuals, are left to interact with each other.

However, although the model can reproduce all of the essential features of observed grooming networks described above, it nevertheless leaves a number of questions unanswered. To what extent, for example, will the model continue to reproduce observed features regardless of variation in the total time which individuals attempt to devote to grooming interactions (A_t)? How will the model be affected by preference among genetic relatives? How accurately can the model predict changes in grooming relations related to changes in reproductive state? The following sections consider the model in light of variations in these parameters. My aim is to show how, by making only a few changes in its properties, the basic model accurately explains female grooming relations in a variety of social situations.

4. Variations in the Model Related to the Time Which Females Attempt to Spend Interacting

At least two points are relevant to any consideration of individual variation in the time which females attempt to spend—and the time which they actually spend—grooming with other adult females. First, as already noted, factors such as the time required for food-gathering and the number of a female's offspring will set an upper limit on the time which individuals can attempt to spend interacting with other adult females. Second, however, even in cases where all individuals attempt to spend a large amount of time, competition will limit the time which low-ranking females can actually devote to grooming interactions. The basic model shows this clearly (see above, Fig. 4), and in doing so offers an explanation of why, in observed grooming networks, there is a positive correlation between rank and the total time which females actually devote to grooming interactions (see Table 1).

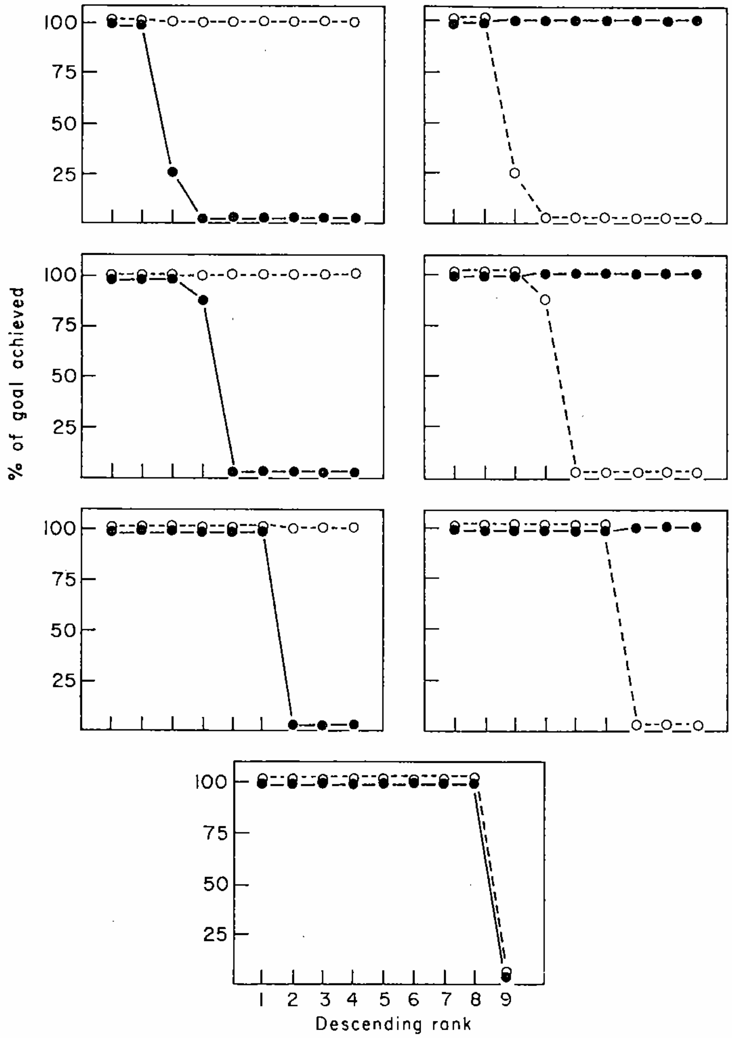


FIG. 4. The proportion of goals for receiving (dark circles) and giving (open circle grooming achieved by females of different ranks in the hypothetical networks shown i Fig. 3. The arrangement of graphs corresponds to the arrangement of grooming network in Fig. 3.

But what about the possibility that factors such as food-gathering and grooming of offspring will set *varying* upper limits on the time which individuals can attempt to spend interacting with other adult females? To test whether such variation affects the basic model, 1000 simulations were run in which (1) individual dominance and attractiveness were fixed (see above), (2) using a random number generator, each female was assigned a goal for A_t within the range 1–20, and (3) each female was randomly assigned

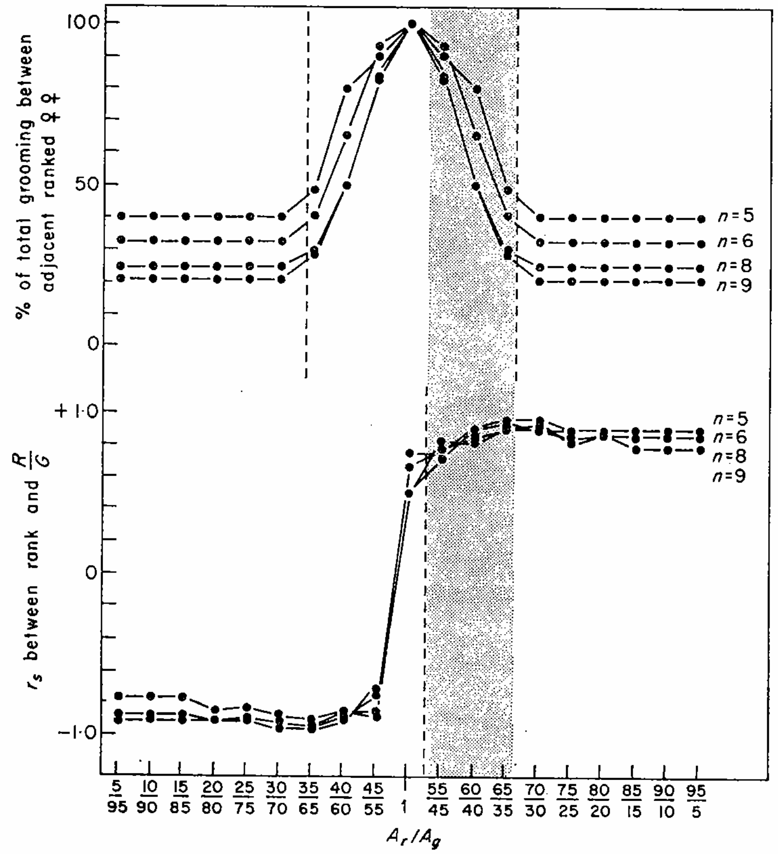


FIG. 5. The extent to which hypothetical grooming networks duplicate the features of observed grooming networks when individuals are assigned different goals for receiving and giving (A_r/A_g). The top graph shows the proportion of grooming accounted for by females of adjacent rank, with vertical lines indicating the limits within which adjacent-ranked females account for more grooming than expected (n = group size). The bottom graph shows Spearman rank correlation coefficients between rank and R/G, with vertical lines indicating the limits within which the correlation is significantly positive. Shaded area indicates the limits within which both features of observed grooming networks are duplicated by the model.

a goal for receiving and giving within the limits set above. The assignmen of goals for A_t within the range 1–20 allows for the possibility that over relatively long period of time one individual may consistently attempt t spend as much as 20 times more time interacting than another (more tha twice the extremes of variation observed in actual populations), and th running of 1000 simulations allows for the possibility that the various goal for A_t assigned to individuals may be positively correlated, negativel correlated, or unrelated to rank. In over 90% of all simulations there wa a positive, significant correlation between rank and R/G (see above), *an* females of adjacent rank accounted for more grooming than expected. Thu if females are regulating their behaviour according to the basic model' principles even very wide individual variations in the time which animal attempt to spend interacting will have only minor effects on the distributio of grooming among individuals. The basic model therefore offers on explanation of why female grooming networks may exhibit similar featur despite wide variations in other aspects of the social group (see Fig. 1).

5. Variations in the Model Related to Preference Among Close Genetic Relatives

(A) SIMULATION

The basic model assumes that each female will be attracted to others i direct relation to their relative ranks. While this pattern of preference ma well exist within some captive groups (see above), adult female preference i other groups will undoubtedly be influenced by the individuals' degree genetic relatedness. How will preference among close genetic relatives affe the basic model?

To modify the model, first assume that females can still be ranked in linear dominance hierarchy, and that close genetic relatives (i.e. mothers an their adult daughters) occupy adjacent ranks [see above, section 2(D) Second, assume that each female will be attracted more to her close relatio than to others, and that within these two general categories (i.e. close genet relations and others) she will prefer individuals according to their relati ranks. Thus if female D is related to female C she will be attracted to othe in the order C, A, B, E, etc.; and if female E is related to females F and she will be attracted to others in the order F, G, A, B, C, etc. Third, assun that regardless of the total time available for any grooming interaction females will attempt to divide their time between giving and receiving suc that $1 < A_r/A_g < 3$.

Given these assumptions, and assuming for the moment that there a no more than two adult female members of the same family within eac

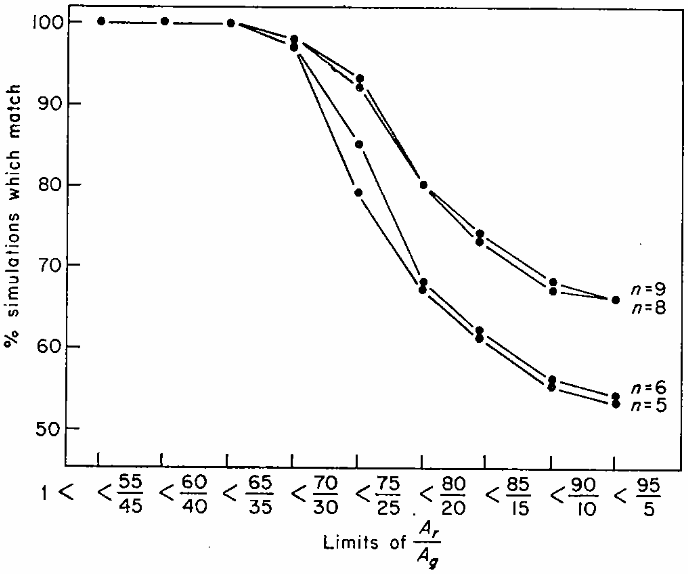


FIG. 6. The extent to which hypothetical grooming networks duplicate the features of observed grooming networks when individuals are assigned goals for receiving and giving (A_r/A_g) at random within increasingly wide limits. Percentage values based on 1000 simulations in which a random number generator was used to assign females goals within each set of limits indicated. A "match" was defined as any simulation in which (i) adjacent-ranked females accounted for more grooming than expected, and (ii) there was a positive, significant correlation between rank and R/G.

group, there are still a number of possible choices open to individuals depending on how they choose to distribute their grooming among related and unrelated individuals. Using a hypothetical group of nine females, Fig. 7 illustrates examples of these choices. The examples are not meant to be exhaustive, but are presented simply to illustrate a number of general points.

In Fig. 7(a)–(c) I assume that each female will attempt to give as much grooming as possible to her relative. In all cases females of adjacent rank account for more grooming than expected, and in two of the three cases individual values for R/G are positively correlated with rank. [The exception is Fig. 7(c), where the lone unrelated female is highest-ranking.] In Fig. 3(d)–(f) I assume that each female will attempt to give some proportion of her grooming (in this case 50 %) to her relative and the remainder to unrelated individuals. In all three cases both features of observed grooming networks are reproduced by the model.

Of course, the networks shown in Fig. 7 are only examples of the possible grooming relations which may result given that group size, A_r/A_g, the

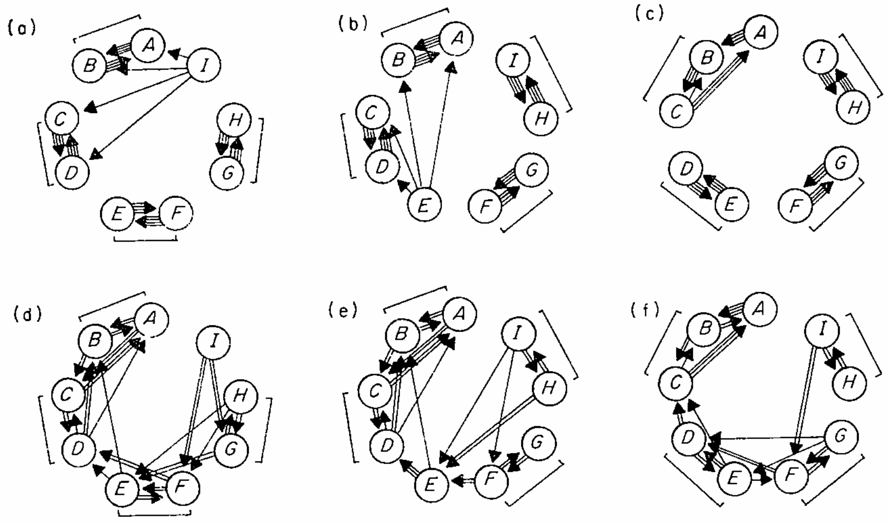


FIG. 7. Hypothetical grooming networks in a group of nine adult females where clo genetic relatives are indicated by brackets. In (a)–(c) I assume that each individual w attempt to give as much grooming as possible to her relative, and then will choose othe for grooming according to their ranks. I also assume, for purposes of illustration onl that for all individuals $A_r/A_g = 10/8$. In (d)–(f) I assume that each individual will attem to give 50% of her total grooming to her relative, and that she will attempt to distribu the remainder among unrelated individuals according to their ranks. In all figures each li represents two units of grooming.

number of related and unrelated individuals, and the proportion of groomir given to relatives may vary. However, computer simulations where all these parameters are allowed to vary indicate that, as long as individu values for A_r/A_g remain within specified limits (see above), the modifie basic model duplicates both features of observed grooming networks over 90% of all cases. The obvious similarities between grooming cause by rank-based preference and grooming caused by kin-based preferen are considered further in the discussion below.

The presence of more than two closely related adult females in the san group raises the question: will grooming within families follow the san principles as grooming between unrelated individuals? Figure 8 provides number of alternative examples.

In Fig. 8(a)–(c) I assume that grooming within families will follow t the same fundamental principles as grooming between families, and th that each adult female in a family group of three will attempt to give much grooming as possible to the higher-ranking of her two relative Although this has no effect on the essential features of grooming networ

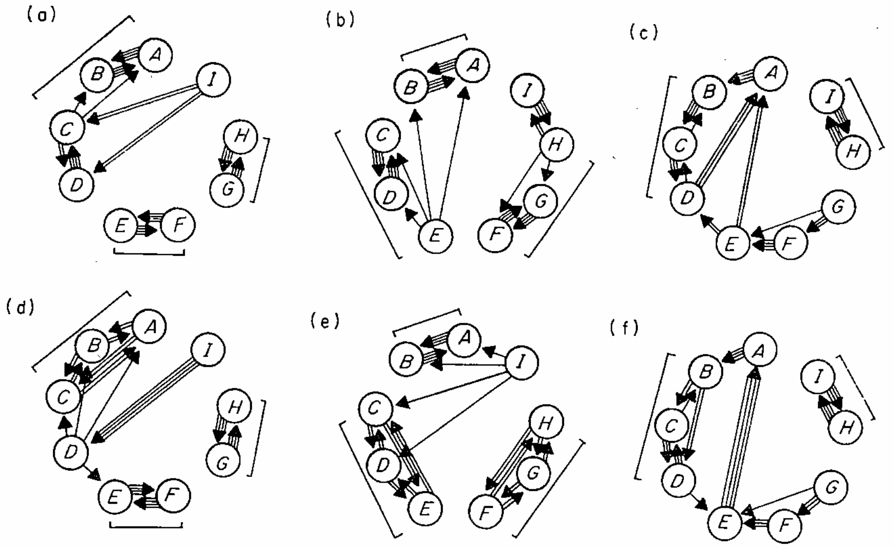


FIG. 8. Hypothetical grooming networks in a group of nine females where there are more than two close genetic relatives present. In (a)–(c) I assume that each adult female in a family group of three will attempt to give as much grooming as possible to the higher-ranking of her two relatives, then will choose her lower-ranking relative for grooming, and finally will choose unrelated animals for grooming according to their ranks. In (d)–(f) I assume that each adult female in a family group of three will attempt to divide her grooming equally among her two close relatives regardless of their ranks. Legend as in Fig. 7.

(since in all cases the features discussed above remain constant), it nevertheless means that some close relatives engage in little or no grooming. In Fig. 8(d)–(f) I assume that grooming within families will follow different principles from those governing interactions between others, and thus that each adult female in a family group of three will attempt to divide grooming proportionately (in this case equally) between her two close relatives regardless of their ranks. As before, this has little effect on the features of grooming networks, however, it does make interactions between close genetic relatives qualitatively different from those between others.

(B) DISCUSSION

As noted above, one of the requirements of any model of female grooming is that it explain why similar networks arise regardless of the number of close genetic relatives present. The basic model (slightly modified) meets this requirement, thus supporting the idea that properties of the model are analogous to the causal factors underlying behaviour.

The modified basic model also emphasizes that unitary explanations, such as "preference among close genetic relatives", are insufficient to explain all of the features of observed grooming networks. In Sade's (1972) study for example, the total amount of grooming received by each female was positively correlated with rank, not family size, and grooming between members of different families, like grooming between members of the same family, occurred primarily between animals of adjacent rank.

In contrast, if female grooming behaviour is considered in terms of a number of interacting causal factors, such as preference among relatives dominance, and the attractiveness of high rank, the features of observed networks are fully explained. Accepting that grooming preferences formed during ontogeny between members of the same family will be an importan cause of adult grooming distributions, the model illustrates how, during adulthood, these preferences will be reinforced by the interaction between dominance and the attractiveness of high rank.

Finally, this explanation of adult female grooming further suggests two predictions concerning social structure and individual behaviour in group of Old World Monkeys. First, the model predicts that the essential feature of grooming relations among the adult females in any group may remain relatively stable over a number of generations, regardless of changes in either the size and composition of the group or the degree of geneti relatedness among individuals. The presence of similar networks among a number of different groups with different degrees of genetic relatednes offers some indirect support for this prediction, but it remains to be tested by long-term observation.

Second, and perhaps more important, the model predicts that bond between members of high-ranking families will be stronger than bond between members of low-ranking families for the following reason. Within high-ranking families, individuals will be attracted to each other becaus of both bonds formed during ontogeny and their high status. In contrast within low-ranking families individuals will be attracted to each othe because of bonds formed during ontogeny and because they are forced t compromise their attraction for high-ranking individuals. Yamada (1963) Fady (1969), and Cheney Seyfarth (1976) present data which suggest tha high-ranking families may indeed be more "cohesive" than others, but a present this prediction also remains to be tested by future research.

6. Variations in the Model Related to the Arrival of Infants

(A) SIMULATION

Thus far the basic model has been compared only with grooming network in which none of the adult females had a young infant. In order to tes whether the model can predict changes in grooming relations when infan are present, I begin with what is known about changes in social behaviour under these conditions.

As noted earlier, when a female has a young infant she receives more grooming, is groomed by a wider variety of individuals, and may have entirely different grooming partners than at other times during her reproductive cycle (see references above). Mothers receive the most grooming when their infants are youngest, and grooming received decreases gradually as infants grow older (e.g. Struhsaker, 1971; Seyfarth, 1976; Hinde & Powell Proctor, 1977). The arrival of infants therefore produces *short-term* changes in the female grooming network, and the age of each infant must be specified when testing any theoretical model against observation.

It is also important to consider the changes in grooming among non-lactating females related to the birth of an infant. Though all adult females are usually attracted to the mother and attempt to groom her (see references above), non-lactating females still continue to groom each other (pers. obs.; Berman, pers. comm.; Simpson, pers. comm.). Thus although birth may produce changes in grooming relations it nevertheless does not entirely disrupt the original grooming network.

Given these observations, the basic model may be modified to predict how individual adult females will distribute their grooming in the presence of one or more females with young infants. To modify the model (leaving dominance relations constant—see above), first assume that all individuals will find females with infants more attractive than females without infants, and that within these two general categories high-ranking females will be more attractive than low-ranking females. Second, assume that individuals will attempt to divide their time between giving and receiving within the limits $1 < A_r/A_g < 3$. Third, because grooming among non-lactating females does not cease entirely when infants are born, assume that no female will attempt to give more than 25% of the total amount of grooming she attempts to give (A_g) to each new mother present.

Predicted grooming distributions, based on the assumptions above, were compared with observed behaviour as follows.

(1) Observed grooming distributions were drawn from 6 weeks' data collected during a 15-month study of adult female baboons (Seyfarth, 1976). One hundred and eighty instantaneous samples (Altmann, 1974) were taken on each female during this period, with samples being equally distributed throughout the daylight hours and during the 6-week period. The period was defined by the first 6 weeks after the troop's sixth-ranking adult female gave birth; no other females had young infants at the time.

(2) Predicted grooming distributions were calculated by a computer simulation based on the assumptions above. To calculate mean predicted

values for each groomer with all possible partners, (i) all females wer assigned equal values of A_t, and (ii) 1000 simulations were run in which eac female's value of A_r/A_g was chosen randomly within the limits above.

Mean predicted values are compared with observation in Table 2, wher I also show the average error for each of the eight individuals. Comparison

Table 2

Comparison between predicted and observed grooming distributions in group of eight adult female baboons when the sixth-ranking female has young infant. Figures represent the observed and (predicted) proportion o each female's total grooming given which she gave to each groomee † = female with infant. $\bar{E}$ *= mean error for each female with all possibl groomees, i.e.* $\sum |Obs-Pred|/7$

	Groomees								
Groomers	H.	Wel.	Lys.	Shir.	LP.	PM†.	M.	Pat.	$\bar{E}$
H.		37·5 (75·0)	25·0 (0)	0 (0)	0 (0)	37·5 (25·0)	0 (0)	0 (0)	10·7%
Wel.	38·0 (75·0)		38·0 (0)	0 (0)	0 (0)	23·0 (25·0)	0 (0)	0 (0)	11·0%
Lys.	18·0 (72·0)	18·0 (3·0)		29·0 (0)	0 (0)	24·0 (25·0)	0 (0)	12·0 (0)	15·9%
Shir.	18·0 (24·0)	0 (42·0)	27·0 (8·0)		0 (0)	36·0 (25·0)	18·0 (0)	0 (0)	13·8%
LP.	11·0 (0)	0 (27·0)	11·0 (48)	0 (0)		44·0 (25·0)	22·0 (0)	11·0 (0)	18·1%
PM.†	25·0 (0)	0 (4·0)	50·0 (82·0)	0 (14·0)	0 (0)		25·0 (0)	0 (0)	14·3%
M.	0 (0)	0 (0)	0 (26·0)	19·0 (49·0)	10·0 (1·0)	71·0 (24·0)		0 (0)	16·0%
Pat.	0 (0)	0 (0)	33·0 (6·0)	0 (58·0)	33·0 (15·0)	33·0 (21·0)	0 (0)		16·4%

Overall $\bar{E} = 15{\cdot}2\%$

between predicted and observed values are illustrated in Fig. 9. The model predictions had a mean accuracy of 84·8% over 56 possible dyads.

As a second test of the model's predictive power, comparison was mac between predicted values and those which were observed during the fir 6 weeks after the same troop's second- and fourth-ranking females ga birth. As before, no other females in the troop had young infants. In th case the model's predictions had a mean accuracy of 93·2% over 56 possib dyads.

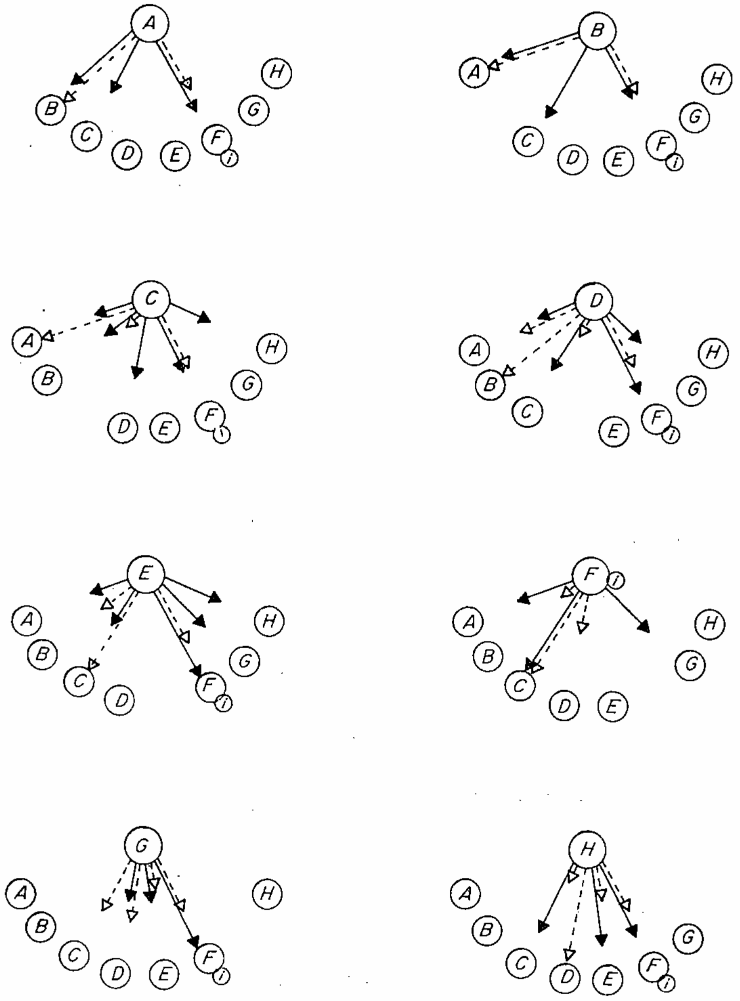


FIG. 9. Comparison between predicted and observed grooming distributions in a group of eight adult female baboons when the sixth-ranking female has a young infant. The lengths of solid and broken arrows indicate the proportion of each female's observed and predicted grooming given to particular other individuals, respectively. Taken from data in Table 2.

(B) DISCUSSION

The modified basic model's ability to predict changes in grooming relations related to birth provides additional evidence for an analogy between the properties of the model and the causal factors underlying behaviour. The model also suggests that, although the birth of an infant may produce short-term changes in its mother's social relationships with others, it does not alter the fundamental principles governing grooming interactions between other adult females in the group. Finally, the model's ability to predict the grooming distributions of mothers as well as those of other individuals suggests that, although mothers are themselves objects of specia interest during their infants' early weeks, they nevertheless make only minor alterations in the principles governing their own grooming behaviour toward others. This supports the more general conclusion that, among adul females, changes in social relationships related to birth are due more to changes in the behaviour of other individuals toward the mother than vice versa.

With regard to these behavioural changes, however, the point to be made is not that *this* particular model with its set of parameters will *always* predic changes in grooming relations, but that slightly different models with slightly different parameters may in future improve our understanding o the ways in which a female's relationships with others are affected by the presence of her infant.

For example, in the first case tested above, I assumed that regardless o her "usual" rank when a female gave birth she became the *most* attractive female in the group. This assumption, however, may not always be correct in particular, low-ranking females in very large troops are often ignored by others, even during their infants' first few weeks. To allow for this individual variation the basic model may be modified so that, for example, female who is usually fifth most attractive becomes either fourth, third second, or first most attractive after giving birth. Then, by comparing series of hypothetical models with observed grooming behaviour and searching for the closest "fit", it should be possible to obtain an accurat measure of the degree to which a female's relative attractiveness in the troop is affected by the birth of her infant.

7. Conclusions

The argument presented in this paper may be summarized by listing th causal principles which appear to determine the essential features of observe grooming networks among adult female monkeys.

(1) Female monkeys groom because they benefit from their interaction in two ways. Animals benefit when they receive grooming because of the removal of their ectoparasites; and animals benefit when they engage i grooming—regardless of who gives or receives—because there is a causa relation between X's interaction with Y and Y's subsequent support of X for example in an aggressive coalition.

(2) Whereas all individuals are equally skilled at removing each other ectoparasites, the likelihood of any individual successfully supportin

another is directly related to the supporting individual's rank (i.e. high-ranking animals are more successful than others). High-ranking animals are therefore more attractive than others, and all females compete to interact with the highest-ranking individual available. As a result of competition and compromise, high-ranking females receive more total grooming than others, and the majority of grooming occurs between females of adjacent rank.

(3) In groups where two or more females are close genetic relatives, principle (2) above is modified such that each female is attractive to others according to some combination of her rank and her degree of relatedness to them. Although the relative importance of rank and relatedness may vary from group to group, these variations will produce only minor changes in the essential features of female grooming networks.

(4) In all groups, during short periods of time after the birth of infants, principle (2) above is modified such that each female with a young infant is attractive according to some combination of her rank, her degree of relatedness, and the age of her infant. Although the relative importance of each of these factors may vary from group to group, consideration of their interaction makes it possible to predict precisely how a female's grooming relations will change whenever she gives birth.

In summary, the model presented here begins with a few simple premises which are derived from, and compatible with, previous studies of grooming relations among adult female Old World Monkeys. The model then demonstrates that the interaction between these premises can explain many of the more complex features of female grooming networks. The model offers a tentative hypothesis, whose explanatory and predictive power remain to be tested by long-term field and laboratory observation.

I am especially grateful to P. P. G. Bateson, who initially encouraged me to write this paper, and to D. Cheney Seyfarth, who played a major role in developing the ideas expressed in the final version. I also thank P. P. G. Bateson, D. Cheney Seyfarth, N. K. Humphrey, M. J. A. Simpson, and especially R. A. Hinde for their criticism of earlier drafts. L. D. Barden, C. M. Berman, J. J. Cherfas, T. Harding, J. Stevenson-Hinde, and L. E. White also provided help and advice at various stages of preparation.

REFERENCES

Altmann, J. (1974). *Behaviour* **49**, 227.
Altmann, S. A. & Altmann, J. (1970). *Baboon Ecology*. Chicago: University of Chicago Press.
Bernstein, I. S. (1975). *Folia primat.* **23**, 50.
Bernstein, I. S. & Sharpe, L. G. (1966). *Behaviour* **26**, 91.
Bramblett, C. A. (1970). *Primates* **11**, 327.

Breuggeman, J. A. (1973). *Folia primat.* **20,** 178.

Bygott, D. (1976). In *Perspectives on Human Evolution*, vol. 5, *Great Apes*. (D. A. Han
burg & J. Goodall, eds). New York: Staples Press.

Clutton-Brock, T. (1974). *Folia primat.* **21,** 161.

Cheney Seyfarth, D. (1976). Ph.D. thesis, University of Cambridge.

Crook, J. H. (1970). In *Social Behaviour in Birds and Mammals*. (J. H. Crook, ed.). Ne
York: Academic Press.

Dunbar, R. I. M. & Dunbar, E. P. (1975). *Social Dynamics of Gelada Baboons*. Base
S. Karger.

Eisenberg, J. F., Muckenhirn, N. A., & Rudran, R. (1972). *Science, N.Y.* **176,** 863.

Fady, J.-C. (1969). *Folia primat.* **11,** 134.

Gartlan, S. J. (1975). In *Symp. 5th Congr. Intl. Primat. Soc.* (S. Kondo, M. Kawai,
Ehara, S. Kawamura, eds). Tokyo: Japan Science Press.

Gouzoules, H. (1975). *Primates* **16,** 405.

Hall, K. R. L. (1962). *Proc. Zool. Soc. Lond.* **139,** 181.

Hall, K. R. L. (1967). In *Social Communication Among Primates*. (S. A. Altmann, ed.
Chicago: University of Chicago Press.

Hinde, R. A. (1976). *Man* **11,** 1.

Hinde, R. A. & Powell Proctor, L. (1977). *Behaviour*.

Jay, P. (1965). In *Primate Behavior*. (I. DeVore, ed.). New York: Holt, Rinehart
Winston.

Kaufmann, J. H. (1966). *Zoologica* **51,** 17.

Kummer, H. (1968). *Social Organization of Hamadryas Baboons*. Chicago: University
Chicago Press.

Kummer, H. (1975). In *Symp. 5th Cong. Intl. Primat. Soc.* (S. Kondo, M. Kawai, A. Ehar
S. Kawamura, eds). Tokyo: Japan Science Press.

Levi-Strauss, C. (1953). In *Anthropology Today* (A. L. Kroeber, ed.). Chicago: Universi
of Chicago Press.

Oki, J. & Maeda, Y. (1973). In *Behavioral Regulators of Behavior*. (C. R. Carpenter, ed.
Lewisburg: Bucknell University Press.

Rhine, R. J. (1972). *Primates* **13,** 181.

Rosenblum, L. A., Kaufman, I. C. & Stynes, A. J. (1966). *Folia primat.* **4,** 438.

Rowell, T. E. (1968). *Anim. Behav.* **16,** 585.

Rowell, T. E. (1969). *Anim. Behav.* **17,** 159.

Saayman, G. S. (1971). *Folia primat.* **15,** 36.

Sade, D. S. (1965). *Am. J. Phys. Anthrop.* **23,** 1.

Sade, D. S. (1967). In *Social Communication Among Primates* (S. A. Altmann, ed.
Chicago: University of Chicago: Press.

Sade, D. S. (1972). *Folia primat.* **18,** 196.

Seyfarth, R. M. (1976). *Anim. Behav.* **24,** 917.

Simpson, M. J. A. (1973). In *Comparative Ecology and Behaviour of Primates*. (J. H. Croo
& R. P. Michael, eds). London: Academic Press.

Sparks, J. (1967). In *Primate Ethology*. (D. Morris, ed.) London: Weidenfeld & Nicolson.

Struhsaker, T. T. (1971). *Anim. Behav.* **19,** 233.

Vaitl, E. (1977). *Primates*.

Weisbard, C. & Goy, R. (1976). *Folia primat.* **25,** 91.

Yamada, M. (1963). *Primates* **4,** 43.