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# 学位申請論文

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**Studies on Grooming Interactions among Wild Chimpanzees.**  
**(野生チンパンジーの毛づくろいインタラクションの研究)**

**A Dissertation**

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Kyoto University**

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## CHAPTER 1.

### Introduction

In the studies of human evolution, we can obtain various information on hardware evolution from such sources as fossil records. However, it is far more difficult to get information on software evolution, such as the evolution of social structures or social interactions, because these developments cannot be known directly from the fossils or from genetic analysis. Thus comparisons of social behaviors with living primates, especially with the great apes, are essential for understanding such aspects of social evolution. Chimpanzees are one of the closest species to humans (Caccone and Powell, 1989), so they have to be fully considered when we talk of evolution.

Social grooming or allogrooming behavior has been widely observed among the taxa (Sparks, 1967; Goosen, 1982), and its original function is supposed to be hygienic, where one individual removes ectoparasites (Tanaka and Takefushi, 1991) or debris from the body of another. However, the behavior is also used socially and is one of the most important social interactions for most primate species. Such social aspects of grooming are sometimes discussed by analogy to human conversation (Morris, 1967; Goosen, 1982; Goodall, 1986; Dunbar, 1996). I do not think it is reasonable to assume that language evolved to replace primate grooming (Dunbar, 1996), nor do I mean to argue that these two are completely equivalent; however, an understanding of the social aspects of grooming behavior is important in order to understand the evolution of social interactions, including conversation, in humans.

Although there are many studies of primate grooming behavior, grooming behavior has usually been measured by its duration (or the number of bouts) with the assumption that all grooming behaviors are equal, or at least that they can be summed and averaged. These

mass measured grooming episodes are often used as if they represent affiliative relationships, degree of reciprocity, etc. Apparently no one has tested whether primate grooming is actually such a simple and homogeneous interaction that we can sum easily. However, chimpanzees often make large grooming clusters (de Waal, 1982; Goodall 1986), and quite a large amount of grooming is polyadic. They also quite often engage in mutual grooming (e.g. Takahata 1990a; 1990b; Oberski, 1993). There are also "social customs" in chimpanzee grooming such as grooming-hand-clasp (McGrew and Tutin, 1978). These customs seem important when we think of chimpanzee "culture" among various locality-specific behaviors of chimpanzees (for review see Whiten et al., 1999), most of which are somehow related to feeding or at least to material objects, whereas grooming-hand-clasp seems almost socially determined.

These characteristics of chimpanzee grooming interaction seem unique even when we include bonobos, who are the closest species to chimpanzees. It is important to understand the uniqueness of chimpanzee social interactions in order to understand the uniqueness of human social behaviors. Then we will be able to understand the commonalities underlying both species' expressions of uniqueness.

## CHAPTER 2.

# Methods

I observed social grooming of the M group chimpanzees (*Pan troglodytes schweinfurthii*) in the Mahale Mountains National Park, Tanzania, between July 1996 and May 1997. For detailed information on the research site, see Nishida (1990). Social grooming is defined here as a series of behavior elements such as stroking of hair, picking of the hair, removing of things with hand(s) or lip(s), and scratching other individuals (see Chapter 5 for detail). Self-grooming or self-scratching was also recorded but was used only for brief comparison with social scratch. In the course of my research, the M group consisted of a total of 53 individuals: 7 adult males (over 15 years), 18 adult females (over 14 years), 5 adolescent males (9-14 years), 5 adolescent females (9-13 years), and 18 juveniles and infants (under 8 years). Normally, only males over 16 years are considered as adult (e.g. Goodall, 1983; Hiraiwa-Hasegawa et al., 1984), but during this study period, a 15-year old male was fourth-ranking (third-ranking in 1997), overtaking some older males, and was the most important coalition partner for the beta male. Therefore, I used that age as adult in this study. There were some fluctuations in the membership because of births, deaths, and disappearances of some individuals. The alpha male Nsaba also disappeared at the end of 1996, and Kalunde became the alpha male after that.

I followed 10 males and 10 females of various age classes (juvenile to adult) as focal target individuals. Each day I followed one target as long as possible and recorded all of the grooming behaviors during the follow. This sampling method aimed to record the structure and membership of grooming clusters in which focal individuals were engaged. Therefore, grooming behaviors were recorded not only for focal individuals but also for non-focal individuals within the grooming cluster, even when they were not directly grooming with

focal individuals. Total duration of follows was 480 hours, during which 137 hours of grooming (total accumulation of individual grooming including non-focal individuals) was recorded. Though visibility was poor in some places, most grooming occurred in relatively open spaces, so grooming within 10 m around the target was recordable. In order to record multiple individuals grooming at the same time, the start and end time of each individual's grooming and changes in partner were recorded on an audio tape recorder. This sampling method enabled wider observation than that of ad libitum sampling of various individuals by minimizing the possibility that observations might be biased toward those individuals who tended to congregate. I sometimes employed different analyses and definitions of terminology and I showed different data sets in each chapter. For details about these, see the Methods section of the corresponding chapter.



## CHAPTER 3.

# Gatherings for Social Grooming among Wild Chimpanzees

### INTRODUCTION

Social grooming, or allogrooming, is one of the most common social interactions and has been observed widely among primate species (Sparks, 1967; Goosen, 1987).

Chimpanzees (*Pan troglodytes*) also allocate a large portion of their daytime hours to grooming each other. Some individuals spend more than 25% of their awake time grooming with others (Goodall, 1986; Kawanaka, 1989). Chimpanzee grooming behavior has often been studied in particular age-sex classes such as among adult males (Simpson, 1973; Takahata, 1990a; Nishida and Hosaka, 1996; Watts, 2000b), among adult males and adult females (Takahata, 1990b), among mothers and offspring (Nishida, 1988), and among adult females (Nishida, 1989; Wrangham et al., 1992). Most of these studies agree with the early observations that grooming is most frequently performed among adult males and mothers with their offspring but less often among adult females (van Lawick-Goodall, 1968; Nishida, 1970; contra Ghiglieri, 1984; Sugiyama, 1988). Given these differences among age-sex classes, together with differences in association, chimpanzee males are often regarded as more social and affiliative with each other than females.

Specific aspects of chimpanzee grooming have also been extensively studied. There have been studies of grooming in the reunion context (Bauer, 1979), as coalition strategies among adult males (Nishida et al., 1992; Nishida and Hosaka, 1996), as means of deception (Nishida, 1998), and as social custom (McGrew and Tutin, 1978; de Waal and Seres, 1997; Nakamura et al., 2000). The most popular topic for grooming studies is perhaps reciprocity (Hemelrijk and Ek, 1991; Oberski, 1993; Watts, 2000a; Boesch and

Boesch-Acherman, 2000). There is evidence that chimpanzees even exchange grooming for food (de Waal, 1997). In most of these studies, researchers measured the amount of grooming and only compared quantities of grooming between dyads. This implies that they assumed grooming to be homogeneous interactions. However, if grooming is used in the different ways described above, we cannot simply accumulate whole grooming interactions as indicators of affiliation or reciprocity. Some authors have mentioned or investigated separately some specific types of grooming interactions. For example, some mentioned that brief grooming (token grooming) is often observed not in the usual grooming context but in relation to greeting, submission, frustration, or mating (Goodall, 1965; Nishida, 1970; Goodall, 1986). In addition, others handled differently the data of simultaneous mutual grooming (Nishida, 1988; Kawanaka, 1989; Takahata, 1990a; 1990b; Oberski, 1993; van Hoof and van Schaik, 1994; Boesch and Boesch-Acherman, 2000) and facial grooming (Nishida and Hosaka, 1996), showing that the frequencies of these specific types of grooming interactions varied among age-sex classes or among dyads. These observations indicate that we have to give more attention to the qualitative aspects of so-called grooming interactions. Hereafter, I focus on another aspect of grooming interaction: grooming as gatherings.

### **Gatherings for Chimpanzee Grooming**

Chimpanzees often groom in gatherings, in which 10 or more individuals groom in the same session and the membership changes frequently (van Lawick-Goodall, 1968). These gatherings are sometimes called "grooming clusters" (de Waal, 1982; Goodall, 1986). In such gatherings, polyadic grooming is often observed (Reynolds and Reynolds, 1965; Hayaki, 1994; Boesch and Boesch-Acherman, 2000; see picture in Goodall, 1986 p. 393 for example). However, such gatherings for grooming have not been examined in detail. We

do not know how often such gatherings are formed, nor the characteristics of such gatherings compared with dyadic grooming episodes. Most chimpanzee researches usually handle the polyadic grooming as a combination of separate dyadic interactions, and such decomposed dyadic interactions are accumulated as if they represent the social relationships of the dyads. When we think of the capability of chimpanzees to understand the significance of the existence of a third party, such as in the context of political fights (de Waal, 1982; Nishida, 1983), it is reasonable to assume that dyadic and polyadic grooming have a different significance. The gathering of chimpanzees in general, the so-called subgroup (Nishida, 1968) or party (Sugiyama, 1968), has been the focus of interest in studies of chimpanzees (Chapman *et al.*, 1994; Chapman *et al.*, 1995; Wrangham *et al.*, 1996; Doran, 1997). These studies usually emphasize two characteristics of chimpanzee grouping, male gregariousness and female solitariness (e.g. Wrangham and Smuts, 1980), and try to explain these characteristics by ecological factors. However, less attention has been given to the possibility that such gatherings are occasions of social interaction for the chimpanzees. It is strange that, considering the abundant studies on gatherings of chimpanzees, data has not been provided on gathering for social interaction. Boesch (1996a) reported that in Tai chimpanzees, resting parties were the second largest parties among all kinds. These surely include grooming parties. It is possible that gathering is done for such social interaction.

### **Complex Grooming Interactions in Other Primate Species**

Grooming interactions seem to be dyadic in most primate species (e.g. Dunbar, 1993). This does not mean that monkeys do not change grooming partners but that they normally groom with only one party at a time. Cheney and Seyfarth (1990) reported that when a high-ranking vervet monkey (*Chlorocebus aethiops*) approached two lower-ranking

conspecifics grooming each other, the subordinate of the two almost always moved away. They showed this in order to argue that vervet monkeys can understand other individuals' ranks, but these episodes also show that their grooming interactions are usually dyadic and rarely triadic. For other primates, there have been other descriptions of more complex grooming interaction such as mutual grooming and polyadic grooming.

Descriptions of mutual grooming can be found in the studies of Macaca mulatta (Boccia, 1983), M. nemestrina (occasional) (Kaufman and Rosenblum, 1966), M. radiata (occasional) (Kaufman and Rosenblum, 1966), M. assamensis (0.8%) (Cooper and Bernstein, 2000), Semnopithecus entellus (rare) (Borries et al., 1994), Cercopithecus mitis (never) (Rowell et al., 1991) and Ateles geoffroyi (never) (Ahumada, 1992). One type of triadic grooming interaction, in which two individuals simultaneously groom a third ( $A \rightarrow B \leftarrow C$ ), has been reported for Cebus apella (often) (Parr et al., 1997), Ateles geoffroyi (sometimes) (Ahumada, 1992), Trachypithecus cristatus (at times) (Bernstein, 1968), Semnopithecus entellus (McKenna, 1978), Macaca mulatta (Sade, 1965), M. fuscata (Furuya, 1957), M. assamensis (7.1%) (Cooper and Bernstein, 2000), Cercopithecus mitis (very rare) (Rowell et al., 1991) and Homo sapiens (|Gui bushman; 13 out of 184 interactions) (Sugawara, 1984). The other type of triadic interaction, in which one grooms a second while the second grooms a third ( $A \rightarrow B \rightarrow C$ ), has been reported for Trachypithecus cristatus (Bernstein, 1968), Macaca mulatta (sometimes) (Sade, 1965), M. fuscata (Furuya, 1957), and Homo sapiens (|Gui bushman; 1 out of 184) (Sugawara, 1984). Polyadic interaction has also been noted for Semnopithecus entellus (common) (McKenna, 1978; Borries et al., 1994) and Pan paniscus (sometimes) (Kuroda, 1980) but these reports did not indicate whether they perform both or either of the two types. Some reports have described grooming interactions that include four or more individuals in such species as Trachypithecus cristatus (Bernstein, 1968),

Semnopithecus entellus (McKenna, 1978), Macaca mulatta (Sade, 1965) and M. assamensis (0.09%) (Cooper and Bernstein, 2000).

Most of these papers only mention that such complex grooming interactions "sometimes" or "rarely" occur, and very few papers provide the frequency of such overlapping. Most studies only refer to triadic grooming, and the largest reported number of individuals grooming simultaneously in a chain is four. Perhaps the scarcity of descriptions of such complex grooming interactions indicates that it is actually infrequent in most primates.

In this paper, I will first describe and give the frequencies of various types and sizes of gatherings of chimpanzees for grooming and show how individuals perform complex grooming interactions in such scenes. Second, in order to test the hypothesis that grooming interactions are not uniform but vary in gatherings, I will compare the levels of participation among all age-sex classes in different sizes of such gatherings. If the hypothesis is correct, it is expected that some new tendencies of age-sex differences will be found in gatherings for grooming when compared with dyadic grooming.

## **METHODS**

I observed the grooming behavior of the M group chimpanzees in the Mahale Mountains National Park, Tanzania, between July 1996 and May 1997. For detailed information on the research site, see Nishida (1990). Grooming is defined here as a series of behavior elements such as stroking of hair, picking of the hair, removing things with hand(s) or lip(s), and scratching other individuals (Nakamura *et al.*, 2000). Self-grooming or leaf grooming (Goodall, 1986; Boesch, 1996b) was not included in the analysis. In the course of

my research, the M group consisted of 53 individuals, 7 adult males (over 15 years), 18 adult females (over 14 years), 5 adolescent males (9-14 years), 5 adolescent females (9-13 years), and 18 juveniles and infants (under 8 years). Normally, only males over 16 years are treated as adults (e.g. Goodall, 1983; Hiraiwa-Hasegawa *et al.*, 1984), but during this study period, a 15-year old male was fourth-ranking (third-ranking in 1997), overtaking some older males, and was the most important coalition partner for the beta male. Therefore, I used that age as adult in this study. There were some fluctuations in the group's membership because of births, deaths, and disappearances of some individuals. The alpha male Nsaba also disappeared at the end of 1996, after which Kalunde assumed the alpha position.

For the purpose of understanding gatherings for grooming, it is obviously not suitable to focus observation on the behavior of only one individual at a time. It is necessary to grasp the behaviors of multiple individuals at any given time. It is also problematic to record the grooming situations randomly because, for example, large grooming clusters occurring in relatively open space would be more often observed than smaller clusters occurring quietly in the bush. Thus, in this study I set the observational viewpoint on one individual for a day and recorded the grooming behaviors of the multiple individuals around him/her even when they were not directly grooming with the focal individual. This methodology enabled the observer to record all kinds of social situations that the target individual experiences in a day. Such situations are expected to differ between individuals or between different age-sex classes. Therefore, I followed 10 males and 10 females of various age classes (juvenile to adult) as focal target individuals (Table I). Adult female targets included about the same number of both lactating and cycling females. Total duration of follows was 480 hours, during which 137 hours of grooming (total accumulation of individual grooming including non-focal individuals) were recorded. In order to record

multiple individuals grooming at the same time, the start and end time of each individual's grooming and changes in partner were dictated on a micro cassette tape recorder.

### **Definition of Grooming Cliques**

Gathering for grooming can occur at two different levels. One is a gathering of directly connected individuals through grooming interactions at the same moment. I use the term grooming clique for this level of gathering, following Dunbar and others who compared conversation cliques and grooming cliques (Dunbar, 1993; Dunbar *et al.*, 1995; also see Nakamura, 2000). For example, when individual A grooms individual B and B grooms individual C at the same time, this is a clique of three individuals. When any change in composition occurred, I considered the newly formed groups to be different cliques.

When describing the grooming cliques, data of their types and the durations of types are more easily obtained than data of individuals taking particular parts. Let us take an example where three individuals A, B, and C groom in series, such as  $A \rightarrow B \rightarrow C$ . When we take the individualities into account, there are potentially 6 patterns,  $A \rightarrow B \rightarrow C$ ,  $A \rightarrow C \rightarrow B$ ,  $B \rightarrow A \rightarrow C$ ,  $B \rightarrow C \rightarrow A$ ,  $C \rightarrow A \rightarrow B$ , and  $C \rightarrow B \rightarrow A$ . In addition, any triad of the 53 members of the M group can be A, B, or C, and so all of the variations in cliques become too many to show even for the triadic cliques. Furthermore, there are larger cliques, so describing the compositions of cliques by membership would be difficult in a limited space. In this paper, therefore, I will not show who is in the particular position in a given clique but instead the grooming status of an individual by an index composed of three numbers. The first number of the index indicates whether the individual grooms mutually (1) or not (0). The second indicates whether he/she grooms another (1) or not (0) at a particular moment. In mutual grooming, both the first and the second numbers are 1. The last number indicates the total

number of individuals by whom he/she is groomed at the moment. For example, 001 indicates the status "not grooming anybody but groomed by only one individual," and 112 indicates the status "grooming mutually while groomed by two including the partner of mutual grooming." Generally, combining individual grooming statuses gives the type of grooming cliques. If, for example, we know five individuals are grooming in statuses 010, 010, 001, 111, and 112, we can figure out that there are two cliques, in one of which two groom unilaterally and in the other two groom mutually, one of whom is groomed by the other (Fig. 3.1.).

### **Definition of Grooming Clusters**

As a grooming clique corresponds to a momentary state of direct grooming connections, its size and composition changes quite frequently. In most cases, such a clique does not occur independently by itself but usually in parallel with other cliques, and such cliques may often exchange their participants with each other. Thus, there appear larger gatherings of grooming within a certain amount of time and space, which are the cumulative consequences of many grooming cliques. I call this larger gathering a grooming cluster, with a nearly equivalent usage to that of de Waal (1982) and Goodall (1986). I consider it a different cluster when there is no grooming for more than 5 minutes, or when others groom more than 3 m away from the nearest member of the cluster. Within this distance, chimpanzees can change their grooming partners easily with only slight movement. When individual A grooms individual B and then B grooms individual C, I define that all of them are included in the same cluster even though A and C do not directly groom each other. With this definition of a cluster, an individual participating in a cluster has to be connected either directly or indirectly with all of the other participants of the cluster. As long as someone



continues to groom, a cluster lasts regardless of compositional change. In such case, the cumulative numbers of the members are used as the size of the cluster. This size does not cause too much overestimation because the membership of a cluster usually does not change dramatically and most members do not move but just alter partners within the cluster.

For the duration of a cluster, I define the following two kinds. Gross duration of a cluster is simply the duration between the beginning time and the end time of a cluster. Thus it includes small gaps without grooming interactions and it does not take into account the number of individuals simultaneously grooming. However, even in clusters of the same size, the number of individuals grooming at one moment varies greatly, so gross duration does not reflect how dense or sparse the grooming interactions are in a given cluster. Thus the accumulation of all of the participants' grooming time in a cluster is defined to be the net duration of the cluster. This surely depends on the size of the cluster, but it is a better indicator of the actual amount of grooming interaction than the gross duration.

## **RESULTS**

### **Grooming at the Individual Level**

Frequencies of grooming by focal targets are shown in Table 3.1. Mean ( $\pm$ SD) frequency of grooming hour was 12.80 ( $\pm$ 7.68)% of the focal observation time. The largest was 32.04% (the oldest adult male) and the smallest was 1.47% (an adolescent male).

### **Grooming Cliques**

Twenty-seven types of grooming cliques were observed (Fig. 3.2.), and the largest consisted of 7 individuals. Figure 3.3. shows the proportion of each type of clique in chimpanzees and Assamese macaques. Although both chimpanzees and Assamese

macaques groomed mostly in the simplest cliques [1], more complex cliques accounted for about 25% of all the cliques in chimpanzees whereas they accounted for only 8% in Assamese macaques. These two data sets cannot be compared directly because the proportion of chimpanzee grooming was calculated with the observed duration while that of Assamese macaques was calculated from the number of "episodes" which were not defined (Cooper and Bernstein 2000). However, it seems that chimpanzees groom more often in complex cliques than do Assamese macaques.

### **Grooming Statuses**

There were 10 status types (Fig. 3.4.), excluding 000 in which the individual is not involved in grooming at all. It is notable that, though rare, as many as four interactions at a time (i.e. 113 and 004) appeared in chimpanzee grooming. About 20% of chimpanzee grooming was performed in more complex statuses than simple 001 and 010 (Fig. 3.5.). 111 and 011 seem similar from an individual's perspective because the individual grooms and at the same time is groomed by one in both of the statuses. However, 111 was more frequent than 011, perhaps because he/she needs only one partner in the former but two in the latter. On the other hand, the number of participants is the same in 011 and 002, but 002 is less frequent than 011. For comparisons, data of Assamese macaques are also shown. It is clear that the more complex statuses are much less frequent in Assamese macaques than in chimpanzees except for 002.

The proportion of complex grooming interactions (i.e. statuses with more than two interactions) differs among age-sex classes (Kruskal-Wallis,  $H=28.2$ ,  $p<0.001$ ), and the difference is significant between adult males and immature individuals and between adult females and immature individuals (Bonferroni's multiple comparison,  $p<0.05$ ). Adult males

showed the least frequent 001 and most frequent 111 among all classes. The pattern of adolescent males was similar to that of adult males, with the second most frequent 111; however, the proportion of 011 was much smaller than adult males (Mann-Whitney:  $N_1=7$ ,  $N_2=5$ ,  $U=0.0$ ,  $p<0.005$ ). The pattern of adult females also resembled those of males, but in comparisons with adult males 111 seems less frequent. The proportion of 002 was highest in this class, implying that the concentration of grooming is frequent in this class. Adolescent females seem to groom more often than to be groomed, as 010 exceeds 50% only in this class. In contrast, 001 accounts for about three-fourths of grooming in immature individuals probably because they usually receive more grooming from their mothers than they give.

### **Frequency of Grooming Clusters**

The size of grooming clusters observed during the study varied from 2 to 23. The percentage of the number of clusters with different sizes is shown in Fig. 3.6. (left). Overall, 926 grooming clusters were observed, in which 66.6% (617/926) were clusters with two individuals. Clusters with five or more individuals occurred in only 7.8% (72/926) of all the events. Small clusters seemed to be dominant if we consider the frequencies only by the number of events. However, when we look at the totals of gross durations of clusters (Fig. 3.6., middle), clusters with two individuals accounted for only 32.4% (2133.2 min./6579.8 min.) while clusters with five or more individuals accounted for 27.9% (1837.5 min./6579.8 min.). Therefore, mean gross duration of clusters with two individuals was very short (3.5 min.) compared to that of clusters with more than 5 individuals (25.5 min.), possibly because the former also include grooming as "tokens" which are often used in different contexts showing submission, frustration, etc. (Goodall, 1986). Figure 3.6. (right) shows the percentages of the net durations of the clusters. Clusters with two individuals dropped to

18.2% (1301.4 min./7377.7 min.), indicating that clusters with two individuals were frequent as events but individuals did not spend a long time grooming in them. They groom most frequently in clusters with four individuals, and those with five or more individuals accounted for 40.8%.

### **Distribution of Grooming in Grooming Clusters of Differing Sizes**

Adult males were both the most active groomers and groomees in clusters with two to four individuals (Fig. 3.7.). In clusters with two individuals, adolescent males groomed adult males quite frequently but the reverse was not the case. Clusters with five and more individuals showed a different tendency in that adult females were the most active groomers and were also most often groomed. Conversely, grooming among adult males decreased to about the same amount as among adult females.

## **DISCUSSION**

### **Overlaps in Chimpanzee Grooming Interactions**

Grooming interactions in chimpanzees are far more complex than so far described or analyzed. In the simplest grooming interaction that is made dyadically and unilaterally without overlap, it is easy to tell who is the actor and who is the recipient of the behavior. However, only one additional interaction can result in the following three different types: 1) Mutual grooming within the original dyad, 2) a triadic clique in series, and 3) also a triadic clique but in concentration. In the last type, the roles of the groomer(s) and the groomee are still clearly separated. On the other hand, the roles of the groomer and the groomee are not easily separated in the former two types. The results showed that these complex grooming interactions occur in chimpanzees so frequently that those characteristics should not be

ignored. Some may question this significance by stating that this kind of overlap can be explained with mere synchronicity of the behavior. However, if one only needs to synchronize the behavior with others, the simplest way would be multiple dyads grooming independently in the unilateral grooming cliques in the vicinity of each other. Thus, synchronicity does not fully explain why complex overlaps emerge in chimpanzees.

As stated in the introduction, few descriptions have been made of complex grooming interactions in primates other than chimpanzees. In many grooming studies, a grooming bout is often defined to continue until a groomer changes its role to a groomee. This definition does not work well when a groomer can be a groomee at the same time, so such a definition also implies the rarity of such a grooming status. Comparisons with Assamese macaques (Cooper and Bernstein, 2000) revealed that although the monkeys sometimes groom mutually and polyadically, the proportion of such overlapping grooming was much lower than that of chimpanzees and that the variations in cliques were also fewer. Thus, it seems reasonable to conclude that the overlapping feature in grooming is more advanced in chimpanzees than in other primate species. One possible explanation for this is the relatively large amount of time spent in grooming by this species. For example, mutual grooming may be no more than accidental overlap between transitions of roles from groomee to groomer, having no particular significance. However, such overlapping is usually not observed in most primates. As we have already seen, most primates usually groom without such overlapping but instead rather tightly alternate their roles. It does not seem reasonable to assume that grooming is randomly distributed only in chimpanzees. Thus, this hypothesis does not explain why some monkey species who spend much time grooming (for review, see Dunbar, 1991) do not overlap grooming as often as chimpanzees.

An alternative explanation is that it may have something to do with the unique

characteristics of the chimpanzee's fission-fusion society. Unlike most primate species who usually stay together with all members of the group, chimpanzees are not always together with a given member of the same community. There exists a period of absence, and this means that their opportunity for social interactions are, to some extent, reduced. Thus, it is assumed that the importance of gathering must be larger in the species that do not stay together all of the time. Members of such species would be more eager to make and maintain such a gathering when there is an opportunity. It seems that grooming provides one such opportunity in chimpanzee society. If this view is correct, such opportunities will be more important for females than for males, since females spend more time alone than males do (Wrangham and Smuts, 1980). Furthermore, this is consistent with my finding that females groomed more often in large grooming clusters. Complex grooming interactions may be a device for formation and maintenance of such social gatherings. If chimpanzees could only use conventional one-to-one grooming, they could not cover all of the partners they want to make relationships with. Overlap makes it possible to interact with multiple individuals at the same time. In addition, they can even interact with an individual who is already engaged in grooming with another individual without manifest competition as shown in the vervet monkeys' cases (Cheney and Seyfarth, 1990). On the other hand, such overlap may obscure who is interacting with whom on a dyadic basis. Therefore, grooming often appears in small clusters between adult males who may have to make it clear for political reasons who is the ally and who is not.

### **Sex Differences in Different Sizes of Grooming Clusters**

When we see the distribution of grooming in different sizes of clusters, the most marked combination of classes was among adult males in relatively smaller clusters. This is

consistent with the known image of chimpanzee grooming being most frequent among adult males. The males' tendency to groom adult males can already be seen in adolescence, as males in this class groomed adult males frequently in clusters of two individuals. However this tendency was not seen in larger clusters, implying that adolescent males only groom adult males when they are alone. Adolescent males are eager to make relationships with adult males, although they often become very tense in doing so (Hayaki, 1988). Under such conditions, it might be difficult for them to handle multiple partners at the same time and the same place. Another explanation for this would be the competitions for adult male grooming partners in large clusters, since an adult male would prefer, when available, another adult male to be the grooming partner rather than adolescent males. Such competition is a problem for an adolescent male when he wants to be groomed by an adult male because the adult male might be preoccupied with grooming another adult male. However, it is not a problem when he wants to groom because he still has the choice of grooming the adult male who is already grooming or being groomed by the other adult male. Therefore, competition may explain why they do not get groomed by adult males, but cannot completely explain why they do not groom adults in larger clusters.

The most remarkable result was that adult females groomed most actively and received grooming most frequently in large grooming clusters, which differed greatly from the conventional knowledge of chimpanzee grooming. Females have been said to be inactive in social interactions with each other (e.g. Nishida, 1979; Wrangham and Smuts, 1980). The fact they groomed less actively in small clusters is consistent with the current view of females, but they groomed most frequently once many individuals gather together. This result could be understood by the difference in the social relationships between adult males and between adult females. Adult male chimpanzees are known to be very political

(de Waal, 1982; Nishida, 1983) and to make every effort to get higher status. One of the effective ways of doing this is to make coalition partners. However, perhaps because of the ascendancy of a young male or the betrayal of the allies, the relationship always faces the possibility of change. Thus, adult males always have to renew or confirm their relationships with each other. This leads to their frequent focused interaction within the clusters with relatively smaller number of partners. On the other hand, adult females do not have to maintain such relationships with particular individuals. They do not seem to be interested in competing for higher status by forming particularly intimate allies. Rather, it seems better for them to get along with many individuals of the community with moderate intimacies. Therefore, females do not have to focus their interactions on particular individuals. Instead, they seem to prefer wider interactions with various individuals at any given moment. More reports from other chimpanzee study sites are required to determine whether this tendency of females is a general feature of chimpanzees or not. The Mahale M group had relatively few prime and old males during the study period and this might have influenced the outcome. Females' sociality does not have to be fixed, but it may take various ways in various social situations.

At least in chimpanzees, so-called grooming interactions are not homogeneous but seem to have a variety of functions and meaning for them. By simply accumulating and comparing the amount of such interactions without considering this fact, one may fail to understand the complexity and richness of their sociality.



## CHAPTER 4.

# Is Human Conversation More Efficient than Chimpanzee Grooming?

## Comparison of Clique Sizes.

### INTRODUCTION

#### Dunbar's Theory on Efficiency of Language

Most primate species show social grooming (or allogrooming) behavior (Sparks, 1967; Goosen, 1987). The original function of grooming may have been hygienic, in that monkeys remove ectoparasites and other debris from their fur or hair (e.g. Tanaka and Takefushi, 1993). However, in most studies, grooming is interpreted as a behavior showing intimate and relaxed relationships among individuals or as a means of establishing such relationships. Consequently, grooming is often considered to be analogous to human conversation (e.g. Morris, 1967; Goodall, 1986; Goosen, 1987).

Robin Dunbar, not stopping at a mere analogy, was the first to compare grooming and conversation theoretically and quantitatively. He hypothesized in his ambitious works that human language evolved as a better bonding mechanism when our ancestors faced difficulties in bonding through conventional primate grooming (Dunbar, 1996). The logic of his theory developed as follows. First, he showed that, at least in catarrhine primates, the frequency of social grooming correlates with group size (Dunbar, 1991) and that group size is a function of relative neocortical volume (Dunbar, 1992). This is because the more group mates one has, the more complex association and coalitions one needs because of the increased intra-group competitions and aggressions. He also estimated that the upper limit for such social time would be about 20% of the day time, while humans would need 42% if

we used conventional primate grooming for bonding in our group sizes (Dunbar, 1993). Therefore, at sometime in the course of brain enlargement, which is also related with the enlargement of the group size, our ancestors had to find a more efficient bonding mechanism than primate manual grooming. In his hypothesis, language was the mechanism we acquired. He also emphasized other social aspects of language, such that it enables gossiping about other individuals and thus provides social information on not only those who are present but also those who are absent.

He supported the above predictions by comparing the efficiencies of human language and primate grooming. Among primate species, chimpanzees (*Pan troglodytes*) have the largest mean group size of about 53.5, while the predicted group size of humans is about 147.8; therefore, language should logically be 2.76 ( $=147.8/53.5$ ) times more efficient than social grooming (Dunbar, 1993: p. 690). Here, by "efficiency" he means "the number of interactants that can be simultaneously reached during social interaction" (ibid.: pp. 689-690). Then, Dunbar et al. (1995) counted clique sizes of human conversation in several public settings and found an upper limit of about four in conversation cliques. He then stated that because "grooming is exclusively a one-to-one interaction" (Dunbar, 1993: p. 690) (i.e. one groomer can reach only one groomee at a time), this clique size of four (i.e. one speaker can reach three listeners at a time) matches the efficiency of language predicted from group size. Finally, he suspected that "human groups are three times larger than those of chimpanzees precisely because humans can reach three times as many social contacts as chimps for a given amount of social effort" (Dunbar, 1996: p. 122).

### **Clique Size of Primate Grooming**

Dunbar's view of primate grooming is that it always occurs on a one-to-one basis and as a

one-sided interaction. This view seems to come mainly from observations of baboon grooming, which he studied for a long time. These characteristics of grooming seem to be true in many primate species. There are many studies of grooming throughout primate taxa (for review, see Goosen, 1987), but most authors seem to take it for granted that grooming is a one-to-one and one-sided interaction, usually giving no discussion about it at all. Some studies, however, have reported that occasionally two participants groom each other simultaneously and that three or more participants engage in grooming at one time, such as  $A \rightarrow B \rightarrow C$  or  $A \rightarrow B \leftarrow C$ . Cooper and Bernstein (2000) reported that they observed 385 triadic episodes, 5 quadratic episodes and 45 mutual episodes in a total of 5397 grooming episodes of Macaca assamensis. Sugawara (1984) observed 14 triadic and no mutual episodes in 184 grooming (lice removal) episodes in Homo sapiens. There are also some descriptions of polyadic and/or mutual grooming for Macaca fuscata (Furuya, 1957), Macaca mulatta (Sade, 1965; Boccia, 1983), Macaca nemestrina and Macaca radiata (Kaufman and Rosenblum, 1966), Presbytis entellus (Mckenna, 1978) and Cebus apella (Parr et al., 1997). However, these studies have only reported that such grooming sometimes or rarely occurs and simply divided them into dyadic episodes for analysis (for example,  $A \rightarrow B \rightarrow C$  is divided into  $A \rightarrow B$  and  $B \rightarrow C$ ). Moreover, the above reports provide no data of frequency.

### **Chimpanzee Grooming to be Compared**

Unlike baboons or macaques, chimpanzees often make large grooming clusters (Goodall, 1986), and quite a large amount of grooming is polyadic. They also quite often engage in mutual grooming (e.g. McGrew and Tutin, 1978; Takahata, 1990a; 1990b; Oberski, 1993). When estimating efficiency, Dunbar compared group size of chimpanzees with that of humans because chimpanzees have the largest mean group size in primates. However, he did not

compare human conversation with chimpanzee grooming. Perhaps the data of chimpanzee polyadic grooming was not available because this kind of grooming is also often divided into dyadic occurrences in studies of chimpanzees (e.g. Nishida, 1988). These characteristics of chimpanzee grooming are important when we compare clique sizes. Furthermore, the chimpanzee is one of the closest species to humans (Caccone and Powell, 1989); they show the highest intelligence among non-human primates as well as some language ability in laboratory studies (e.g. Savage-Rumbaugh *et al.*, 1978; Kojima, 1984).

It is a difficult question whether cliques of grooming and those of conversation can be directly compared in the way Dunbar did. However, even under the assumption that they can, is conversation really three times more efficient than chimpanzee grooming? Here, I would like to discuss the issue.

## **METHODS**

In the first half of the paper, I will point out a few simple mistakes in Dunbar's calculation of the efficiency of conversation in relation to primate grooming. In the latter half, I will compare clique sizes of chimpanzee grooming, based on my own data, with the data of clique sizes of human conversation.

### **Data on Human Conversation**

Here, I use the clique size data of human conversation presented by Dunbar *et al.* (1995).

### **Data on Chimpanzee Grooming**

The field observation was conducted on a wild chimpanzee (*P. t. schweinfurthii*) group (M group) of the Mahale Mountains National Park, Tanzania, during the period of July 1996 to

May 1997. For detailed information about the research site, see Nishida (1990). I selected 10 males and 10 females as focal target individuals (Table 4.1.) and followed them as long as possible while recording all of the grooming that occurred around the target. This sampling method enabled wider observation than that of ad libitum sampling of various individuals by minimizing the possibility that observations might be biased toward those individuals who tended to congregate. Total duration of observation was about 480 hours. In order to record the sizes and patterns of cliques in large grooming clusters, a micro tape recorder was used to check the time when any individual in the cluster made a change in the grooming status (i.e. started grooming, stopped grooming, or changed partner). Grooming is a series of behavioral elements with other individuals such as stroking hair, picking hair, removing things with hand(s) or lip(s), and scratching (Nakamura *et al.*, 2000). Self-grooming and leaf grooming was not included in the analysis. A grooming cluster was defined as a gathering of individuals who at least once groomed or were groomed. A cluster begins when one or some individuals begin to groom and ends when no individuals are grooming for more than five minutes. Because some data were incomplete, I only use the 38 sets of complete grooming clusters that were observed from beginning to end and lasted more than 30 minutes. I only analyzed clusters that lasted more than 30 minutes because shorter grooming is often used as a token (Goodall, 1986). The human conversation data of Dunbar *et al.* (1995) were collected at cafeterias and reception parties in which conversation would last long. Therefore, their data was also likely free of brief conversations such as greetings when two persons meet on the street. Total duration of these complete grooming clusters was about 30 hours.

## **Definition of Terms**

Clique: Following Dunbar *et al.* (1995), I define "clique" as "the number of individuals taking part in a particular conversation (or grooming)". In other words, it is a subgroup of individuals who are directly connected through conversation (or grooming) in a larger gathering of conversation (or grooming). This usage of clique is different from that in graph theory or network analysis (Scott, 1991).

Actor: In grooming, the one who acts to make bonding is a "groomer," while in conversation it is a "speaker." In this article both of these types of individuals are referred to as "actor."

Recipient: The one who receives the action is a "groomee" in grooming and is a "listener" in conversation. These two types of individuals are referred to as "recipient."

Theoretical Monkey: I define theoretical monkeys as those who always groom one-to-one and one-sidedly, as Dunbar has assumed and as most primates usually, but not always, do. In other words, theoretical monkey grooming always consists of only one actor and only one recipient, so clique size is always two.

## **RESULTS**

### **1) Average Clique Size of Human Conversation**

Dunbar argued that because usual primate (i.e. theoretical monkey) grooming is one-to-one (i.e. clique size is 2) while the clique size of human conversation is 4, human conversation is three times more efficient than grooming (Dunbar, 1996: p. 121). This clique size of four in human conversation seems to be derived from their finding that "human clique size reached an asymptotic value of 3.0-3.5 at a group size of about four individuals" (Dunbar *et al.*, 1995).

This means that when the number of people present is smaller than four, all the group's participants usually engage in only one clique, and therefore clique size becomes larger when group size becomes larger. However, when group size exceeds four, it breaks down into two or more cliques. Therefore, "asymptotic value of 3.0-3.5" only means that cliques of larger than four are not likely to occur, but does not mean the average size of human conversation cliques is about four. When we compare the efficiency of grooming with that of conversation, we have to consider the average efficiency of each, not the potential efficiency. If reality follows what theory requires, human conversation must be three times more efficient than grooming on average. Recalculations of the data from Dunbar et al. (1995) revealed that the average clique size of human conversation was 2.72 (Table 4.2.). This means that there are 1.72 recipients for one actor on average; therefore, human conversation is only 1.72 times more efficient than theoretical monkey grooming on average.

## **2) Role Alternation Model**

Dunbar does not seem to have taken role alternation into account. He argued that conversation is three times more efficient than theoretical monkey grooming when clique size of conversation is four. This seems true when we count the number of arrows of social interaction flows in Fig. 4.1-a. There are three arrows coming out of individual **A** in human conversation, while there is only one arrow in theoretical monkey grooming. If we only see this moment, it is three times more efficient for **A** to be an actor in conversation than in grooming, as Dunbar mentioned. However, in reality **A** cannot perform as an actor all the time but instead has to be in the role of recipient while others are playing the actor's role. In Fig. 4.1.-b, role alternation is taken into account. In grooming, **A** takes the actor's role in the first turn, has to be a recipient in the second, then can again take an actor's role in the third,

and so on. In conversation, **A** can take the actor's role over three other individuals at a time in the first turn, but **A** has to wait as a recipient during the following three turns.

In grooming with role alternation, **A** can have two arrows (i. e. social interaction flows) as an actor and two arrows as a recipient, therefore, in total, **A** can have 4 arrows in this certain amount of time. In conversation, **A** can have 6 arrows, three as an actor and three as a recipient. Therefore when we consider the alternation of roles, conversation in the clique size of four is only 1.5 times more efficient than theoretical monkey grooming whose clique size is always two. In Fig. 4.1., I only considered conversation in the clique size of four, but there are of course various sizes of cliques. In general, to calculate efficiency while considering the role alternation model is precisely the same as calculating the ratio of arrows in a certain moment with equaled numbers of participants in grooming and conversation. When clique size of conversation is  $n$ , the number of arrows in the conversation is  $n-1$  (all the participants minus one actor), and if these  $n$  individuals groom as theoretical monkeys, the number of arrows becomes  $n/2$ . Therefore, the efficiency of  $n$  clique conversation over theoretical monkey in general is  $2(n-1)/n$ .

### **3) Chimpanzee Grooming Cliques**

Dunbar seems to assume that primate grooming is almost always like that of the theoretical monkey (Dunbar, 1993; 1996). This view might come from his observations of the grooming of baboons, which he studied for a long time. Actually, it seems physically impossible for an actor to groom multiple recipients, which we can do easily in conversation. However, in grooming it is possible that a recipient is groomed by multiple actors or an individual plays both an actor's role and a recipient's role at the same time, which is quite common in chimpanzees.



Fig. 4.2. shows all of the types of chimpanzee grooming cliques actually observed. There were 23 patterns of cliques, the largest size of which was 7. The frequencies of these cliques are shown in Table 4.4.

Chimpanzees often engage in mutual grooming in which two participants groom each other simultaneously. For one adult male, the proportion of mutual grooming accounted for about 30% of all of his grooming time. In mutual grooming, the number of arrows, i.e. the number of grooming flows, is 2 even when clique size is 2. If the problem is the efficiency of social flows among interactants, this grooming is twice as efficient as normal grooming even though the number of participants remains the same.

#### **4) Comparisons**

First, let us compare clique sizes in a simple way. A clique size of two was the most common in chimpanzee grooming as well as in human conversation; however, cliques larger than three accounted for 15% in chimpanzees. The largest size of 7 in chimpanzee grooming was the same as that of human conversation. The average clique size for chimpanzee grooming was 2.18 (Table 4.2.), while that for human conversation was 2.72, as we have seen earlier.

Table 4.3. compares the efficiency of human conversation with that of theoretical monkey grooming while taking the effect of role alternation into account. Overall, the average number of arrows in human conversation was 1.72, while it was 1.36 in theoretical monkey grooming. This means that when we take role alternation into account, human conversation was only 1.27 ( $=1.72/1.36$ ) times more efficient than theoretical monkey grooming.

Table 4.4. compares the efficiency of chimpanzee grooming with that of theoretical

monkey grooming in the same way as in Table 4.3. The average number of arrows in chimpanzee grooming was 1.36 and 1.09 for theoretical monkeys. Consequently, chimpanzee grooming was 1.25 ( $=1.36/1.09$ ) times more efficient than theoretical monkey grooming. Both human conversation and chimpanzees grooming are 1.2-1.3 times more efficient than theoretical monkey grooming.

## DISCUSSION

Most studies of language evolution emphasize its special features, for example its ability to express abstract meaning or things that are not present by using complex vocalization and complex syntax. If we only see these complex and special features of language, non-human primates are far from comparable. Language seems unique to humans, which makes a comparison of species ridiculous. However, primitive but very basic features of language seem to be forgotten or too much taken for granted. It is a very simple fact that conversation (which is made with language) is without doubt the most common social interaction among humans. Of course there usually is much information contained in conversation, but do we not we often talk just for its own sake even about redundant topics? In such talks, the aspect of conveying information becomes small, and the bonding or maintaining of social relationships is not negligible. Furthermore, this bonding mechanism exists even when language conveys information. When we see non-human primates, our close relatives, their most common social interaction is grooming. In this respect Dunbar's works are quite valuable. He tried to compare primate grooming and human conversation from the viewpoint that both of them have the same function of making social bonds among individuals in a group.

In his theory, one of the major reasons for the evolution of language is that language

is three times more efficient than primate grooming. However, it is too simple to assume that language is more efficient than grooming. It is more efficient than theoretical monkey grooming, but not to the extent that Dunbar has argued. As I have shown, chimpanzee grooming has about the same efficiency as human conversation when we consider the quantities of these social interactions. I do not, however, want to argue that chimpanzee grooming is equivalent to human conversation. It is still unknown whether the same duration of conversation or grooming is really comparable solely from the viewpoint of efficiency.

It should be noted that conversation itself is quite diverse, and thus even the same quantities of conversations do not always have the same efficiency. How can one compare the efficiency of a serious talk between two people and a garrulous chatter among many friends only by their durations? Chimpanzee grooming also seems to be diverse, and it looks quite different when they groom in a large grooming cluster and when they groom one-to-one, often face-to-face. Thus perhaps we will have to consider not only quantitative efficiency but also qualitative aspects of the social interactions.

Chimpanzee grooming was shown to be as efficient as human conversation precisely because they do not always groom like theoretical monkeys but often mutually and polyadically. These characteristics of chimpanzee grooming also make their grooming cliques quite diverse, as we have seen in Fig. 4.2. It is not clear whether mutual and polyadic grooming is really performed less often in other primates than chimpanzees because there are very limited descriptions of mutual grooming and polyadic grooming for species other than chimpanzees. However, in most of these descriptions (Furuya, 1957; Kaufman and Rosenblum, 1966; Sparks, 1967; Mckenna, 1978; Boccia, 1983), primates are said to groom mutually or polyadically only sometimes or rarely. The rareness of this kind of

description may also imply that these observations themselves are rare. Perhaps they have the potential to groom in the same way as chimpanzees but simply do not have to because their group size is usually smaller than that of chimpanzees. However, there is also the possibility that it requires some kind of cognitive abilities to be an actor and a recipient of different interactions at the same time, which might prevent monkeys from grooming in the way chimpanzees do. Chimpanzees are also known to use grooming in quite complex and various ways such as trading with food (de Waal, 1997), as deceptive tactics (Nishida, 1998), and in many other social situations (e.g. Goodall, 1986). There is also some "cultural" diversity in chimpanzee grooming (McGrew and Tutin, 1978; Nakamura *et al.*, 2000), which implies that their grooming is more socially determined than other primates. Perhaps various patterns of cliques may also be related to this kind of complex use of grooming in chimpanzees to some extent.

One would think that primate grooming and human conversation are intrinsically different because, for example, chimpanzees can groom simultaneously with each other whereas humans cannot do so in conversation. This is nearly true in English speaking people (Sacks *et al.*, 1978) and perhaps in Japanese as well. In these cultures, the speakers must alternate in a way quite similar to how theoretical monkeys behave in grooming. When simultaneous speeches occur, they are usually taken as mistakes in conversation and one or both speakers stop talking. However, it is not really correct to assume that this characteristic is universal among humans because some hunter-gatherer people often talk simultaneously for quite a long time (e.g. the !Gui Bushman, Sugawara, 1998; the Baka Pygmy, Kimura, 1995). These simultaneous speeches are sometimes agonistic as they usually are in our heated debates, but they are often cooperative or parallel (Sugawara, 1998). Chorus or co-singing may be another example of simultaneous vocalization. Chorus is not strictly

conversation, but it surely helps bonding among the participants. We have to be cautious about the fact that both grooming and conversation can potentially be mutual or alternating. If we include these kinds of conversations or chorus, not only English conversation, the efficiency of human conversations would become larger. However, there is not such data available so far. At this point, data on clique size of both primate grooming and conversation are very limited. In this paper I only presented the data from one population of chimpanzees. Comparisons among many primate species and also among different human cultures are needed.

Grooming and conversation both have an aspect that functions as a group bonding mechanism. However, of course, these two are not the only mechanisms nor are they incompatible. For example, in bonobos (*Pan paniscus*), female estrous is prolonged (Furuichi, 1992) and sexual behavior has some aspect of functioning as a group bonding mechanism apart from its original function of reproduction (de Waal, 1989; Kano, 1992). The original function of grooming may have been to remove ectoparasites (e.g. Tanaka and Takefushi, 1993), while that of language (or vocal communication) may have been to convey some information to a remote individual. However, they now both seem to be used as bonding mechanisms as well. Group bonding mechanisms do not have to evolve only for their own sake but also by a diversion of other mechanisms that used to have different functions. As for humans, we can think of various different ways of bonding such as conversation, sexual or non-sexual contact, co-feeding, exchange of goods, eye contact, facial expression and so on. We will have to explore the possibility that the group bonding mechanism may be a mosaic of many elements of behavior, not only grooming or conversation.

## CHAPTER 5.

### Social Scratch.

#### Another Custom in Wild Chimpanzees?

##### INTRODUCTION

When Dawkins (1976) chose "You scratch my back, I'll ride on yours" as the title of Chapter 10 of The Selfish Gene, he likely did not know that scratching other individuals is uncommon in most chimpanzee populations. Although self-scratching is observed throughout primate taxa including chimpanzees (for review, see Maestriperi et al., 1992), to scratch socially is rare.

The chimpanzees of Mahale scratch other individuals' bodies while they groom them, hence the term "social scratch" Nishida (1983) briefly described the pattern as "scratch and rub" in the context of alloparental care among Mahale K-group chimpanzees. Mothers and allomothers scratch infants as part of their maternal behavior. Nishida did not publish a detailed report of the pattern because it was so commonplace at Mahale that he did not consider that it might be absent in other populations.

There are many locality-specific behavioral patterns in chimpanzees, and these fuel an ongoing debate as to whether chimpanzees have "culture" (e.g. Nishida, 1987; Tomasello & Call, 1997; Boesch & Tomasello, 1998; McGrew, 1998; Whiten et al., 1999). Local differences such as tool-use or food preferences (for review, see McGrew, 1992) can be characterized as the relationships between an individual and inanimate objects. On the other hand, locality-specific social behavioral patterns are used in relationships among individuals. For example, a variant of social grooming called the grooming-hand-clasp occurs in a few populations: Mahale (McGrew & Tutin, 1978), Kibale Forest (Ghiglieri, 1984), Kalinzu

Forest, Uganda (Hashimoto, pers. comm.), Lope (Tutin, pers. comm.) and Tai (Boesch & Boesch, 2000). It also occurs in the captive colony of the Yerkes Regional Primate Research Center (de Waal & Seres, 1997). However, the pattern has never been recorded at Gombe despite more than 37 years of research, nor at other long-term sites such as Bossou or Budongo. Likewise, the leaf-clipping courtship display (Nishida, 1980) has been observed at Mahale but not at Gombe. This also regularly occurs at Bossou (Sugiyama, 1981) and Tai (Boesch, 1995), but the contexts vary from place to place. Some researchers (e.g. Nishida, 1987; Boesch, 1996; McGrew, 1998; Whiten *et al.*, 1999) argue that these social patterns should be regarded as cultural. However, Tomasello and Call (1997) assert that most, or all, of such patterns could be explained by ontogenetic ritualization or conventionalization, in which two organisms essentially shape one another's behavior in repeated instances of social interaction. As social scratch has not been seen at Gombe or other sites, it may be another example of a locality-specific social behavioral pattern that adds more information to the debate.

Here, we report the details of this behavior and discuss its hypothetical origins and function of this behavioral pattern and the mechanisms that may facilitate the transmission of this custom among group members.

## **METHODS**

We observed 53 chimpanzees of M group in the Mahale Mountains National Park, Tanzania. For detailed information about the research site, see Nishida (1990).

### **Methods of MN (Michio Nakamura)**

From July 1996 to May 1997, MN followed 10 males and 10 females as focal target

individuals. Each day MN followed one target as long as possible and recorded all the grooming behavior during the follow. This sampling method primarily aimed to record structure and membership of grooming clusters in which focal individuals engaged. Therefore, grooming behavior was recorded not only on focal individuals but also on non-focal individuals within the grooming cluster, even when they were not directly grooming with focal individuals. Total duration of follows was 480 hours, during which 137 hours of grooming (total accumulation of individual grooming) was recorded. Though visibility was poor in some places, most grooming occurred in relatively open spaces, so that grooming within 10 m around the target was recordable. When multiple individuals were grooming at the same time, the start and end time of each individual's groom or scratch and changes in partner were recorded on a tape recorder. This sampling method enabled wider observation than that of ad libitum sampling on various individuals by minimizing the possibility that observations might be biased toward those individuals who tended to congregate. Unless otherwise stated, MN's data include all grooming recorded during the follow, not just the focal subjects'. Only data after November 1996 were used in calculating a focal subject's frequency of behavior per follow, as there was some bias in the focal data before then. Only 9 focal males were available after November 1996.

### **Methods of WCM (William C. McGrew) and LFM (Linda F. Marchant)**

Between 12 September and 18 December 1996, WCM and LFM collected data on laterality of hand function on 44 members of M group, ranging in age from 3-41 years (only babes in arms were excluded). We sought comprehensive and balanced coverage of the group and so used a scheme of switching focal sampling. When a party was encountered, the observer chose as targets the individuals with the least data accumulated up to the point. If a party split up, or



fused, the same criterion was used to change subjects. Length of observation session was proportional to data accumulated, that is, when shy or peripheral individuals were present, they were given priority, opportunistically. To economize on effort, an arbitrary ceiling of 100 data-points (bouts) per behavioral category per individual was imposed.

We defined a bout of social scratch (see Results) to be separated from another by other elements of grooming (e.g. stroke, pick). For age-sex classes, we defined "mature males" as males after puberty (over 9 years old, the reported age of first ejaculation), "cycling females" as those who showed estrous swelling cycles, and "lactating females" as those who suckled infants (therefore not cycling) during the period of observation. "Youngsters" were subjects below the age of sexual maturity (infants and juveniles).

For comparison, we used the chi-square test, Spearman's rank correlation coefficient test, Mann-Whitney's U-test, and the Binomial test. All p-values presented are two-tailed.

## **RESULTS**

### **Observations**

In social scratch, one individual rakes the hand back and forth across the body of another, usually with the nails but sometimes with the distal finger pads of the four fingers (Fig. 5.1.). This manual motor pattern is the same as that of self-scratch. Social scratches always occurred during sessions of social grooming, none occurred separately. Recipients of social scratch showed no specific reaction to it; instead they just continued to sit or lie still while being groomed.

MN observed 391 bouts of social scratch, WCM and LFM observed 139 (Table 5.1.). Thirty-one (27 in MN's data, 26 in WCM and LFM's data) of 53 individuals of M group's

members were seen to perform the pattern. Thirty-eight individuals received social scratch (MN's data). Using the same methods, WCM and LFM studied laterality of hand function in Gombe National Park from September to December 1992 but never observed social scratch there.

### **Concordance of the Two Data Sets**

For the 31 individuals who were observed at least once to do social scratch, the relative frequency of social scratch across individuals in MN's data is significantly correlated with that in WCM and LFM's data (SS vs. SSg in Table 5.1.,  $r_s=0.43$ ,  $p<0.05$ ,  $N=31$ ). The concordance of the two data sets is impressive, despite their having been obtained by different sampling methods.

### **Frequency of Social Scratch**

Duration of follows (observation hours), number of social scratches, and duration of grooming bouts of MN's focal targets between November 1996 and May 1997 are shown in Table 5.2. The 19 focal individuals averaged  $0.31 \pm 0.09$  (mean  $\pm$  SE) social scratches per observation hour and  $1.99 \pm 0.57$  social scratches per grooming hour. They received an average of  $0.39 \pm 0.13$  social scratches per observation hour and  $2.53 \pm 0.64$  per grooming hour. With the inclusion of MN's data on non-focal individuals, social scratch was seen 0.81 times in every observation hour, and 2.84 times in every grooming hour.

For the 24 individuals who both gave and received social scratch, the frequency of giving social scratch was not correlated with the frequency of receiving social scratch (SSg vs. SSr in Table 5.1.,  $r_s = 0.36$ ,  $p=0.09$ ,  $N=24$ ).

There was no sex difference in giving social scratch (SSg in Table 5.1.,  $U=80$ ,

N[male]=12, N[female]=15,  $p=0.62$ ; SS in Table 4.1.,  $U=75.5$ , N[male]=12, N[female]=14,  $p=0.66$ ) nor in receiving social scratch (SSr in Table 5.1.,  $U=129.5$ , N[male]=16, N[female]=22,  $p=0.17$ ).

### **Comparisons of Social Scratch with Social Groom and Self-Scratch**

For those subjects who exhibited social scratch, its frequency was correlated with the duration of their social grooming in MN's data (SSg vs. GRg(h) in Table 5.1.,  $r_s=0.65$ ,  $p<0.001$ ,  $N=27$ ) as well as in WCM and LFM's data (SS vs. GR in Table 5.1.,  $r_s=0.43$ ,  $p<0.05$ ,  $N=26$ ).

Those who groom others longer tend to scratch others more often. The correlation was the same for the frequency of received social scratch and the duration of being groomed (SSr vs. GRr(h) in Table 5.1.,  $r_s=0.61$ ,  $p<0.001$ ,  $N=38$ ). The frequency of social scratch also correlated with that of self-grooming (SS vs. SG in Table 5.1.,  $r_s=0.42$ ,  $p<0.05$ ,  $N=26$ ). The latter correlation may reflect a connection between social and self-grooming (GR vs. SG in Table 5.1.,  $r_s=0.62$ ,  $p<0.001$ ,  $N=42$ ).

The frequency of social scratch did not correlate with that of self-scratch (SS vs. SC in Table 5.1.,  $r_s=0.43$ ,  $p=0.11$ ,  $N=15$ ). Those who often scratch themselves do not scratch others more often.

### **Distribution of Social Scratch by Age-Sex Class**

More than half (220/391) of social scratches were given in only two combinations of age-sex classes: mature males to mature males (MM in Fig. 5.2.) and lactating females to youngsters (LY in Fig. 5.2.). Although the duration of grooming was also long in these two combinations, the number of social scratches was larger than expected from duration of grooming (the line in Fig. 5.2.). Cycling females groom others as often as lactating females

groom youngsters but they seem to scratch others less than expected from grooming. The observed distribution of social scratch was significantly different from that expected from grooming distribution ( $\chi^2=220.86$ ,  $df=15$ ,  $p<0.001$ ).

Among mature males, the frequency of received social scratch per grooming time was correlated with their dominance rank ( $r_s=-0.84$ ,  $p<0.01$ ,  $N=12$ , see Table 5.1.). This means that higher-ranking males received more social scratches than expected from the duration of the grooming they received. Social scratch was also positively correlated with age ( $r_s =0.85$ ,  $p<0.01$ ,  $N=12$ , see Table 5.1.). However, the frequency of giving social scratch per grooming by mature males was neither correlated with rank ( $r_s =-0.51$ ,  $p=0.08$ ,  $N=12$ ) nor with age ( $r_s =0.48$ ,  $p=0.47$ ,  $N=12$ ).

### **Body Parts Scratched**

Body parts to which each class gave and received social scratch are shown in Fig. 5.3. and Fig. 5.4., respectively. In total, the back was most often scratched and accounted for 65% (256/391) of bouts. However, lactating females showed a different tendency, in that they scratched the back less than did other age-sex classes (the back and other body parts were not evenly scratched in different age-sex classes,  $\chi^2=44.57$ ,  $df=3$ ,  $p<0.01$ ). The same tendency was seen in the parts where youngsters received social scratches ( $\chi^2=24.76$ ,  $df=3$ ,  $p<0.01$ ). This is because the lactating females who frequently scratched youngsters were mostly mothers scratching their offspring. They usually groomed infants in their lap and often placed infants horizontally, holding their limbs. This enabled mothers to scratch all parts of the infant's body more freely than when others scratched adult conspecifics.

## **Laterality of Social Scratch**

For 19 individuals who were observed (in both data sets) often enough for statistical testing (Binomial test,  $N > 6$ ), two (DG and NK) were significantly left-preferent, three (FT, HB and NS) were significantly right-preferent, and the other 14 were ambidextrous (Fig. 5.5.). This is level 1 in the 5-tier framework of laterality proposed by McGrew and Marchant (1996).

## **DISCUSSION**

Although there were large individual differences in social scratch (for example, MJ and DG gave many and DE received many), this pattern was not restricted to a few individuals but occurred widely among members of M group. Eighty-one percent (43/53) of M group members either gave or received social scratch; of the 10 who did not, none was older than 9 years. Infants seldom showed social scratch, but this may be because they also seldom groomed others until about 3 years old (Nishida, 1988), while most adult individuals showed this behavior. The frequency of occurrence was high enough to conclude that social scratch was neither anecdotal, idiosyncratic, nor habitual, but was customary (McGrew & Marchant, 1997). Social scratch has not been seen at other sites of chimpanzee studies, such as Gombe (Goodall, pers. comm.), Taï (Boesch, pers. comm), Bossou (Sugiyama, pers. comm.; Matsuzawa, pers. comm.; Yamakoshi, pers. comm.), or Ndoki (Kuroda, pers. comm.). Plooi (1984, p. 173) listed a general category of "SCR (scratch)", but he did not specify its form or its context.

### Function and Origin of Social Scratch

There are several hypotheses on the function and origin of social scratch:

### (1) Effective Way of Grooming

Scratching makes the groomee's hair erect, which enables the groomer to find more easily ectoparasites or other materials in the hair or on the skin. Or, scratching may remove ectoparasites (Tanaka, 1998), such as ticks, or sticky fruit sap, such as of Saba, from the hair. Such substances seem less easy to remove by conventional grooming.

### (2) Extension of Grooming Context

Grooming is often regarded as an expression of an intimate relationship between participants. However, grooming is tedious because it requires taking care to pick at tiny objects. Those who seek to service intimate relationships but are reluctant to engage in bothersome behavior may use social scratch as an easier alternative to keep grooming contact. Social scratches are brief, but they may be used to fill gaps between bouts of grooming.

### (3) Relief of Tension

Self-scratch can be related to social tension or stress in chimpanzees (de Boekhorst *et al.*, 1991; Aureli & de Waal, 1997). Thus, social scratch may emerge for displacement or release of tension or stress for the giver, as it does for self-scratch.

### (4) Reducing Itchiness of the Recipient

Chimpanzees may scratch others in order to reduce the recipients' itchiness. It is easy to imagine that chimpanzees (like humans) feel pleasure when an itch is scratched. They may scratch others in order to get scratched in return, or to make others more comfortable, if making them feel good would make them less likely to be aggressive.

Even if these hypotheses explain social scratch at Mahale, they also must explain why social scratch does not occur at other localities. Hypothesis (1) is plausible, given that social scratch is mostly given to the dorsum of the body (where scratching oneself is difficult), and that it is often given from mothers to their infant or juvenile offspring. If there were

more detritus or ectoparasites at Mahale than at other sites, this could explain why social scratch occurs only in Mahale. For example, in Mahale, there are three species of buffalo bean (*Mucuna* spp., Papilionaceae) (Nishida & Uehara, 1981) whose pods are covered with many transparent tiny filaments. In the dry season the needle-like filaments are dispersed by wind and stick to everything from soil and rocks to the trunk, branches and leaves of trees and woody vines. If you touch such a substratum coated with the needles, you will itch and scratch. At Gombe and Tai, there are no buffalo beans (Nishida, personal observation). This abundance of buffalo beans also supports hypothesis (4). These hypotheses can be tested by systematically comparing the frequency of self-scratch of Mahale and other localities lacking these plants. WCM and LFM's frequency data on self-scratch at Gombe and Mahale do not differ.

The fact that higher-ranking males receive more social scratch implies that there are social factors involved in this behavior, which suggests that hypotheses (2) and (3) have merit. Lower-ranking males always seek to better their relationships (e.g. by grooming) with higher-ranking males, but the latter seldom groom the former. As a result, lower-ranking males have to groom one-sidedly in order to extend grooming contacts, so they more often social scratch as a function of (2). For hypothesis (3), it is reasonable to assume that lower-ranking males are tense when they groom higher-ranking males, so that social scratch appears more often. However, hypotheses (2) and (3) cannot explain why it does not occur in other localities. These hypotheses also cannot explain the frequent social scratches from lactating females to youngsters. Perhaps social scratch originated as (1) or (4) and was given mainly from mothers to offspring, then it acquired an added function of (2) or (3) which is now often used by males.

### Learning Process of Social Scratch

Because it is a social behavior, the process of learning social scratch might be an example of ontogenetic ritualization, as suggested by Tomasello and Call (1997). According to them, ontogenetic ritualization is when individual A performs behavior X, and individual B reacts consistently with behavior Y, so this repetition causes A to ritualize behavior X in order to elicit Y from B. Here if behavior X is social scratch, then what corresponds to behavior Y? In social scratch, the recipient shows no specific reaction, so the typical reaction that corresponds to behavior Y, is "no-response". For example, recipients do not react negatively by leaving or by aggressing, but instead allow the scratcher to go on scratching. Moreover, the scratcher need not ritualize social scratch in order to elicit "no-response", which can be most easily evoked by doing nothing! Therefore, it is difficult to explain social scratch as ontogenetic ritualization.

What learning processes may be involved (Zentall, 1996)? First, it would seem to be easy for a chimpanzee to acquire this behavior by individual learning, because the motor pattern is just self-scratch redeployed. If so, why do not individual chimpanzees in any other locality learn it as at Mahale? Perhaps the environmental causes discussed in the first hypothesis enhance individual learning by local enhancement (Zentall, 1996), but this seems unlikely to explain the differences at Mahale across ranks or age-sex classes. This would require (for example) more dominant individuals to have dirtier hair.

Second, if the fourth hypothesis is true, a chimpanzee could learn to social scratch from the experience of being scratched by others. Chimpanzees may be intelligent enough to remember the pleasurable feeling of being scratched when they are itchy. It may be that they can take the groomer's perspective when they groom, given their ability to reciprocate, but why should they? Local differences across populations could also be explained (for



example) by environmental factors that cause itchiness, but this fails to account for the rank and class differences within a population.

Third, chimpanzees may learn from watching other individuals engage in social scratch (Zentall, 1996). Social scratch sometimes is noisy enough to be an attention-getter. This third type of learning could be program level imitation, in which the goal of the behavior is learned, or action level imitation, in which the behavioral sequence is copied (Byrne & Russon, 1998). Either is a reasonable explanation for skillful tool use such as nut cracking, given that these complex patterns have a beneficial payoff to the performer (Whiten, 1998). Social scratch, on the other hand, achieves no obvious benefit for the scratcher, but instead is beneficial to the recipient. Thus, it is hard to see a goal for emulation. Social scratch seems to be a custom of the Mahale population, the origin and dissemination of which requires further study.

## SUMMARY

To understand the social evolution of humans (Homo sapiens), it is essential to compare our social behaviors with those of living primates, especially with the great apes. I have studied grooming interactions of wild chimpanzees (Pan troglodytes schweinfurthii) in Mahale Mountains National Park, Tanzania, in order to extract the characteristics of their social interactions. In the first part, I analyze their grooming behavior as "gatherings." Primate grooming behavior usually occurs on a one-to-one basis and unilaterally, and thus it is typically regarded as characteristics of dyadic relationships. However in chimpanzee grooming, 27 types of grooming cliques (the momentarily connections of individuals engaged in grooming interactions) were observed. The largest clique consisted of 7 individuals. I defined grooming clusters as larger gatherings that are accumulative of cliques. Adult females groom each other more often in large clusters than in smaller ones, whereas adult males groom each other most frequently in clusters of two individuals. In the second part, I tested Robin Dunbar's hypothesis that human language evolved because, as a bonding mechanism, it is three times more efficient than primate grooming. Comparisons of clique sizes in human conversation and in chimpanzee grooming revealed that these two behaviors have about the same number of social interactions that one can make at a given moment. In the third part, I showed that a grooming pattern called "social scratch" is unique to Mahale chimpanzees. This behavior was frequently observed among adult and adolescent males and from mothers to infants or juveniles. Among males, more dominant individuals tended to receive more social scratches. Chimpanzees and humans have similarities in the complexity of their social interactions, and subtle social customs occur within such complex interactions. It is suggested that the origins of such complex interaction and so-called "cultural" differences may be even older than the origin of vocal language.

## REFERENCES

- Ahumada, J. A. (1992). Grooming behavior of spider monkeys (*Ateles geoffroyi*) on Barro Colorado Island, Panama. *Int. J. Primatol.* 13: 33-49.
- Aureli, F. and de Waal, F. B. M. (1997). Inhibition of social behavior in chimpanzees under high-density conditions. *Amer. J. Primatol.*, 41: 213-228.
- Bauer, H. (1979). Agonistic and grooming behavior in the reunion context of Gombe Stream chimpanzees. In: Hamburg, D. A., and McCown, E. R. (eds.), *The Great Apes*, Benjamin/Cummings, Menlo Park, pp.395-403.
- Bernstein, I. (1968). The lutong of Kuala Selangor. *Behaviour* 32: 1-16.
- Boccia, M. L. (1983). A functional analysis of social grooming patterns through direct comparison with self-grooming in rhesus monkeys. *Int. J. Primatol.* 4: 399-418.
- Boesch, C. (1995). Innovation in wild chimpanzees (*Pan troglodytes*). *Int. J. Primatol.*, 16: 1-16.
- Boesch, C. (1996a). Social grouping in Tai chimpanzees. In: McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), *The Great Ape Societies*, Cambridge University Press, Cambridge, pp. 101-113.
- Boesch, C. (1996b). Three approaches for assessing chimpanzee culture. In: Russon, A. E., Bard, K. A., and Parker, S. T. (eds.), *Reaching into Thought: The Minds of the Great Apes*, Cambridge University Press, Cambridge, pp. 404-429.
- Boesch, C. and Boesch-Achermann, H. (2000). *The Chimpanzees of the Tai Forest*, Oxford University Press, Oxford.
- Boesch, C. and Tomasello, M. (1998). Chimpanzee and human cultures. *Curr. Anthropol.*, 39: 591-614.
- Borries, C., Sommer, V., and Srivastava, A. (1994). Weaving a tight social net allogrooming

- in free-ranging female langurs (Presbytis entellus). Int. J. Primatol. 15: 421-443.
- Byrne, R. W. and Russon, A. E. (1998). Learning by imitation: a hierarchical approach. Behav. Brain Sci., 21: 667-721.
- Caccone, A., and Powell, R. (1989). DNA divergence among hominoids. Evolution 43:925-942.
- Chapman, C. A., White, F. J., and Wrangham, R. W. (1994). Party size in chimpanzees and bonobos: a reevaluation of theory based on two similarly forested sites. In: Wrangham, R. W., McGrew, W. C., de Waal, F. B. M., and Heltne, P. G. (eds.), Chimpanzee Cultures, Harvard University Press, Cambridge, Mass, pp. 41-57.
- Chapman, C. A., Wrangham, R. W., and Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. Behav. Ecol. Sociobiol. 36: 59-70.
- Cheney, D. L. and Seyfarth, R. M. (1990). How Monkeys See the World, the University of Chicago Press, Chicago and London.
- Cooper, M. A., and Bernstein, I. S. (2000). Social grooming in Assamese macaques (Macaca assamensis). Am. J. Primatol. 50: 77-85.
- Dawkins, R. (1976). The Selfish Gene, Oxford University Press, Oxford.
- de Waal, F. B. M. (1982). Chimpanzee Politics, Jonathan Cape, London.
- de Waal, F. B. M. (1989). Peacemaking Among Primates. Harvard University Press, Cambridge, Mass.
- de Waal, F. B. M. (1997). The chimpanzee's service economy: food for grooming. Evol. Hum. Behav. 18: 375-386.
- de Waal, F. B. M., and Seres, M. (1997). Propagation of handclasp grooming among captive chimpanzees. Am. J. Primatol. 43: 339-346.

- Doran, D. (1997). Influence of seasonality on activity patterns, feeding behavior, ranging and grouping patterns in Tai chimpanzees. Int. J. Primatol. 18 183-206.
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. Folia Primatol. 57: 121-131.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. Journal of Human Evolution 20:469-493.
- Dunbar, R. I. M. (1993). Coevolution of neocortical size, group size and language in humans. Behav. Brain Sci. 16: 681-735.
- Dunbar, R. I. M. (1996). Grooming, Gossip and Evolution of Language, Harvard University Press, Cambridge, Mass.
- Dunbar, R. I. M., Duncan, N. D. C., and Nettle, D. (1995). Size and structure of freely forming conversational groups. Human Nature 6: 67-78.
- Furuichi, T. (1992). The prolonged estrus of females and factors influencing mating in a wild group of bonobos (Pan paniscus) in Wamba, Zaire. In Itoigawa, N., Sugiyama, Y., Sackett, G. P. and Thompson, R. K. R. (eds.), Topics in Primatology, Vol.2: Behavior, Ecology, and Conservation, University of Tokyo Press, Tokyo, pp. 179-190.
- Furuya, Y. (1957). Grooming behavior in the wild Japanese monkeys. Primates 1: 47-68.
- Ghiglieri, M. P. (1984). The Chimpanzees of Kibale Forest, Columbia Univ. Press, New York.
- Goodall, J. (1983). Population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. Z.Tierpsychol. 61:1-60.
- Goodall, J. (1986). The Chimpanzees of Gombe: Patterns of Behavior, Harvard University Press, Cambridge, Mass.
- Goosen, C. (1987). Social grooming in primates. In: Mitchel, G. and Erwin, J. (eds.), Comparative Primate Biology, vol 2B: Behavior, Cognition, and Motivation, Alan R. Liss,

- Inc., New York, pp. 107-131.
- Hayaki, H. (1988). Association partners of young chimpanzees in the Mahale Mountains National Park, Tanzania. Primates 29: 147-161.
- Hayaki, H. (1994). Social relations of the second ranking male chimpanzee at M group of the Mahale Mountains National Park, Tanzania. Primate Res. 10: 289-305.
- Hemelrijk, C. K., and Ek, A. (1991). Reciprocity and interchange of grooming and 'support' in captive chimpanzees. Anim. Behav. 41: 923-935.
- Hiraiwa-Hasegawa, M., Hasegawa, T., and Nishida, T. (1984). Demographic study of a large-sized unit-group of chimpanzees in the Mahale Mountains, Tanzania: a preliminary report. Primates 25: 401-413.
- Kano, T. (1992). The Last Ape: Pygmy Chimpanzee Behavior and Ecology, Stanford University Press, Stanford, CA.
- Kaufman, I. C., and Rosenblum, L. A. (1966). A behavioral taxonomy for Macaca nemestrina and Macaca radiata: based on longitudinal observation of family groups in the laboratory. Primates 7: 205-258.
- Kawanaka, K. (1989). Age differences in Social interaction of young males in a chimpanzee unit-group at the Mahale Mountains National Park, Tanzania. Primates 30: 285-305.
- Kimura, D. (1995). Speech overlap and long silence among the Baka Pygmy. Journal of African Studies 46:1-19 (in Japanese with English abstract).
- Kojima, T. (1984). Generalization between productive use and receptive discrimination of names in an artificial visual language by a chimpanzee. International Journal of Primatology 5:161-182
- Kuroda, S. (1980). Social behavior of the pygmy chimpanzees. Primates 21: 181-197.
- Maestriperi, D., Schino, G., Aureli, F., and Troisi, A. (1992). A modest proposal:

- displacement activities as an indicator of emotions in primates. Anim. Behav., 44: 967-979.
- McKenna, J. (1978). Biosocial functions of grooming behavior among the common Indian langur monkey (Presbytis entellus). Am. J. Phys. Anthropol. 48: 503-510.
- McGrew, W. C. (1992). Chimpanzee Material Culture: Implications for Human Evolution, Cambridge University Press, Cambridge.
- McGrew, W. C. (1998). Culture in nonhuman primates? Ann. Rev. Anthropol., 27: 301-328.
- McGrew, W. C., and Marchant, L. F. (1996). On which side of the apes? Ethological study of laterality of hand use. In :McGrew, W. C.; Marchant, L. F.; Nishida, T. (eds.), Great Ape Societies Cambridge University Press, Cambridge, pp. 255-272.
- McGrew, W. C., and Marchant, L. F. (1997). Using the tools at hand: Manual laterality and elementary technology in Cebus spp. and Pan spp. Int. J. Primatol., 18: 787-810.
- McGrew, W. C., and Tutin, C. E. G. (1978). Evidence for social custom in wild chimpanzees? Man 13: 234-251.
- Morris, D. (1967). The Naked Ape, Jonathan Cape, Ltd, London.
- Nakamura, M. (2000). Is human conversation more efficient than chimpanzee grooming?: Comparison of clique size. Human Nature, 11: 281-297.
- Nakamura, M., McGrew, W. C., Marchant, L. F., and Nishida, T. (2000). Social scratch: Another custom in wild chimpanzees? Primates 41: 237-248.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. Primates 9: 167-224.
- Nishida, T. (1970). Social behavior and relationships among chimpanzees of Mahali Mountains. Primates 11: 47-87.
- Nishida, T. (1980). The leaf-clipping display: a newly-discovered expressive gesture in wild

- chimpanzees. J. Hum. Evol., 9: 117-128.
- Nishida, T. (1983a). Alloparental behavior in wild chimpanzees of the Mahale Mountains, Tanzania. Folia Primatol., 41: 1-33.
- Nishida, T. (1983b). Alpha status and agonistic alliance in wild chimpanzees (Pan troglodytes schweinfurthii). Primates 24: 318-336.
- Nishida, T. (1987). Local traditions and cultural transmission. In: Smuts, B. B.; Cheney, D. L.; Seyfarth, R. M.; Wrangham, R. W.; Struhsaker, T. T. (eds.), Primate Societies, University of Chicago Press, Chicago, pp. 462-474.
- Nishida, T. (1988). Development of social grooming between mother and offspring in wild chimpanzees. Folia Primatol. 50: 109-123.
- Nishida, T. (1989). Social interaction between resident and immigrant female chimpanzees. In: Heltne, P. G., and Marquardt, L. A. (eds.), Understanding Chimpanzees, Cambridge Harvard University Press, Cambridge, pp. 68-89.
- Nishida, T. (1990). (ed.) The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies, University of Tokyo Press, Tokyo.
- Nishida, T. (1998). Deceptive tactic by an adult male chimpanzee to snatch a dead infant from its mother. Pan Africa News 5:13-15.
- Nishida, T., Hasegawa, T., Hayaki, H., Takahata, Y., and Uehara, S. (1992). Meat-sharing as a coalition strategy by an alpha male chimpanzee? In: Nishida, T., McGrew, W. C., Marler, P., Pickford, M., and de Waal, F. B. M. (eds.), Topics in Primatology, Vol.1: Human Origins, University of Tokyo Press, Tokyo, pp. 159-174.
- Nishida, T. and Hosaka, K. (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), The Great Ape Societies, Cambridge University Press, Cambridge, pp. 114-134.



- Nishida, T. and Uehara, S. (1981). Kitongwe name of plants: a preliminary listing. Afr. Study Monogr., 1: 109-131.
- Oberski, I. M. (1993). A method for the analysis of grooming reciprocation at the dyadic level. In: Roeder, J. J., Thierry, B., Anderson, J. R., and Herrenschildt, N. (eds.), Current Primatology. Vol. II. Social Development, Learning and Behaviour,
- Parr, L. A., Matheson, M. D., Bernstein, I. S., and de Waal, F. B. M. (1997). Grooming down the hierarchy: allogrooming in captive brown capuchin monkeys, Cebus apella. Anim. Behav. 54 361-367.
- Plooi, F. X. (1984). The Behavioral Development of Free-Living Chimpanzee Babies and Infants, Ablex Publishing Co., Norwood.
- Reynolds, V., and Reynolds, F. (1965). Chimpanzees of the Budongo Forest. In: DeVore, I. (ed.) Primate Behavior, Holt, Rinehart and Winston, New York, pp. 368-424.
- Rowell, T. E., Wilson, C., and Cords, M. (1991). Reciprocity and partner preference in grooming of female blue monkeys. Int. J. Primatol. 12: 319-336.
- Sacks, H., Schegloff, E. A. and Jefferson, G. (1978). A simplest systematics for the organization of turn taking for conversation. In: Schenkein, J. (ed.) Studies in the Organization of Conversational Interaction, Academic Press, New York, pp. 7-55.
- Sade, D. S. (1965). Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. Am. J. Phys. Anthropol. 23: 1-18.
- Savage-Rambaugh, E. S., Rambaugh, D. M., and Boysen, S. (1978). Symbolic communication between two chimpanzees (Pan troglodytes). Science 201:641-644
- Scott, J. (1991) Social Network Analysis: A Handbook, Sage, London.
- Simpson, M. J. A. (1973). The social grooming of male chimpanzees. A study of eleven free-living males in the Gombe Stream National Park, Tanzania. In: Michael, R. P., and Cook,

- J. H.(eds.) Comparative Ecology and Behaviour of Primates, Academic Press, London and N. Y., pp. 411-505.
- Sparks, J. (1967). Allogrooming in primates: a review. In: Morris, D. (eds.), Primate Ethology, Morrison and Gibb Ltd., London, pp. 148-175.
- Sugawara, K. (1984). Spatial proximity and bodily contact among the Central Kalahari San. Afr. Study Monogr. 3: 1-43.
- Sugawara, K. (1998). The 'egalitarian' attitude in everyday conversation among the |Gui. In: Bank, A. (ed.) The Proceedings of the Khoisan Identities and Cultural Heritage Conference, The Institute for Historical Research, Cape, pp. 232-240.
- Sugiyama, Y. (1968). Social organization of chimpanzees in the Budongo Forest, Uganda. Primates 9: 225-258.
- Sugiyama, Y. (1981). Observations on the population dynamics and behavior of wild chimpanzees of Bossou, Guinea, 1979-1980. Primates, 22: 435-444.
- Sugiyama, Y. (1988). Grooming interactions among adult chimpanzees at Bossou, Guinea with special reference to social structure. Int. J. Primatol. 9: 393-407.
- Takahata, Y. (1990a). Adult males' social relations with adult female. In: Nishida, T. (ed.), The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies, University of Tokyo Press, Tokyo, pp. 133-148.
- Takahata, Y. (1990b). Social relationships among adult males. In: Nishida, T. (ed.) The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies, University of Tokyo Press, Tokyo, pp. 149-170.
- Tanaka, I. (1998). Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. Anim. Behav., 56: 1229-1236.
- Tanaka, I., and Takefushi, H. (1993). Elimination of external parasite (lice) is the primary

- function of grooming in free-ranging Japanese macaques. Anthropol. Sci. 101: 187-193.
- te Boekhorst, I. J. A., de Weerth, C., and van Hooff, J. A. R. A. M. (1991). Does scratching signal stress in chimpanzees? In: Social Structure of Three Great Ape Species: an Approach Based on Field Data and Individual Oriented Models, Ph. D. Thesis of te Boekhorst, I. J. A., University of Utrecht, Netherlands, pp. 157-175.
- Tomasello, M., and Call, J. (1997). Primate Cognition, Oxford University Press, Oxford.
- Thierry, B. (1984). Clasp ing behaviour in Macaca tonkeana. Behaviour 89.
- van Hoof, J. A. R. A. M., and van Schaik, C. P. (1994). Male bonds: affiliative relationships among nonhuman primate males. Behaviour 130: 309-337.
- van Lawick-Goodall, J. (1968). The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. 1: 161-311.
- Watts, D. P. (2000a). Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and diversity and grooming reciprocity. Int. J. Primatol. 21: 189-210.
- Watts, D. P. (2000b) Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Influence of male rank and possible competition for partners. Int. J. Primatol. 21: 211-238.
- Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes). J. Comp. Psychol., 112: 270-281.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W., and Boesch, C. (1999). Cultures in chimpanzees. Nature, 399: 682-685.
- Wrangham, R. W., and Smuts, B. B. (1980). Sex differences in the behavioural ecology of chimpanzees in the Gombe National Park, Tanzania. J. Reprod. Fert., Suppl. 28: 13-31.
- Wrangham, R. W., Clark, A. P., and Isabirye-Basuta, G. (1992). Female social relationships

and social organization of Kibale Forest chimpanzees. In: Nishida, T., McGrew, W. C., Marler, P., Pickford, M., and de Waal, F. B. M. (eds.), Topics in Primatology, Vol.1: Human Origins, University of Tokyo Press, Tokyo, pp. 81-98.

Wrangham, R. W., Chapman, C. A., Clark-Arcadi, A. P., and Isabirye-Basuta, G. (1996).

Social ecology of Kanyawara chimpanzees: implication for understanding the costs of great ape groups. In: McGrew, W. C., Marchant, L. F., and Nishida, T. (eds.), The Great Ape Societies, Cambridge University Press, Cambridge, pp. 45-57.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In: Heyes, C. M.; Galef, B. G. (eds.), Social Learning in Animals, Academic Press, San Diego, pp. 221-243.

**Table 3.1 Hours of observation and grooming of focal individuals.**

Names	Sex	Year of Birth <sup>a</sup>	Rank/Status	Kin <sup>b</sup>	Hours of Total Observation	Hours of Grooming <sup>c</sup>	Groom/Obs. (%)
Kalunde	m	1963?	2		29.6	9.5	32.0
Nsaba	m	1973	1		15.7	3.6	23.0
Fanana	m	1978?	3		30.9	4.8	15.6
Hanby	m	1980	5		20.7	3.1	14.7
Dogura	m	1981?	4		31.1	5.6	17.9
Bonobo	m	1981	8		13.7	0.3	2.5
Alofu	m	1982	5	mo, ys, ys	25.5	0.4	1.5
Carter	m	1985	adolescent	mo, yb	24.6	0.7	2.9
Sinsi	m	1985?	adolescent	ys	13.8	1.0	7.3
Darwin	m	1988	juvenile		33.2	2.8	8.3
Gwekulo	f	1962?	cycling		25.8	5.5	21.2
Fatuma	f	1963?	lactating	so, da	22.8	4.3	18.9
Ikocho	f	1965?	lactating	so, da	26.2	4.2	15.9
Nkonbo	f	1970?	cycling		28.0	3.3	11.8
Pinky	f	1972?	cycling	so	26.8	2.9	10.9
Christina	f	1975?	lactating	so	23.2	3.3	14.0
Abi	f	1982	cycling		23.8	4.2	17.8
Serena	f	1987	cycling(adolescent)	mo, ys	21.3	1.9	8.8
Maggy	f	1987	adolescent	ob	22.4	0.6	2.7
Ai	f	1988	juvenile	mo, ob, yb	21.0	1.8	8.5

a. ? indicates estimated years of birth.

b. mo=mother, ob=older brother, yb=younger brother, ys=younger sister, so=son, da=daughter.

c. Only grooming during their focal follow is shown here.

**Table 4.1** Information of 20 focal individuals.

Names	Year of birth <sup>a</sup>	rank/ status	Kin <sup>b</sup>	Total observation (h)
<b>Males</b>				
Kalunde	1963?	2		29.55
Nsaba	1973	1		15.67
Fanana	1978?	3		30.85
Hanby	1980	5		20.74
Dogura	1981?	4		31.10
Bonobo	1981	8		13.72
Alofu	1982	5	mo,ys,ys	25.50
Carter	1985	adolescent	mo,yb	24.63
Sinsi	1985?	adolescent	ys	13.82
Darwin	1988	juvenile		33.19
<b>Females</b>				
Gwekulo	1962?	cycling		25.84
Fatuma	1963?	lactating	so,da	22.80
Ikocha	1965?	lactating	so,da	26.18
Nkonbo	1970?	cycling		28.03
Pinky	1972?	cycling	so	26.84
Christina	1975?	lactating	so	23.22
Abi	1982	cycling		23.75
Serena	1987	cycl.(adol.)	mo,ys	21.30
Maggy	1987	adolescent	ob	22.40
Ai	1988	juvenile	mo,ob,ys	20.95

a ? indicates estimated year of birth.

b "mo"=mother, "ob"=older brother, "yb"=younger brother, "ys"=younger sister, "so"=son, "da"=daughter.

**Table 4.2: Distribution of Clique Sizes for Human Conversation and Chimpanzee Grooming.**

Clique size	Human <sup>a</sup>					Total	Overall %	Chimp <sup>b</sup>	
	Sample 1	Sample 2	Sample 3	Sample 4	Overall %			Overall %	
2	237	231	25	77	570	53.93	84.36		
3	98	93	27	66	284	26.87	13.88		
4	57	44	20	22	143	13.53	1.34		
5	22	16	7	5	50	4.73	0.34		
6	0	3	2	2	7	0.66	0.02		
7	0	1	2	0	3	0.28	0.05		
Average clique size <sup>c</sup>	2.67	2.63	3.28	2.77		2.72	2.18		

a Source: Dunbar et al., 1995. They use 4 samples from different public settings.

b Source: Author's data.

c Calculated as  $\sum (k \times P_k)$ , where  $k$  = clique size and  $P_k$  = proportion of appearance of  $k$ -size clique.

**Table 4.3. Efficiency of Human Conversation Compared with Theoretical Monkey Grooming.**

Clique size	Frequency (%) <sup>a</sup>	Number of arrows <sup>b</sup>		Efficiency <sup>e</sup>
		Human <sup>c</sup>	Monkey <sup>d</sup>	
2	53.93	1	1	1.00
3	26.87	2	1.5	1.33
4	13.53	3	2	1.50
5	4.73	4	2.5	1.60
6	0.66	5	3	1.67
7	0.28	6	3.5	1.71
Average number of arrows <sup>f</sup>		1.72	1.36	1.27

a Source: Dunbar et al., 1995

b An arrow means a social interaction flow.

c For humans, the number of arrows is  $n-1$  when clique size is  $n$ .

d Calculated as the total participants at equal number to clique size of humans.

Therefore, the number of arrows is  $n/2$  when clique size is  $n$  for human.

e The number of arrows of human divided by the number of arrows of monkey.

f Calculated as  $\sum (N_k \times E_k/100)$ , where  $N_k$ = the number of arrows when clique size is  $k$ , and

$E_k$ = Frequency (%) of appearance of  $k$ -size clique.



**Table 4.4** Efficiency of Chimpanzee Grooming Compared with Theoretical Monkey Grooming.

Cliques type <sup>a</sup>	Cliques size	Frequency (%)	Number of arrows <sup>b</sup>		Efficiency <sup>c</sup>
			Chimp <sup>c</sup>	Monkey <sup>d</sup>	
2-1	2	69.44	1	1	1.00
2-2	2	14.92	2	1	2.00
3-1	3	7.40	2	1.5	1.33
3-2	3	2.39	3	1.5	2.00
3-3	3	0.10	3	1.5	2.00
3-4	3	3.98	2	1.5	1.33
4-1	4	0.52	3	2	1.50
4-2	4	0.08	4	2	2.00
4-3	4	0.13	3	2	1.50
4-4	4	0.09	4	2	2.00
4-5	4	0.39	3	2	1.50
4-6	4	0.03	4	2	2.00
4-7	4	0.10	3	2	1.50
5-1	5	0.03	4	2.5	1.60
5-2	5	0.05	4	2.5	1.60
5-3	5	0.05	4	2.5	1.60
5-4	5	0.02	4	2.5	1.60
5-5	5	0.08	4	2.5	1.60
5-6	5	0.09	5	2.5	2.00
5-7	5	0.01	5	2.5	2.00
6-1	6	0.02	5	3	1.67
7-1	7	0.02	6	3.5	1.71
7-2	7	0.03	7	3.5	2.00
Average number of arrows <sup>f</sup>			1.36	1.09	1.25

a See Figure 4.2.

b An arrow means a social interaction flow.

c For chimps, the number of arrows is counted directly from Figure 2.

d Calculated as the total participants at equal number to cliques size of chimps.

Therefore number of arrows is  $n/2$  when cliques size is  $n$  for chimp.

e Number of arrows of chimp divided by the number of arrows of monkey.

f Calculated as  $\sum (N_k \times E_k/100)$ , where  $N_k$ = the number of arrows when cliques type is  $k$ , and  $E_k$ = Frequency (%) of appearance of  $k$ -type cliques.

Table 5.1. Frequency of Scratching and Grooming by M Group.

Names	Year of birth *	Rank of males	Data of WM & LM					Data of MN						
			SG**	GR**	SC**	SS**	GRg(h)**	SSg**	SSg/GRg	GRr(h)**	SSr**	SSr/GRr		
Males														
DE	1963?	2	45	100	83	1	11.66	19	1.63	9.54	84	8.81		
NS	1973	1	93	99	100	7	6.83	7	1.02	5.54	16	2.89		
MA	1977	6	92	37	100	3	3.03	10	3.30	2.94	7	2.38		
FN	1978?	3	58	52	58	8	4.20	17	4.05	8.46	23	2.72		
HB	1980?	6	51	68	100	22	3.69	38	10.30	2.87	7	2.44		
DG	1981?	4	62	53	100	1	9.19	94	10.22	7.59	19	2.50		
BB	1981	8	66	32	71	0	2.00	0	0.00	1.06	3	2.84		
AL	1982	6	100	22	100	4	2.68	6	2.24	4.29	10	2.33		
IW	1982	9	60	45	100	23	1.02	2	1.97	1.25	0	0.00		
CL	1985?	12	51	63	100	4	3.39	2	0.59	1.34	1	0.75		
CT	1985	10	54	8	100	1	1.18	1	0.85	2.88	6	2.08		
SS	1985?	11	43	31	100	0	0.72	0	0.00	0.66	1	1.52		
PM	1988		8	26	27	1	2.91	3	1.03	2.13	5	2.35		
DW	1988		41	30	91	3	2.61	3	1.15	3.56	31	8.70		
PR	1991		6	16	37	0	1.23	0	0.00	2.20	8	3.63		
OR	1991		32	15	52	0	1.20	0	0.00	0.90	0	0.00		
CD	1991		3	3	17	0	0.04	0	0.00	0.24	0	0.00		
XT's inf.	1995						0.00	0	0.00	1.94	1	0.51		
LD's inf.	1996						0.00	0	0.00	0.10	0	0.00		
MJ's inf.	1996						0.00	0	0.00	0.31	18	57.24		
Females														
SL	1955?		1	9	4	0	2.66	2	0.75	1.55	1	0.64		
CA	1960?		21	14	33	2	1.14	0	0.00	1.41	3	2.13		
WX	1961?		23	71	39	1	5.12	4	0.78	9.89	12	1.21		
GW	1962?		57	100	100	0	13.59	3	0.22	4.52	6	1.33		
FT	1963?		34	84	53	2	6.77	19	2.81	2.88	1	0.35		
IK	1965?		43	94	88	7	2.50	4	1.60	4.65	11	2.37		
NK	1970		32	27	80	2	2.34	6	2.57	2.25	8	3.55		

(Continued)

(Table 51. Continued)

OP	1971?	40	55	100	0	1.65	0	0.00	3.43	12	3.50
PI	1972?	47	89	100	5	6.90	7	1.01	3.88	1	0.26
JN	1974?	34	12	86	1	0.13	0	0.00	0.50	0	0.00
XT	1975?	58	91	100	4	6.57	4	0.61	4.38	11	2.51
AA	1977?	7	3	6	0	0.53	1	1.89	0.94	0	0.00
LD	1980?	37	41	78	0	1.10	0	0.00	1.30	2	1.54
MJ	1980?	45	98	44	21	3.32	88	26.54	5.01	11	2.20
AK	1981?	27	35	98	5	3.30	17	5.15	1.97	2	1.02
AB	1982	32	56	100	6	5.93	25	4.22	5.19	29	5.59
TZ	1982	13	28	55	0	6.61	7	1.06	6.10	4	0.66
CY	1982?	28	7	37	0	0.44	0	0.00	1.99	1	0.50
RB	1986	23	38	41	2	0.54	0	0.00	0.80	3	3.74
SY	1987?					0.38	0	0.00	0.24	0	0.00
SE	1987	4	9	30	1	2.68	0	0.00	1.45	0	0.00
MG	1987	15	15	95	0	0.76	0	0.00	0.34	0	0.00
AI	1988	10	51	63	0	2.39	0	0.00	2.37	1	0.42
PP	1990	14	2	40	0	1.26	0	0.00	4.14	12	2.90
CS	1990	21	0	59	0	0.29	0	0.00	1.61	2	1.24
FU	1991	45	51	36	2	0.63	1	1.59	0.76	0	0.00
PE	1993	6	3	11	0	0.39	0	0.00	2.16	14	6.48
IV	1993	6	4	19	0	0.29	1	0.00	1.44	4	2.79
SL's inf.	1994					0.00	0	0.00	0.39	0	0.00
AA's inf.	1995					0.00	0	0.00	0.04	0	0.00
JN's inf.	1995					0.00	0	0.00	0.02	0	0.00
WX's inf.	1996					0.00	0	0.00	0.37	0	0.00
TZ's inf.	1996					0.00	0	0.00	0.02	0	0.00
Total		1588	1787	2931	139	137.77	391		137.77	391	

\* ? indicates estimated years.

\*\* SG=Self(Auto)-Groom; GR=Social Groom (GRg = GR given, GRr = GR received); SC = Self(Auto)-Scratch;

SS = Social-Scratch (SSg = SS given, SSr = SS received)

Table 5.2. Observation Hours, Frequency of Social Scratching, and Duration of Grooming of Focal Targets of MN  
(Data from Nov. 1996-May 1997 shown here).

Names	SSg*	SSr**	obs.time(h)	SSg/obs.	SSr/obs	GR* time(h)	SSg/GR	SSr/GR
<b>Males</b>								
NS	4	2	8.23	0.49	0.24	1.52	2.63	1.32
DE	9	54	23.22	0.39	2.33	7.36	1.22	7.34
FN	13	12	21.07	0.62	0.57	3.57	3.65	3.37
DG	27	10	20.28	1.33	0.49	4.57	5.91	2.19
HB	20	6	17.78	1.12	0.34	2.08	9.63	2.89
BB	0	0	0.00	0.00	0.00	0.00	-	-
AL	0	2	18.00	0.00	0.11	0.36	0.00	5.62
CT	1	0	18.08	0.06	0.00	0.71	1.41	0.00
SS	0	0	8.92	0.00	0.00	0.73	0.00	0.00
DW	0	20	27.07	0.00	0.74	2.54	0.00	7.88
<b>Females</b>								
IK	3	9	15.07	0.20	0.60	2.08	1.44	4.32
FT	4	1	13.15	0.30	0.08	1.60	2.50	0.63
PI	3	0	14.43	0.21	0.00	1.28	2.34	0.00
GW	2	2	21.57	0.09	0.09	4.03	0.50	0.50
XT	1	0	17.80	0.06	0.00	1.80	0.56	0.00
NK	5	8	20.32	0.25	0.39	2.71	1.85	2.96
AB	12	22	16.75	0.72	1.31	2.88	4.16	7.63
MG	0	0	13.50	0.00	0.00	0.17	0.00	0.00
AI	0	1	12.55	0.00	0.08	0.67	0.00	1.49
SE	0	0	12.93	0.00	0.00	0.24	0.00	0.00
<b>Total</b>	<b>104</b>	<b>149</b>	<b>320.72</b>	<b>0.32</b>	<b>0.46</b>	<b>40.88</b>	<b>2.54</b>	<b>3.64</b>

\* For abbreviations see Table 5.1.

## FIGURE LEGENDS

**Fig. 3.1. Examples of grooming status indices of individuals.**

**Fig. 3.2. All types<sup>a</sup> of grooming cliques observed during the study.**

<sup>a</sup> I have already shown the preliminary list of types and frequencies of grooming cliques in Nakamura (2000), where I only showed data of clusters that lasted more than 30 minutes because the main topic of the study was comparisons with human conversation cliques.

**Fig. 3.3. Proportion of each grooming clique type<sup>a</sup> for chimpanzees and Assamese macaques<sup>b</sup>.**

<sup>a</sup> For grooming clique types, see Fig. 3.2.

<sup>b</sup> Data from Cooper and Bernstein (2000). Cliques of 3 and 4 individuals probably correspond to clique type [4] and type [10] in Fig. 3.2., respectively, not to [3] and [7], because they stated “multiple animals sometimes groomed a single recipient.”

**Fig. 3.4. Individual grooming status observed during the study period.**

Numbers indicate corresponding grooming status indices. Circles in the figure indicate individuals, and arrows indicate the flow of grooming interaction.

**Fig. 3.5. Proportion of each grooming status<sup>a</sup> of chimpanzees in different age-sex classes and that of Assamese macaques<sup>b</sup>.**

<sup>a</sup> For grooming status indices see Fig. 3.4.

<sup>b</sup> Original data from Cooper and Bernstein (2000). Statuses are reconstructed from the clique types. Cliques with 3 individuals are treated as [4] and cliques with 4 individuals as [10], although the authors did not specify clearly this.

**Fig. 3.6. Proportion of each size of grooming clusters with three measures: the number of events (left), gross duration (middle), and net duration (right).**

For details on the three measures, see text.

**Fig. 3.7. Duration of grooming among age-sex classes per dyad in different sizes of grooming clusters.**

**Fig. 4.1. Two models of efficiency of human conversation over theoretical monkey grooming when the clique size is four in conversation.**

Circled letters indicate individuals and black arrows indicate social interaction (grooming or conversation) flows. In 4.1-b, the flow of the time is indicated with large white arrows. One box indicates a certain period of time after which role alternation takes place.

**Fig. 4.2. All types of chimpanzee grooming cliques observed.**

Circles indicate individuals and arrows indicate direction of grooming.

**Fig. 5.1. Typical Social Scratch (Photo by L. F. Marchant).**

**Fig. 5.2 Total Number of Social Scratches in each Combination of Age-Sex Classes Plotted against Total Duration of Grooming in the Combination.**

Letters in the figure indicate combinations of the classes. The first of the two letters indicates the giver of social scratches and grooming, and the second indicates the recipient of these behaviors; where **M**=mature males, **L**=lactating females, **C**=cycling females, **Y**=youngsters. Therefore **LY**, for example, means value of social scratches (in y axis) and grooming (in x axis) that lactating females gave to youngsters. The line in the figure indicates expected number of social scratches when we assume the distribution of them equals to that of grooming duration.

**Fig. 5.3. Percentage of Body Parts by Scratcher.**

Body parts combined as follows; back=[back, waist, hip], front=[belly, chest, armpit], shoulder=[shoulder], limb=[arm, hand, leg, thigh, foot], head=[head, face, neck].

**Fig. 5.4. Percentage of Body Parts by Recipient.**

**Fig. 5.5. Percentage of Right-Preferent Social Scratch.**

Only individuals who social scratched often enough for Binomial testing ( $N > 6$ ) are shown. Number in parenthesis indicates (right-handed / right-handed + left-handed).  
"\*L" and "\*R" indicate individuals who are significantly left-preferent, and right-preferent respectively, all others are ambi-preferent.

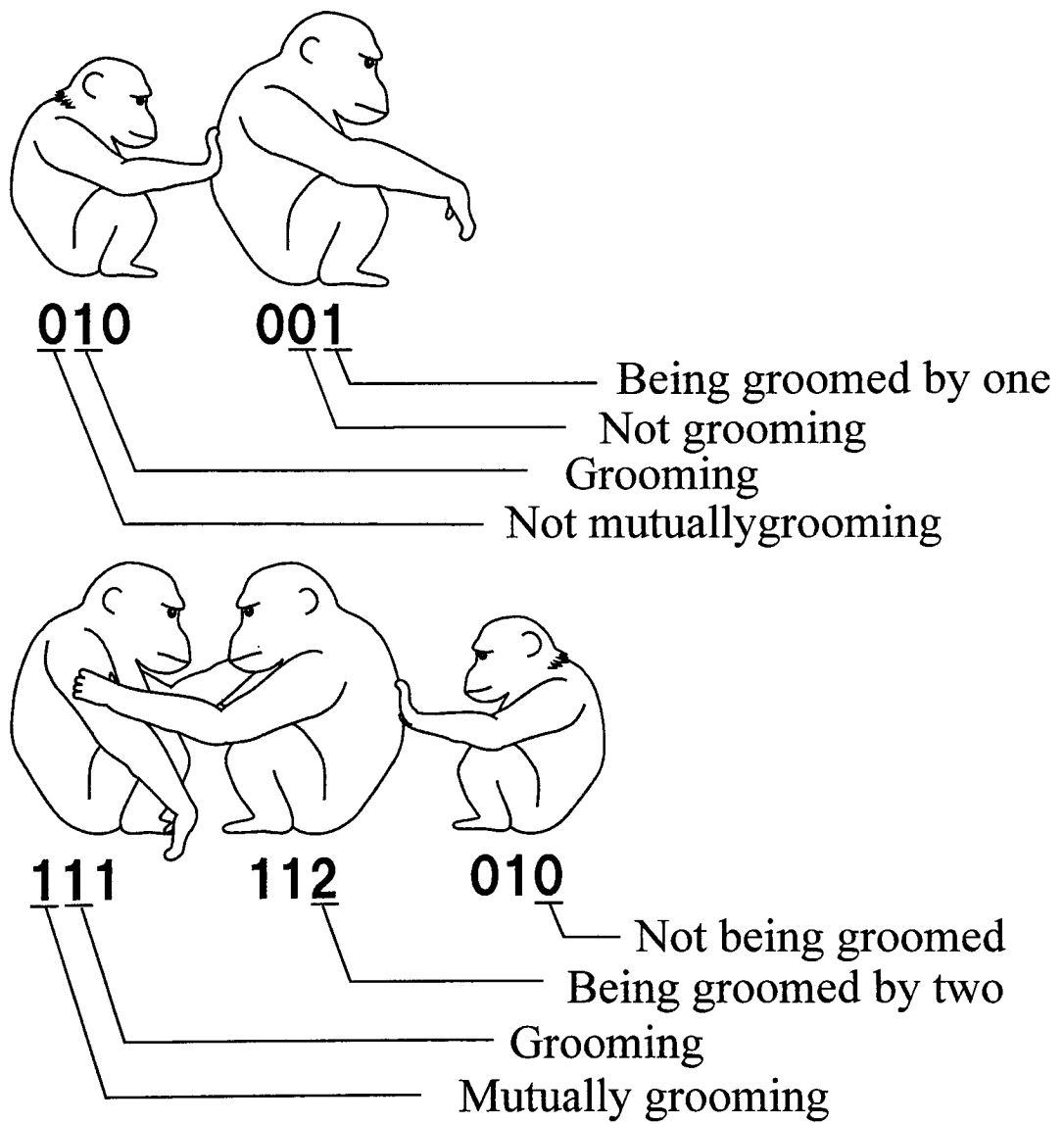


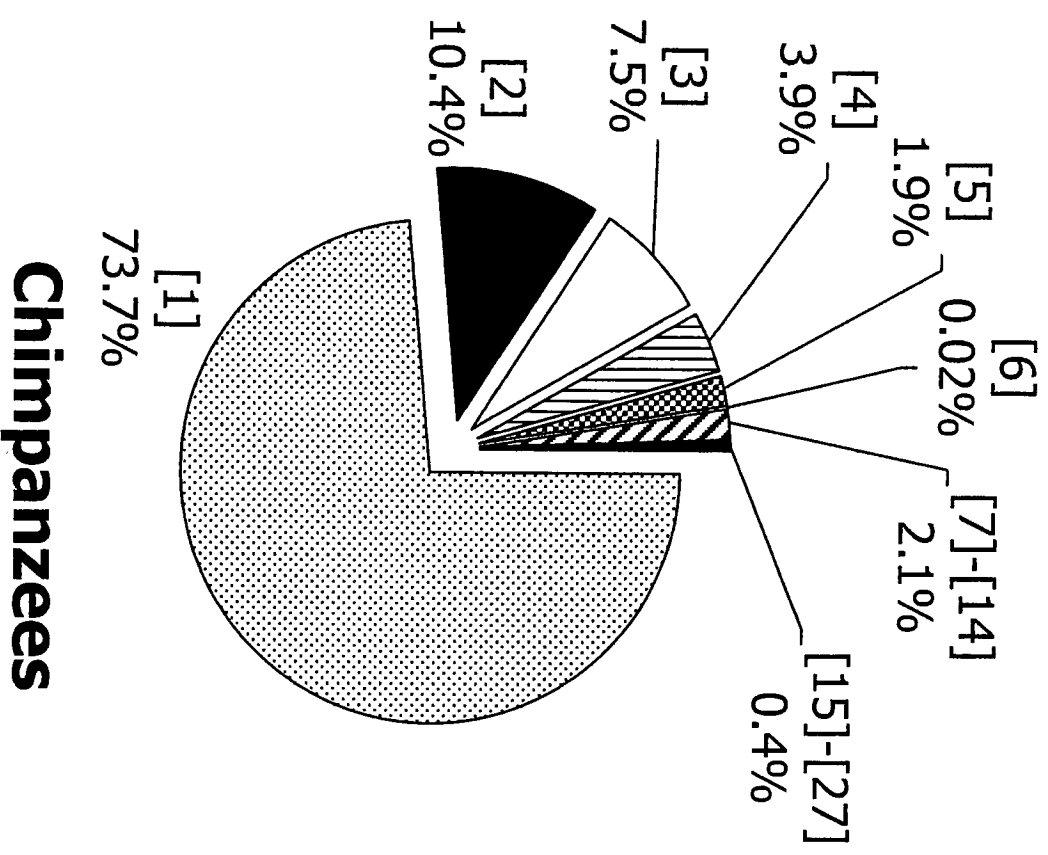
Fig 3 1.



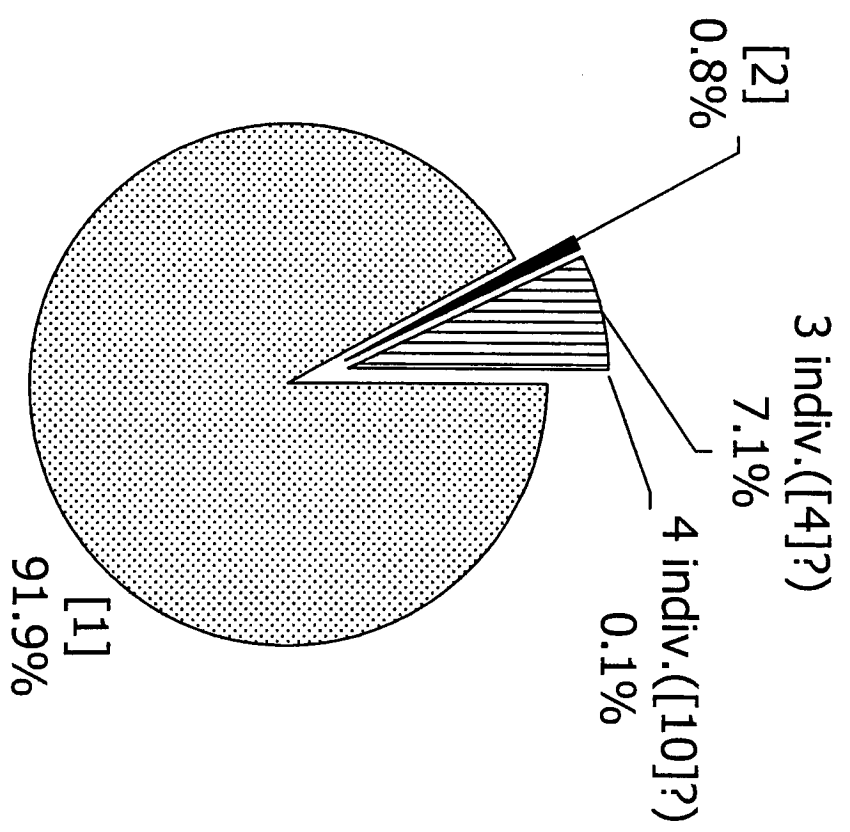
# Individuals	Clique Types		
2	[1]	[2]	
	[3]	[5]	[6]
3	[4]		
	[7]	[11]	[14]
	[8]	[12]	
	[9]	[13]	
4	[10]		

# Individuals	Clique Types	
5	[15]	[21]
	[16]	
	[17]	[22]
	[18]	[23]
	[19]	
	[20]	[24]
	[25]	[26]
6		
7	[27]	

Fig 3 2.



**Chimpanzees**



**\*Assamese macaques**

Fig 3 3.


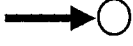

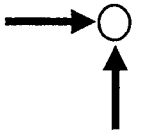
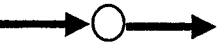

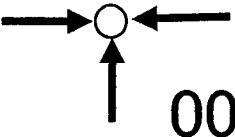
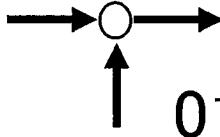
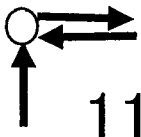
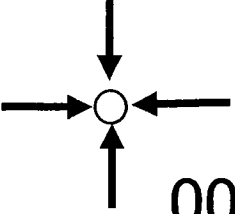
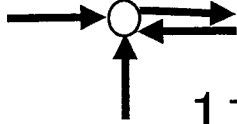
# of interactions	Grooming Status		
0	 000		
1	 001	 010	
2	 002	 011	 111
3	 003	 012	 112
4	 004		 113

Fig 3 4

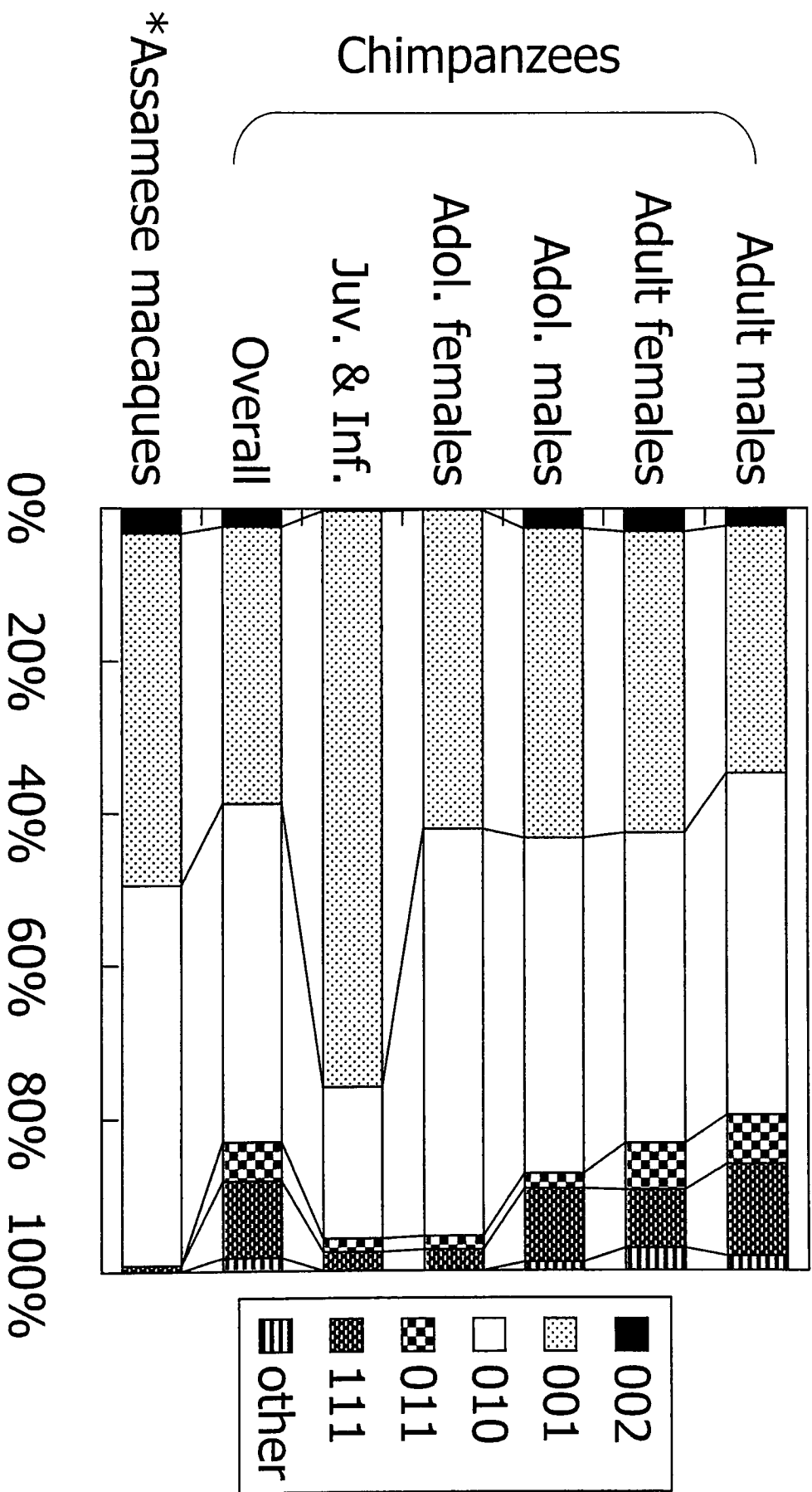


Fig 3.5

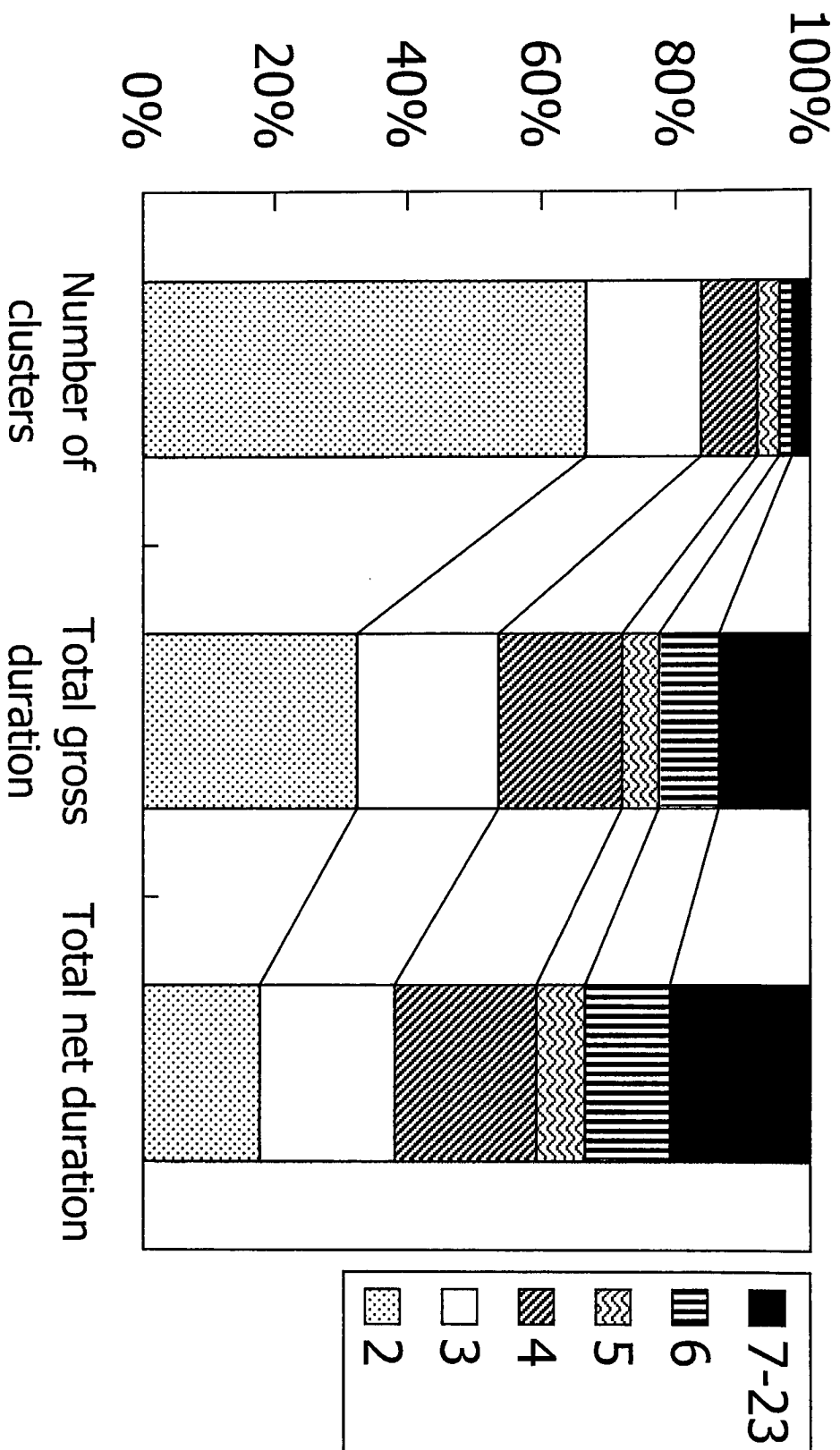


Fig. 3.6

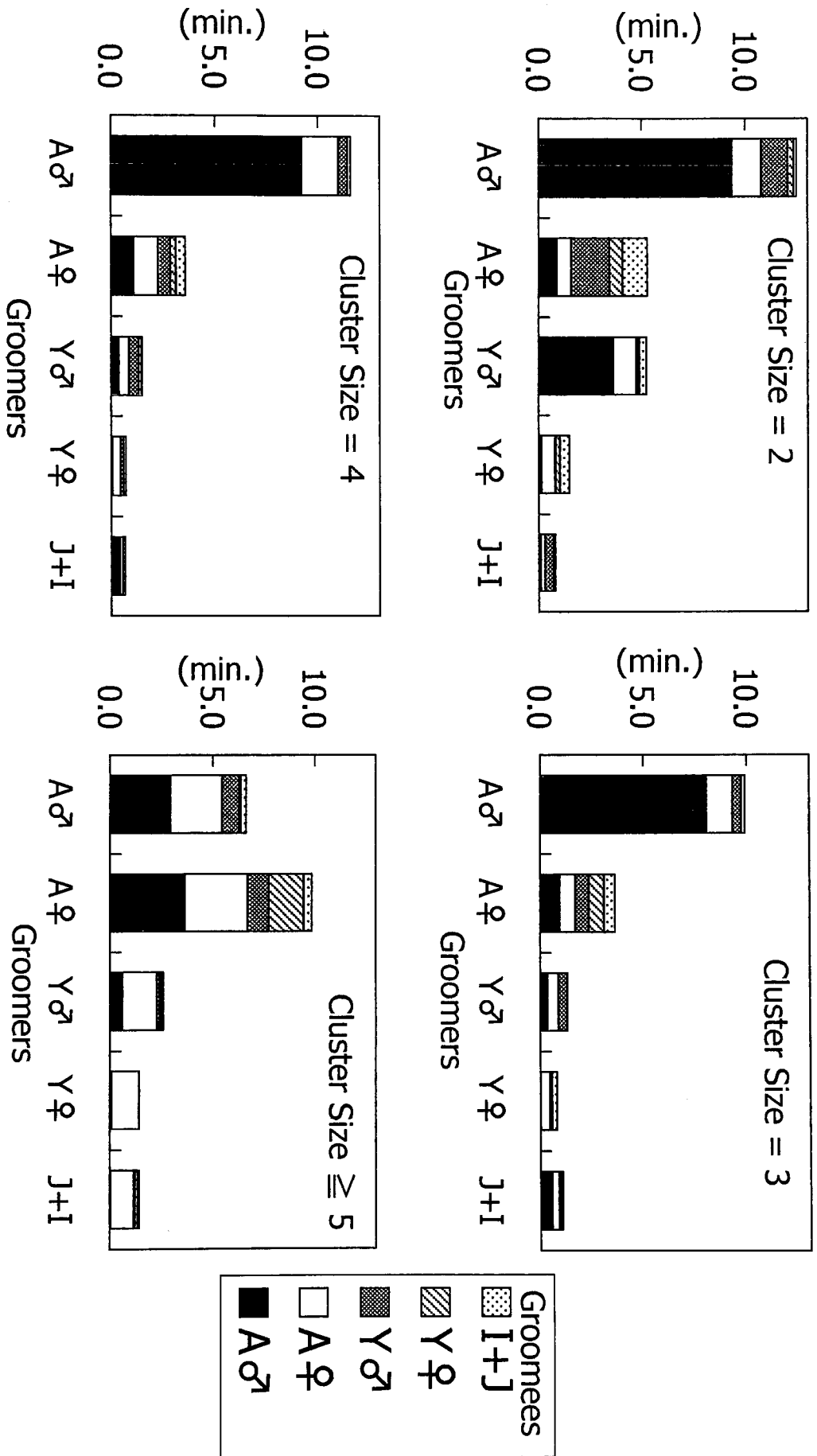


Fig 37

	<b>Role Alternation Model.</b>				
	<b>a. Dunbar's Model</b>	<b>b.</b>			
<b>Theoretical Monkey Grooming</b>	 A → B	 A → B, B → A, C → D, D → C			
<b>A's perspective</b>	<b>Actor to B.</b>	<b>Actor to B.</b>	<b>Recipient of B.</b>	<b>Actor to C.</b>	<b>Recipient of C.</b>
<b>Conversation</b>	 A → B, C, D	 A → B, C, D B → A, C, D C → A, B A → C, B → C D → A, B			
<b>A's perspective Ratio of Arrows for A.</b>	<b>Actor to B, C, D.</b>  1:3	<b>Actor to B, C, D.</b>  <b>4:6 = 2:3</b>			

Fig 4 1

Number of Participants	Not Including Mutual Grooming	Including Mutual Grooming	Circle
2	2-1 	2-2 	
3	3-1 	3-2 	3-3 
4	4-1 	4-2 	
	4-3 	4-4 	
	4-5 	4-6 	
	4-7 		

Fig 4.2

Number of Participants	Not Including Mutual Grooming	Including Mutual Grooming
5	5-1 	
	5-2 	
	5-3 	
6	6-1 	
	6-2 	
	6-3 	
7	7-1 	
	7-2 	
	7-3 	





Fig 5 1

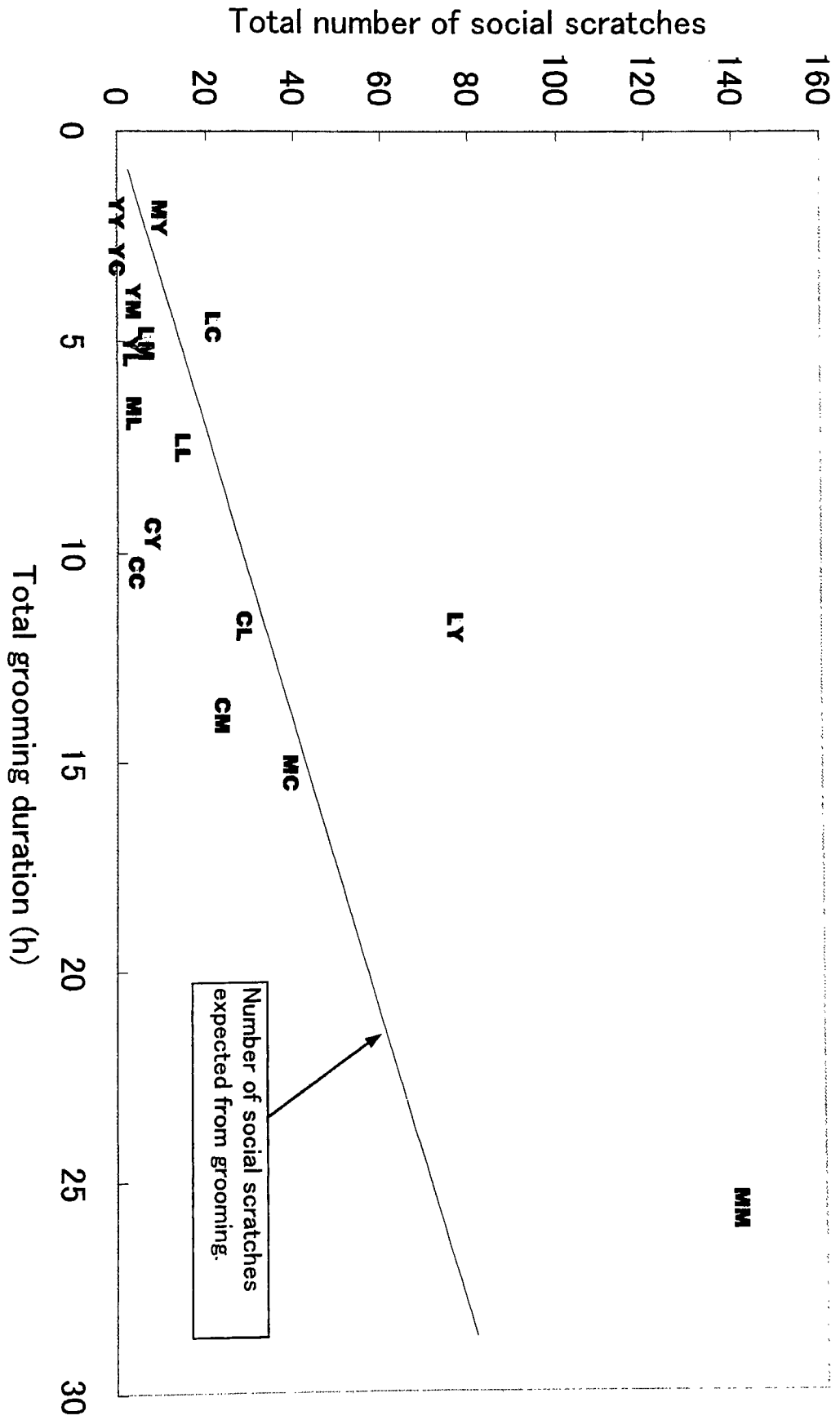


Fig. 5 2

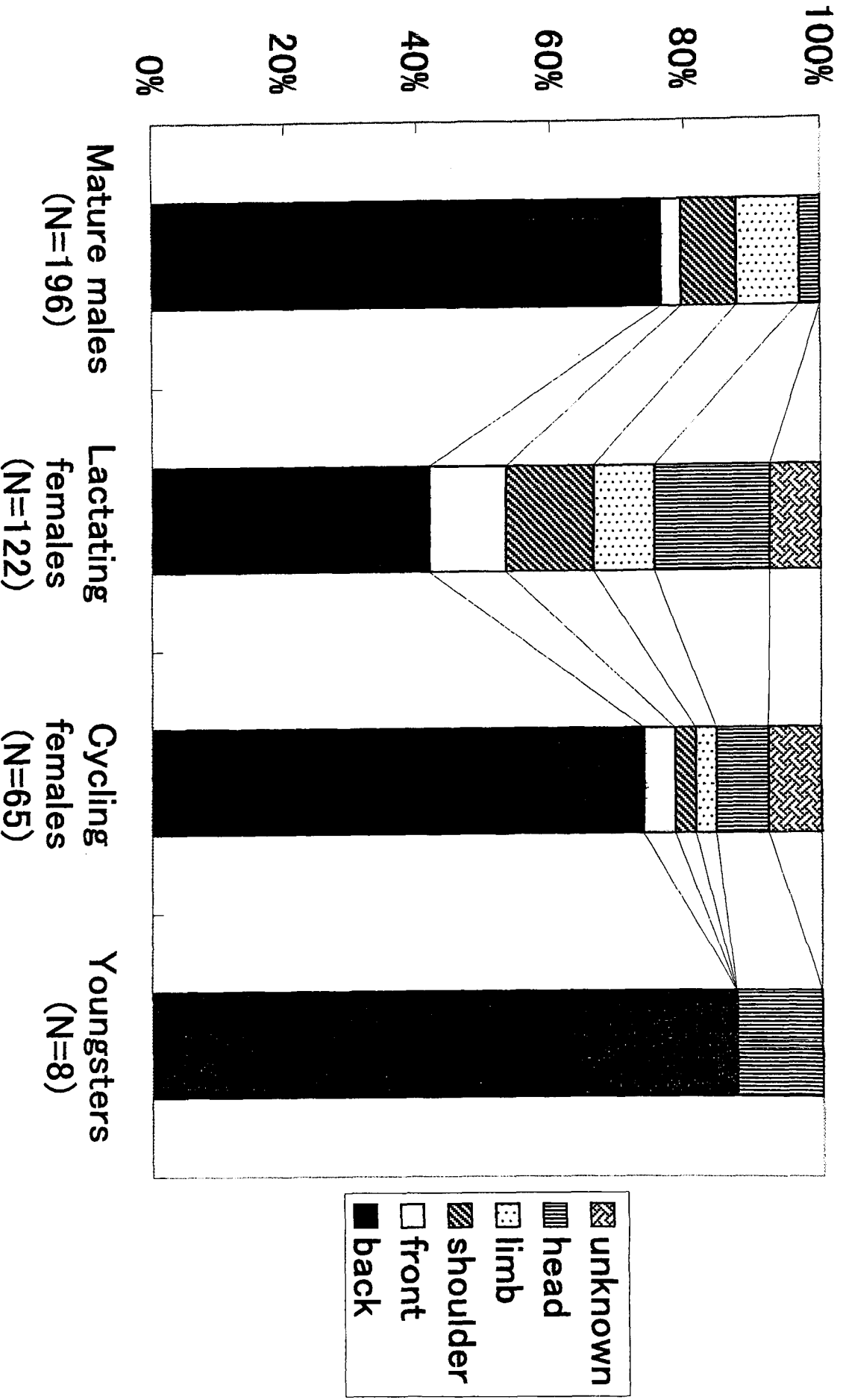


Fig. 5 3

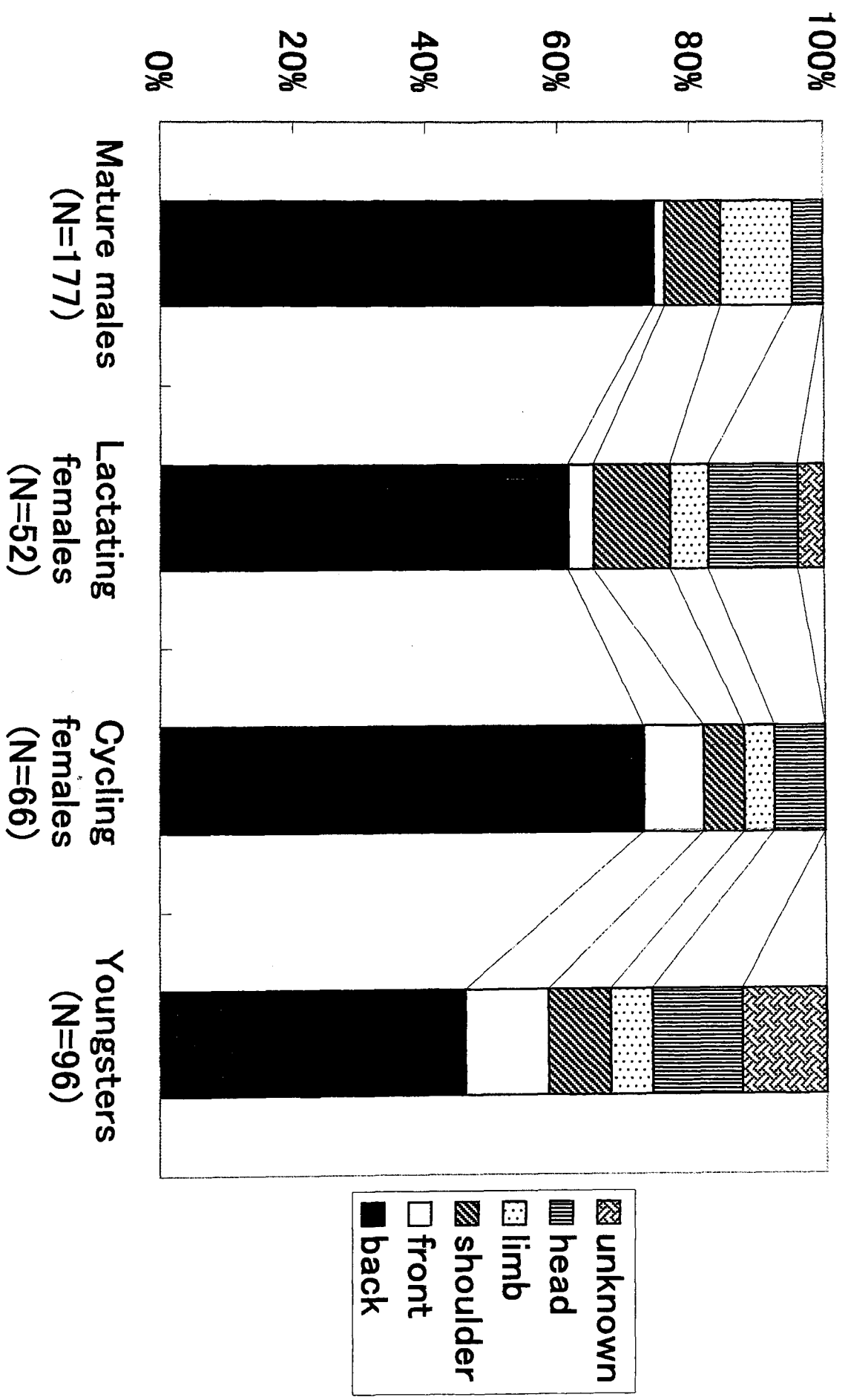


Fig. 5 4

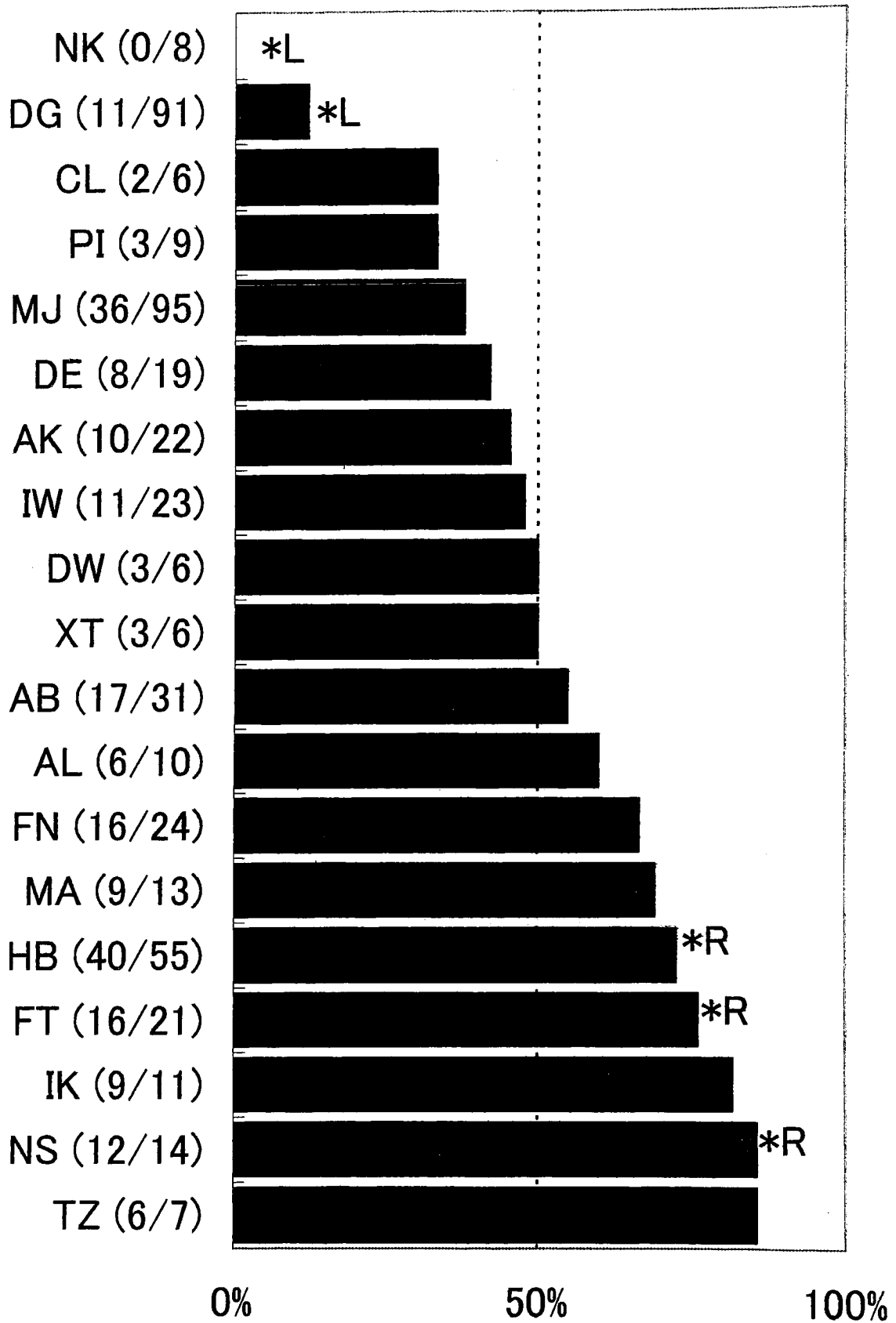


Fig 5.5.