Nakamura M (2000) Is human conversation more efficient than chimpanzee grooming?: comparison of clique sizes. *Human Nature* 11: 281–297. DOI 10.1007/s12110-000-1014-2

Is Human Conversation More Efficient than Chimpanzee Grooming? Comparison of Clique Sizes

Michio Nakamura
Kyoto University

ABSTRACT

Clique sizes for chimpanzee (*Pan troglodytes*) grooming and for human conversation are compared in order to test Robin Dunbar's hypothesis that human language is almost three times as efficient a bonding mechanism as primate grooming. Recalculation of the data provided by Dunbar et al. (1995) reveals that the average clique size for human conversation is 2.72 whereas that of chimpanzee grooming is shown to be 2.18. The efficiency of human conversation and actual chimpanzee grooming over Dunbar's primate grooming model (always one-to-one and a one-way interaction) is 1.27 and 1.25, respectively, when we take role alternation into account. Chimpanzees can obtain about the same efficiency as humans in terms of quantity of social interactions because their grooming is often mutual and polyadic.

Key Words: Bonding mechanisms; Chimpanzees (*Pan troglodytes*); Clique size; Conversation; Efficiency; Grooming.

DUNBAR'S THEORY OF THE EFFICIENCY OF LANGUAGE

Most primate species show social grooming (or allogrooming) behavior (Goosen 1987; Sparks 1967). The original function of grooming may have been hygienic, in that monkeys remove ectoparasites and other debris from each other's 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., Goodall 1986; Goosen 1987; Morris 1967).

Robin Dunbar, not stopping at a mere analogy, was the first to compare grooming and conversation theoretically and quantitatively. He hypothesized that human language evolved as a better bonding mechanism when our ancestors faced difficulties in bonding through conventional primate grooming (Dunbar 1996). 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 neocortical volume (relative to whole brain volume; Dunbar 1992). Larger groups require more complex levels of association and coalitions because of increased intra-group competition and aggression. He also estimated that the upper limit for social time would be about 20% of the daytime whereas humans would need 42% if we used conventional primate grooming for bonding, given our group sizes (Dunbar 1993). Therefore, sometime in the course of the evolution of larger brains, which is also related to the increase in group size, our ancestors had to find a more efficient bonding mechanism than primate grooming. In his hypothesis, language was the mechanism we acquired. He also emphasizes other social aspects of language, such as the fact 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 supports the above predictions by comparing the efficiencies of human language and primate grooming. Among nonhuman primate species, chimpanzees (*Pan troglodytes*) have the largest mean group size at about 53.5; 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 1993:690). Here, by "efficiency" he means "the number of interactants that can be simultaneously reached during social interaction" (1993:689–690). Then, Dunbar et al. (1995) counted clique sizes of human conversational groups 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 1993:690) (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: 122).

CLIQUE SIZE FOR 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 not discussing any other options 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→B→C or A→B→C. Cooper and Bernstein (2000) observed 385 triadic episodes, 5 quadratic episodes, and 45 mutual episodes in a total of 5,397 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), M. mulatta (Boccia 1983; Sade 1965), *M. nemestrina* and *radiata* (Kaufman and Rosenblum 1966), *Presbytis entellus* (McKenna 1978), and *Cebus apella* (Parr et al. 1997). However, these studies only report that such grooming sometimes or rarely occurs, and the authors simply divided them into dyadic episodes for analysis (for example, A→B→C is divided into A→B and B→C). Moreover, the above reports provide no data on frequency.

Unlike baboons or macaques, chimpanzees often form 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; Oberski 1993; Takahata 1990a, 1990b). When estimating efficiency, Dunbar compared group size of chimpanzees with that of humans because chimpanzees have the largest mean group size among nonhuman primates. However, he did not compare human conversation with chimpanzee grooming. Perhaps the data on chimpanzee polyadic grooming were not available because this kind of grooming is also often divided into dyadic occurrences in chimpanzee studies (e.g., Nishida 1988). These characteristics of chimpanzee grooming are important when we compare clique sizes. Furthermore, the chimpanzee is genetically one of the closest species to humans (Caccone and Powell 1989) and also they show the highest intelligence among nonhuman primates as well as some language ability in laboratory studies (Kojima 1984; Savage-Rumbaugh et al. 1978).

It is difficult to say whether grooming and conversation clique sizes can be directly compared in the way Dunbar did. And even under the assumption that they can, is conversation really three times more efficient than chimpanzee grooming? In the next section, I will point out a few simple mistakes in Dunbar's calculation of the efficiency of conversation in relation to primate grooming. In the following section, I will compare clique sizes of chimpanzee grooming, based on my own data, with the data on human conversation cliques provided in Dunbar et al. 1995.

METHODS

The field observation was conducted on a wild chimpanzee (*P. t. schweinfurthii*) group (M group) in Mahale Mountains National Park, Tanzania, between July 1996 and May 1997. For detailed information about the research site, see Nishida 1990. I selected 10 males and 10 females as focal target individuals (Table 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 grooming status (i.e., started grooming, stopped grooming, or changed partners). Grooming comprises 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 were not included in the analysis. A grooming cluster is defined as a gathering of individuals who exhibit at least one grooming behavior. A cluster begins when one or some individuals begin to groom and ends when no individuals have groomed for more than five minutes. Because some data are incomplete, I only use the 38 sets of complete grooming clusters that were observed from beginning to end. I only analyzed clusters that lasted more than 30 minutes because shorter grooming is often used as a token (Goodall 1986). Total duration of these complete grooming clusters is about 30 hours.

Dunbar and colleagues (1995) collected their data at cafeterias and receptions in which conversation would last for extended periods. Therefore, their data are also likely free of brief conversations such as greetings when two persons meet on the street.

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 is the "groomer," while in conversation he or she is the "speaker." In this article both of these types of individuals are referred to as "actors."

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

RESULTS

Average Clique Size for Human Conversation

Dunbar argued that because usual primate grooming is one-to-one (i.e., clique size is two) whereas clique size for human conversation is four, human conversation is three times more efficient than grooming (Dunbar 1996:121). This clique size of four seems to be derived from the 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. 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; it 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) reveal that the average clique size for human conversation is 2.72 (Table 2). This means that there are 1.72 recipients for one actor on average; therefore, human conversation is only 1.72 times more efficient on average than grooming as modeled by Dunbar.

Role Alternation Model

Dunbar does not seem to have taken role alternation into account. He argues that conversation is three times more efficient than grooming when conversational clique size is four. This seems true when we count the number of arrows representing social interaction in Figure 1a. There are three recipients of conversation from individual A, but only one recipient in Dunbar's grooming model. If we only consider 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; instead A has to be in the role of recipient while others are playing the actor's role. In Figure lb, 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 and direct his conversation toward 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 four arrows in this certain amount of time. In conversation, A can have six 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 in Dunbar's grooming model in which clique size is always two. In Figure 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 in Dunbar's model, the number of arrows becomes n/2. Therefore, the efficiency of conservation over grooming is 2(n - 1)/n.

Chimpanzee Grooming Cliques

Dunbar's model of primate grooming (1993,1996) makes intuitive sense because it seems impossible for an actor to groom multiple recipients simultaneously, whereas a speaker routinely has multiple listeners. However, a recipient can be groomed by multiple actors or an individual can play both an actor's role and a recipient's role at the same time, as is quite common in chimpanzees.

Figure 2 shows the types of chimpanzee grooming cliques actually observed. There were 23 patterns, the largest of which involved seven participants. The frequencies of these cliques are shown below in Table 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 interactions) is two even when clique size is two. If the issue is the efficiency of social interaction, mutual grooming is twice as efficient as normal grooming even though the number of participants remains the same.

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 with more than three accounted for 15% of the patterns observed. The largest clique size for chimpanzee grooming (7) was the same as that for human conversation. The average clique size for chimpanzee grooming was 2.18 (Table 2), while that for human conversation was 2.72, as we have seen earlier.

Table 3 compares the efficiency of human conversation with that of grooming in Dunbar's model while taking the effect of role alternation into account. Overall, the average number of arrows in human conversation is 1.72, while it is 1.36 in the grooming model. Thus, human conversation is only 1.27 (1.72 / 1.36) times more efficient than grooming.

Table 4 compares the efficiency of chimpanzee grooming with that of Dunbar's grooming model in the same way as in Table 3. The average number of arrows is 1.36 for chimpanzee grooming and 1.09 for Dunbar's model. Consequently, chimpanzee grooming is 1.25 (1.36 / 1.09) times more efficient than Dunbar's model. Both human conversation and chimpanzee grooming are 1.2-1.3 times more efficient than Dunbar's model.

DISCUSSION

Most studies of language evolution emphasize its special features, for example its ability to express abstract meaning or refer to things that are not present by using complex vocalization and syntax. If we see only these complex and special features of language, communication of nonhuman primates is far from comparable. However, primitive but very basic features of language seem to be forgotten or taken for granted. Conversation (which is made with language) is without doubt the most common form of social interaction among humans. Although much information is usually contained in conversation, do we not often talk just for its own sake? In such conversation, the aspect of conveying information becomes minor, and the bonding or maintaining of social relationships aspect is considerable. Furthermore, this bonding mechanism exists even when language conveys information. The most common social interaction exhibited by our close relatives the nonhuman primates is grooming. In this respect Dunbar's work is quite valuable. He compared primate grooming and human conversation from the viewpoint that both have the same function of making social bonds among individuals in a group.

According to Dunbar, one of the major reasons for the evolution of language is that language is three times more efficient than primate grooming as a means of social bonding. However, 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 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 chimps 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 the monkeys in Dunbar's model, but often mutually and polyadically. These characteristics of chimpanzee grooming also make their grooming cliques quite diverse, as we have seen in Figure 2. It is not clear whether mutual and polyadic grooming really occurs less often in other primates than in chimpanzees because there are very limited descriptions of mutual grooming and polyadic grooming for species other than chimpanzees. However, in most of these descriptions (Boccia 1983; Furuya 1957; Kaufman and Rosenblum 1966; McKenna 1978; Sparks 1967), primates are said to groom mutually or polyadically only sometimes or rarely. The scarcity of this kind of description may imply that these occurrences themselves are rare. Perhaps other species 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. It is also possible that some set of cognitive abilities is required 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 for food (de Waal 1997), using deceptive tactics (Nishida 1998), and in many other social situations (e.g., Goodall 1986). The "cultural" diversity in chimpanzee grooming (McGrew and Turin 1978; Nakamura et al. 2000) implies that their grooming is more socially determined than that of other primates. Perhaps the various patterns of cliques are also related to this kind of complex use of grooming.

One would think that primate grooming and human conversation are intrinsically different because, for example, chimpanzees can groom each other simultaneously whereas humans cannot do so in conversation. This is nearly true for English-speaking people (Sacks et al. 1978) and perhaps for Japanese as well. In these cultures, the speakers must alternate in a way quite similar to the way in which the monkeys in Dunbar's model 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 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 communication, the efficiency of human conversations would become greater. However, no such data are available thus far. At this point, data on clique sizes 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, these are not the only mechanisms, nor are they incompatible. For example, in bonobos (*Pan paniscus*), female estrus is prolonged (Furuichi 1992) and sexual behavior has some aspects of a group bonding mechanism apart from its reproductive function (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 have evolved only for their own sake. As for humans, we can think of various bonding mechanisms, such as conversation, sexual or nonsexual contact, co-feeding, exchange of goods, eye contact, and facial expressions. 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.

The fieldwork was supported by a grant from the International Scientific Research Program (07041138 to T. Nishida) of the Monbusho (Japanese Ministry of Education, Science, Sports, and Culture). I would like to express my thanks to the Tanzania Commission for Science and Technology (COSTECH), Serengeti Wildlife Research Institute (SWRI), Tanzania National Parks (TANAPA), Mahale Mountains Wildlife Research Centre (MMWRC), and Mahale Mountains National Park (MMNP) for permission to do the research. Thanks are also due to K. Kawanaka, S. Uehara, H. Sasaki, W. C. McGrew, L. F. Marchant, R. Kitopeni, M. B. Kasagula, M. Matumula, and K. Athumani for cooperation in the field. I also express gratitude to F. Fukuda, T. Nemoto, and H. Kayunbo for their help in various ways in Tanzania; T. Nishida and G. Yamakoshi for comments on an early version of the manuscript; and all the members of the Laboratory of Human Evolution Studies, Kyoto University for useful comments and suggestions. Michio Nakamura is a research fellow at Japan Monkey Centre. He received his Master of Science degree from Kyoto University in 1996. He is carrying out research on the grooming behavior of chimpanzees at Mahale, Tanzania, for his doctorate.

REFERENCES

Boccia, M. L.
1983 A Functional Analysis of Social Grooming Patterns through Direct Comparison with Self-Grooming in Rhesus Monkeys. *International Journal of Primatology* 4:399–418.

Caccone, A., and R. Powell
1989 DNA Divergence among Hominoids. *Evolution* 43:925–942.

Cooper, M. A., and I. S. Bernstein
2000 Social Grooming in Assames Macaques (*Macaca assamensis*). *American Journal of Primatology* 50:77–85.

de Waal, F. B. M.
1989 *Peacemaking among Primates*. Cambridge: Harvard University Press.
1997 The Chimpanzee's Service Economy: Food for Grooming. *Evolution and Human Behavior* 18:375–386.

Dunbar, R. I. M.
1991 Functional Significance of Social Grooming in Primates. *Folia Primatologica* 57:121–131.
1992 Neocortex Size as a Constraint on Group Size in Primates. *Journal of Human Evolution* 20:469–493.
1993 Coevolution of Neocortical Size, Group Size and Language in Humans. *Behavioral and Brain Sciences* 16:681–735.
1996 *Grooming, Gossip and Evolution of Language*. Cambridge: Harvard University Press.

Dunbar, R. I. M., N. D. C. Duncan, and D. Nettle
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 *Topics in Primatology, Vol. 2: Behavior, Ecology, and Conservation*, N. Itoigawa, Y. Sugiyama, G. P. Sackett, and R. K. R. Thompson, eds. Pp. 179–190. Tokyo: University of Tokyo Press.

Furuya, Y.
1957 Grooming Behavior in Wild Japanese Monkeys. *Primates* 1:47-68.

Goodall, J.
1986 *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press.

Goosen, C.
1987 Social Grooming in Primates. In *Comparative Primate Biology, Vol. 2B: Be-havior, Cognition, and Motivation*, G. Mitchel and J. Erwin, eds. Pp. 107–131. New York: Alan R. Liss.

Kano, T.
1992 *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford: Stanford University Press.

Kaufman, I. C., and L. A. Rosenblum
1966 A Behavioral Taxonomy for *Macaca nemestrina* and *Macaca radiata*: Based on Longitudinal Observation of Family Groups in the Laboratory. *Primates* 7: 205–258.

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.

McGrew, W. C., and C. E. G. Tutin
1978 Evidence for Social Custom in Wild Chimpanzees? *Man* 13:234–251.

McKenna, J.
1978 Biosocial Functions of Grooming Behavior among the

Common Indian Langur Monkey (*Presbytis entellus*). *American Journal of Physical Anthropology* 48:503–510.

Morris, D.
1967 *The Naked Ape*. London: Jonathan Cape.

Nakamura, M., W. C. McGrew, L. F. Marchant, and T. Nishida
2000 Social Scratch: Another Custom in Wild Chimpanzees? *Primates* 41 (in press).

Nishida, T.
1988 Development of Social Grooming between Mother and Offspring in Wild Chimpanzees. *Folia Primatologica* 50:109–123.
1998 Deceptive Tactic by an Adult Male Chimpanzee to Snatch a Dead Infant from Its Mother. *Pan Africa News* 5:13–15.

Nishida, T., ed.
1990 *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*. Tokyo: University of Tokyo Press.

Oberski, I. M.
1993 A Method for the Analysis of Grooming Reciprocation at the Dyadic Level. In *Current Primatology, Vol. II: Social Development, Learning and Behaviour*, J. J. Roeder, B. Thierry, J. R. Anderson and N. Herrenschmidt, eds. Pp. 175–183 Strasbourg: University Louis Pasteur.

Parr, L. A., M. D. Matheson, I. S. Bernstein, and F. B. M. de Waal
1997 Grooming down the Hierarchy: Allogrooming in Captive Brown Capuchin Monkeys, *Cebus apella*. *Animal Behaviour* 54:361–367.

Sacks, H., E. A. Schegloff, and G. Jefferson
1978 A Simplest Systematics for the Organization of Turn Taking for Conversation. In *Studies in the Organization of Conversational Interaction*, J. Schenkein, ed. Pp. 7–55. New York: Academic Press.

Sade, D. S.
1965 Some Aspects of Parent-Offspring and Sibling Relations in a Group of Rhesus Monkeys, with a Discussion of Grooming. *American Journal of Physical Anthropology* 23:1–18.

Savage-Rambaugh, E. S., D. M. Rambaugh, and S. Boysen
1978 Symbolic Communication between Two Chimpanzees (*Pan troglodytes*). *Science* 201:641–644.

Scott, J.
1991 *Social Network Analysis: A Handbook.* London: Sage.

Sparks, J.
1967 Allogrooming in Primates: A Review. In *Primate Ethology*, D. Morris, ed. Pp. 148–175. London: Morrison and Gibb.

Sugawara, K.
1984 Spatial Proximity and Bodily Contact among the Central Kalahari San. African Study Monographs 3:1-43.
1998 The “egalitarian” attitude in everyday conversation among the |Gui. In *The Proceedings of the Khoisan Identities and Cultural Heritage Conference*, A. Bank, ed. Pp. 232–240. Capetown: Institute for Historical Research.

Takahata, Y.
1990a Adult Males’ Social Relations with Adult Female. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, T. Nishida, ed. Pp. 133–148. Tokyo: University of Tokyo Press.
1990b Social Relationships among Adult Males. In *The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies*, T. Nishida, ed. Pp. 149–170. Tokyo: University of Tokyo Press.

Tanaka, I., and H. Takefushi
1993 Elimination of External Parasite (Lice) Is the Primary Function of Grooming in Free-Ranging Japanese Macaques. *Anthropological Science* 101:187–193.

Table 1. Information on 20 Focal Individuals

Names	Year of Birth[a]	Rank/Status	Kin[b]	Hours of Total Observation
MALES				
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
FEMALES				
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	cycling (adolescent)	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 2. Distribution of Clique Sizes for Human Conversation and Chimpanzee Grooming

	Human[a]						Chimp[b]
Clique Size	Sample 1	Sample 2	Sample 3	Sample 4	Total	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[c]	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 3. Efficiency of Human Conversation Compared with Dunbar's Grooming Model

Clique Size	Frequency (%)[a]	Number of Arrows[b]		
		Human[c]	Dunbar's Model[d]	Efficiency[e]
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[f]		1.72	1.36	1.27

[a] Source: Dunbar et al. 1995

[b] An arrow means a social interaction.

[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 humans.

[e] The number of arrows for humans divided by the number of arrows for Dunbar's Model.

[f] Calculated as $\sum(N_k \times F_k /100)$, where N_k = the number of arrows when clique size is *k*, and F_k = Frequency (%) of appearance of k-size clique.

Table 4. Efficiency of Chimpanzee Grooming Compared with Dunbar's Model of Grooming

Clique Type[a]	Clique Size	Frequency (%)	Number of Arrows[b]		Efficiency[e]
			Chimp[c]	Dunbar's Model[d]	
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[f]			1.36	1.09	1.25

[a] See Figure 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 clique size of chimps. Therefore number of arrows is n/2 when clique size is n for chimps.

[e] The number of arrows for chimps divided by the number of arrows for Dunbar's Model.

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

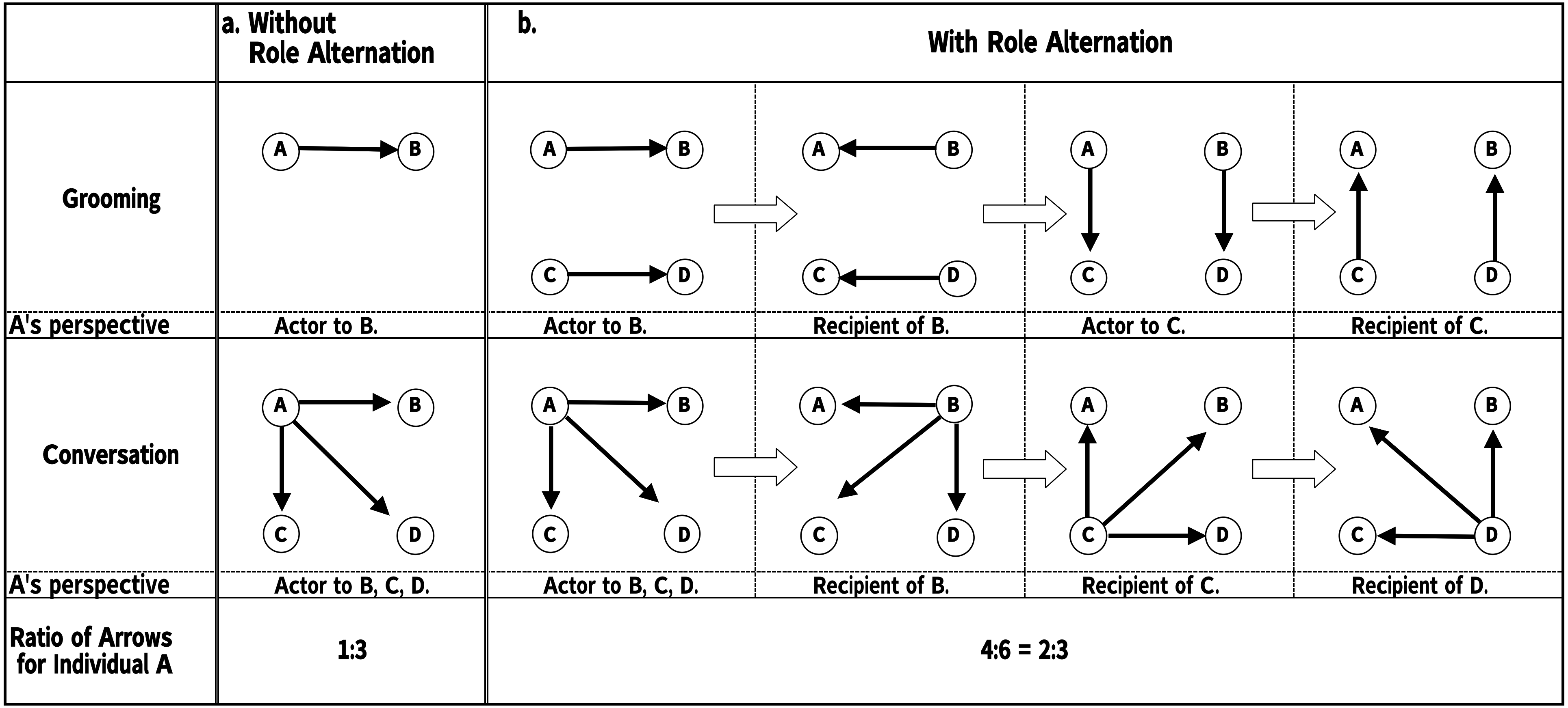

Figure 1.

Two models of efficiency of human conversation and primate grooming, ideally supposing that conversation clique sizes are always four and grooming cliques are always dyadic and one-sided as in Dunbar's model. Circled letters indicate individuals and black arrows indicate social interaction (grooming or conversation) flows. In 1b, the flow of time is indicated with large arrows. One box indicates a certain period of time after which role alternation takes place.

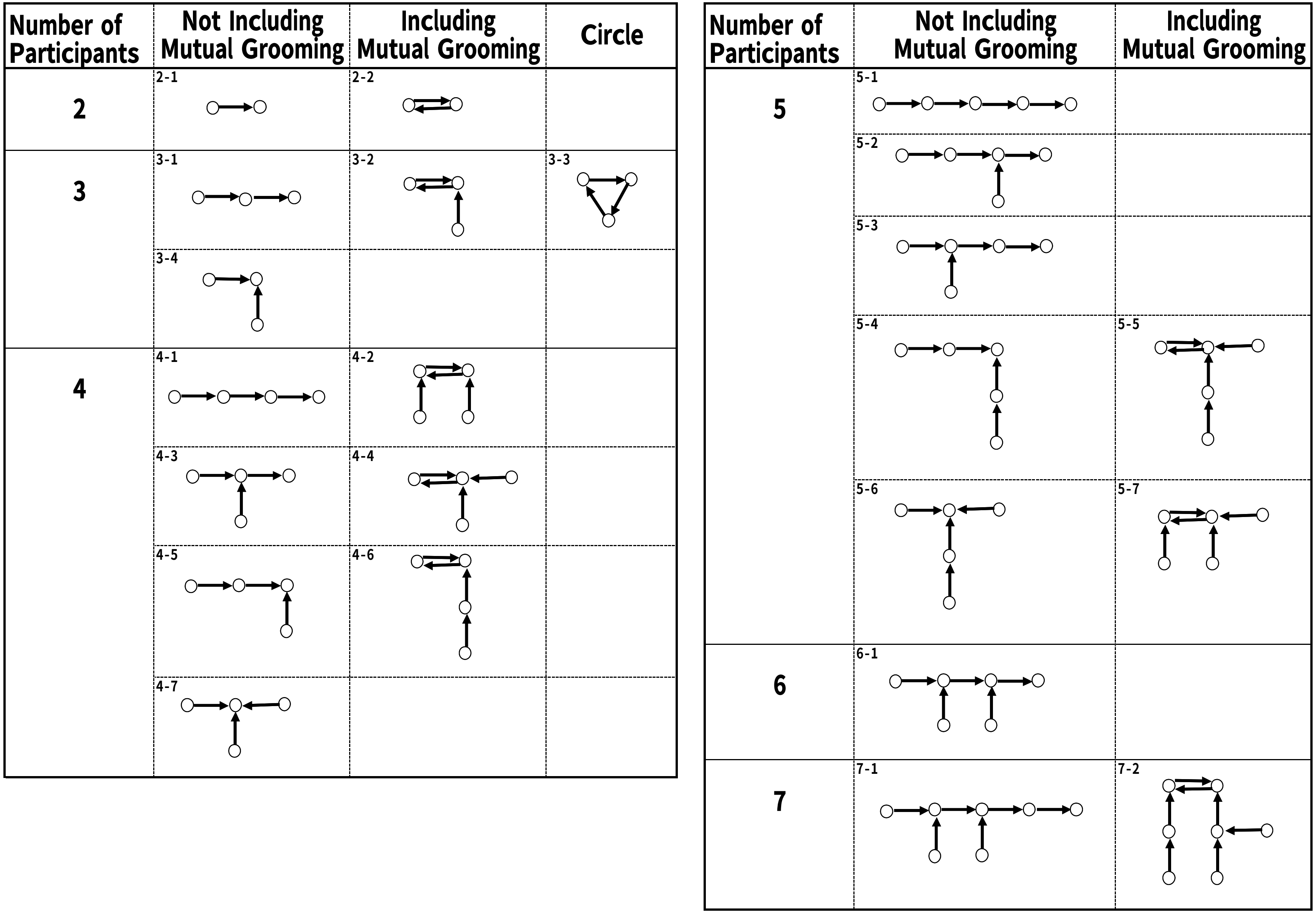

Figure 2. All types of chimpanzee grooming cliques observed. Circles indicate individuals and arrows indicate direction of grooming.