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'Gatherings' of social grooming among wild chimpanzees: implications for evolution of sociality

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Abstract

Chimpanzees (*Pan troglodytes*) often groom in gatherings that cannot simply be divided into unilateral dyadic grooming interactions. This feature of grooming is studied at two different levels: grooming cliques and grooming clusters. *Grooming cliques* are defined as directly connected configurations of grooming interactions at any given moment, and when any member of a clique successively grooms any member of another clique within 5 min and within a distance of 3 m, all the members of both cliques are defined as being in the same *grooming cluster*. Twenty-seven types of cliques are observed, with the largest one consisting of seven individuals. Mutual and/or polyadic cliques account for more than 25% of all cliques. The size of grooming clusters varies from two to 23 individuals, and almost 70% of the grooming time is spent in polyadic clusters. Although adult males groom the longest in relatively smaller clusters (size = 2–4), adult females groomed the longest in clusters of five or more individuals. A review of the literature implies that mutual and polyadic cliques occur less often in other primate species than in chimpanzees. The importance of overlapping interactions for these kinds of gatherings and its possible significance in the evolution of sociality is discussed in this article.

Keywords: Chimpanzees; Social grooming; Mahale Mountains National Park; Overlaps of interactions; Gatherings; Evolution of sociality

1.Introduction

The evolution of sociality is one of the most important topics when we consider the overall evolution of *Homo sapiens* and of primate taxa (e.g. Imanishi, 1960; van Schaik, 1983; Itani, 1985; Wrangham, 1987). Sociality can be studied from various viewpoints. Some may study macroscopic aspects such as 'social structure' or 'social organization', while others may study microscopic aspects such as 'social behaviors' or 'social tactics' of an individual that are believed to ultimately increase its reproductive fitness. Both approaches are useful, but it is apparent that the social structure cannot simply be constructed by summing up individual social behaviors. Many more steps that connect these two aspects of sociality need to be studied in order to understand how behaviors are integrated to form a society. One example of such attempts is the study of human social 'gathering' (Goffman, 1963). Goffman defined gathering as "any set of two or more individuals whose members include all and only those who are at the moment in one another's immediate presence", and vividly described the aspects of everyday social life in modern human society. It is important that 'gathering' is neither a society itself nor an attribution of a particular individual, but lies somewhere in between. Being a sociologist, Goffman did not conduct his studies from the evolutionary perspective, but the same kind of approach may be also useful for understanding primate sociality and its evolution.

Social grooming is one of the most common everyday social interactions among chimpanzees (*Pan troglodytes*) as well as among various other primate species (Sparks, 1967; Goosen, 1987). Chimpanzees allocate a large portion of their daytime hours grooming each other. Some individuals spend more than 25% of their waking time grooming with others (Goodall, 1986; Kawanaka, 1989). Being common behavior, grooming is used frequently, and often too easily, as an index for affiliation in primate studies (Cords, 1997). In such cases, it is implicitly regarded that the groomer pays some cost and the recipient gains some benefit. With this assumption, grooming is often regarded as being exchanged for grooming itself, collaboration in fighting, copulation, or sometimes food. In this kind of analysis, the grooming interaction is usually broken down into dyadic and unilateral interactions such as 'A/B', and such segmented interactions are cumulated on a dyadic basis.

However, chimpanzees often groom in gatherings, sometimes called 'grooming clusters' (de Waal, 1982; Goodall, 1986), in which 10 or more individuals groom in the same session and the membership changes frequently (van Lawick-Goodall, 1968). In such gatherings, individuals can, and often do, participate in multiple interactions simultaneously; for example, an individual may groom another while being groomed by a third, or he/she may receive grooming from two or more partners at the very same time. Such overlaps of interactions form polyadic chains of grooming (see picture in Goodall, 1986, p. 393, for example). However, such gatherings of grooming and overlaps of grooming interactions have not been examined in detail. We do not know how often such gatherings are formed, nor the characteristics of such gatherings compared to the dyadic grooming interactions.

Humans often form social gatherings and interact with multiple partners at the same time in everyday interactions, such as conversations. Given the phylogenetic closeness of humans and chimpanzees, some similarity in sociality could be expected. Especially in grooming, the most frequent everyday interactions in chimpanzees, such polyadic characteristics of social gathering are expected to be observed frequently. Accordingly, this article describes the frequencies of various types and sizes of gatherings of chimpanzee grooming and explains, by focusing on overlaps of the interactions, as to how individuals perform grooming behaviors in such scenes. Next, the age–sex differences of participation in different size of gatherings are briefly examined followed by a discussion on the implication of this phenomenon in chimpanzees on the evolution of sociality.

2.Methods

The grooming behavior of the M group chimpanzees in the Mahale Mountains National Park, Tanzania, was studied between July 1996 and May 1997. For detailed information on the research site, see Nishida (1990). Grooming is defined here as a series of behavioral elements, such as stroking the hair, picking the hair, removing things with hand(s) or lip(s), and scratching other individuals (Nakamura et al., 2000). Self-grooming and leaf grooming (Zamma, 2002) were not included in the analysis. In the course of my research, the M group consisted of 53 individuals: seven adult males (over 15 years), 18 adult females (over 14 years), five adolescent males (9–14 years), five adolescent females (9–13 years), and 18 juveniles and infants (under 8 years).

To understand gatherings made for grooming, it is necessary to grasp the behaviors of multiple individuals at any given time. However, ad libitum sampling of any grooming is not suitable because large grooming clusters occurring in relatively open spaces are more likely to be observed than smaller clusters occurring quietly in the bush. Thus, in this study, the observational viewpoint is set on one individual for a day, and the grooming behaviors of the multiple individuals around him/her were recorded even when they were not directly grooming with the focal individual. In this methodology, all kinds of social situations that the target individual experienced in a day could be observed. Ten males and 10 females of various age classes (juvenile to adult) were followed as focal target individuals (Table 1). Total duration of follow-ups was 480 h, during which 137 h of grooming (total accumulation of individual grooming including non-focal individuals) were recorded. The entire non-focal grooming was included in analysis unless otherwise stated.

2.1. Definition of grooming cliques

Grooming clique (Dunbar, 1993; Nakamura, 2000) is defined as a configuration of directly connected individuals through grooming interactions at one moment. For example, when individual A grooms individual B and B grooms individual C at the same time (A/B/C), this is a triadic clique in a serial chain. When any change in composition or configuration occurs, the newly formed groups are considered different cliques. *Polyadic cliques* are cliques containing three or more members, and *multi-interaction-cliques* means polyadic cliques plus dyadic mutual grooming cliques. This term is used because in both polyadic and mutual cliques, two or more grooming interactions (such as to groom and to be groomed) simultaneously occur for at least one individual.

2.2. Definition of grooming clusters

As a grooming clique corresponds to a momentary state of direct grooming connections, its size and composition change quite frequently. In most cases, such cliques do not occur independently, but are usually in parallel with other cliques, and they may often exchange their members with each other. Thus, all members of two or more cliques are defined to be in the same *grooming cluster* when any member of a clique successively grooms any member of another clique within 5 min and within the distance of 3 m. Within this distance, chimpanzees can change their grooming partners easily with only slight movement. With this definition of a cluster, an individual participating in a cluster is connected to all the members of the cluster by either direct or indirect (i.e. through other individuals) grooming interactions. As long as someone continues to groom, a cluster lasts regardless of compositional change. In such a case, the cumulative number of the members is used as the size of the cluster.

3.Results

3.1. Grooming cliques

Twenty-seven types of grooming cliques were observed (Fig. 1), and the largest consisted of seven members. At a maximum, four interactions were observed for one individual at a time. For example in cliques [12] and [24], an individual groomed one partner and was in turn groomed by three partners, including the one he was grooming; and in clique [22], an individual was groomed by four individuals simultaneously.

Fig. 2 shows the proportion of total duration of each type of clique. Polyadic cliques ([3]–[27]) accounted for 16.0% of all the cliques, and with the inclusion of clique [2], multi-interaction-cliques accounted for 26.3%. Among various types of multi-interaction-cliques, chimpanzees groomed frequently in clique [2] (dyadic mutual grooming: 10.4%) and clique [3] (triadic series chain grooming: 7.5%). Total duration of clique [4] (dual grooming to the third: 4.0%) was less than that of clique [3], although both of them are triadic cliques with two grooming interactions.

The proportion of single and multiple grooming interactions in different age–sex classes are shown in Fig. 3 as mean of individuals in each class. The proportion of multiple interactions varied among age–sex classes (Kruskal–Wallis, $H = 28.2$, $p < 0.001$). Significant differences were found between adult males (22.7% ± 7.8 SD) and youngsters (infants and juveniles, 4.5% ± 6.8, Bonferroni's multiple comparison, $p < 0.05$).

3.2. Grooming clusters

The size of grooming clusters observed during the study varied from two to 23 individuals (almost half of the M group members). Day party size (the number of individuals observed in a day) surely limits the maximum size of clusters because the latter cannot exceed the former. Therefore, I have examined the observed maximum cluster size for each size of day party (2–50), but there was no correlation between them (Spearman, $r_s = 0.25$, $N = 38$, $p = 0.13$). Relative frequencies of clusters with different sizes are shown in Fig. 4 (left). Overall, 926 grooming clusters were observed, of which 66.6% (617/926) were clusters with two individuals. Clusters with five and more individuals occurred in only 7.8% (72/926) of all events. Small clusters seemed to be dominant if we only consider the number of events. However, when we look at the relative duration of clusters (Fig. 4, right), 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, the mean duration of clusters with two individuals was very short (3.5 min) compared to that of clusters with five or more individuals (25.5 min). Although the previously mentioned durations include even time when they were not actually engaged in grooming, data on 20 focal individuals showed similar tendencies: they virtually groomed an average of 42.0% (± 25.7), 16.9% (± 14.1), 19.9% (± 20.5), 21.5% (± 20.7), and were groomed 37.5% (± 24.1), 20.4% (± 16.3), 22.7% (± 20.9), 19.4% (± 21.8), in clusters of two, three, four, and more than five individuals, respectively.

Fig. 5 shows the relative duration of multi-interaction-cliques of different sizes of clusters. Polyadic cliques could not occur in clusters with two individuals by definition. In every cluster larger than three, polyadic cliques were observed at least more than 10% (11.6–48.4%) of the time. In the overall duration of such larger clusters, 22.7% of time was performed in polyadic cliques. The larger cluster size did not affect the occurrence of either the dyadic mutual cliques ($r_s = 0.14$, $N = 12$, $p = 0.64$) or the polyadic cliques ($r_s = 0.47$, $N = 12$, $p = 0.11$).

3.3. Grooming duration in clusters of different sizes

Fig. 6 shows mean total grooming duration of individuals of different age–sex classes in different sizes of clusters. There are marked differences among the age–sex classes (ANOVA, df=2, $F = 35.2$, $p<0.0001$), and adult males groomed the longest followed by adult females (Bonferroni test, adult males vs. adult females $p<0.01$, adult males vs. others $p<0.0001$, adult females vs. others $p<0.0001$). Although no significant differences were found among cluster sizes (ANOVA, df=3, $F = 2.5$, $p = 0.058$), there was a significant interaction between age–sex classes and cluster sizes (ANOVA, df=6, $F = 2.4$, $p<0.05$). Grooming duration particularly increased in adult females when they were in clusters of five or more individuals.

4.Discussion

4.1. Comparison with other primates

Although the aspects of polyadic grooming in chimpanzees have been previously described, the results may not be easy to evaluate without comparisons with other species. Unfortunately, almost no information is available on grooming clusters in other species. However, there are some descriptions of multi-interaction-cliques from 13 Anthropoidea primates (Table 2). Most of the articles only note that such cliques occur 'sometimes' or 'rarely' without any quantitative data (Table 2, (A)), and the scarceness of descriptions about such grooming in other primates may indicate the actual rareness of such grooming. When the four species with some quantitative data (namely, *Macaca assamensis*, *M. mulatta*, *H. sapiens* and *P. troglodytes*) are compared in Table 2 (B), chimpanzees seem to be more often engaged in multi-interaction-cliques than other species (26.3% in chimpanzees vs. 5.2–8.1% in others). Note that direct comparisons or statistical tests were not possible due to the different measures among studies and the difficulty of identifying such measures from the previous articles (e.g. 'episodes' are not defined in Cooper and Bernstein, 2000). One famous example would also support this view: 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. This indicates that their grooming interactions are normally dyadic and rarely triadic, resulting in this kind of competition over grooming partners. Chimpanzees, on the other hand, can interact with an individual who is already involved in grooming with another, without manifesting competition, which may obscure who is interacting with whom on a dyadic basis.

Judging from the fragmentary information, there seems to be more frequent reporting on clique [4] (dual grooming to the third) than clique [2] (dyadic mutual grooming) or clique [3] (triadic serial chain grooming). Furthermore, in all of those species with quantitative data, the proportion of clique [4] always exceeds that of [2] or [3], although the number of interactions are the same in these cliques with the only exception of chimpanzees, where [2] and [3] are much more frequent than [4]. In clique [4], such as A/B)C, although two interactions are overlapped on B, his/her role is still a groomee. On the other hand, in clique [3], such as X/Y/Z, Y plays the two roles of groomer and groomee. Playing two different roles is also the case in mutual grooming, where both of the two participants play groomers and groomees at the same time. Therefore, playing two different roles simultaneously may be a key characteristic of chimpanzee grooming. It is also important that the former type of overlap (concentration on one individual) cannot easily increase the size of a clique because of the limitation of physical space. Five or more individuals cannot groom one individual simultaneously, but the same number of individuals can make a chain.

4.2. Sex differences in 'gatherings' of grooming

Female chimpanzees have been said to be relatively inactive in social interactions with each other (e.g. Nishida, 1979; Wrangham and Smuts, 1980), and the result that they groomed less often than longer than males in large grooming clusters. This adult males in small clusters is consistent with this may be understood by the difference in the social current knowledge. However, they groomed even relationships between males and between females. Adult male chimpanzees are known to be very political (de Waal, 1982; Nishida, 1983), and many of them usually compete for 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, this coalitional relationship always faces the possibility of change. Thus, these males always have to renew or confirm their relationships with each other. This leads to their frequent and long grooming in relatively small clusters. On the other hand, adult females do not have to maintain such relationships with particular individuals. They do not seem to compete for higher status by forming particularly intimate allies. Rather, it seems better for them to get along with many individuals of the community. Therefore, females may not have to focus their interactions on particular individuals in small clusters. Instead, they may prefer wider interactions with various individuals at any given moment, making it practical to groom in larger grooming clusters.

4.3. Implications for evolution of sociality

If chimpanzees groom more often in gathering than other primates, what implications does it have on their social life and the evolution of sociality? Three non-exclusive hypotheses are subsequently proposed.

First, the formation of gathering in chimpanzees may have something to do with the unique characteristics of their fission–fusion society (Nishida, 1968). As a chimpanzee is 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. Members of such a species would be more eager to make and maintain a gathering when there is an opportunity. It is suggested that grooming provides one such opportunity in chimpanzee society. If this is the case, individuals would groom those others in a large cluster who do not usually range with them in small parties.

Second, the relatively egalitarian sociality of chimpanzees may be one explanation. It is known that dominance among chimpanzees (Bygott, 1974; Hayaki et al., 1989), especially among females (Nishida, 1989), is not as strict as that among macaques. Also, food is occasionally shared among non-related adults (Nishida et al., 1992; Nakamura and Itoh, 2001). Such a general tolerance may permit many individuals to gather together in one place and to participate in a single social scene. If so, the more egalitarian bonobos would also perform similar gatherings in some social scenes; however, they do not seem to do this at least in grooming.

The other possibility is related to their cognitive ability. Social behavior would require a more complex cognitive process than the behavior with inanimate objects, because the actor of the behavior has to coordinate its behavior with the response from the partner. In this sense, it is more difficult for an individual to interact with multiple individuals at the same time than with only one individual, and it is more difficult to play two roles at the same time than one. Thus, it is likely that at the preliminary stage of the evolution of sociality, individuals would have interacted with only one partner at a time, even in groups of multiple members. At the next stage, they would have started to interact with two individuals duplicating the single interaction. Then, they would have begun to interact with more individuals, sometimes performing two different roles simultaneously. Investigating multiple social interactions in other great apes would test this hypothesis.

The previously mentioned three characteristics are also common to humans, and we also form gatherings of social interactions (especially in conversation), where we interact with multiple individuals at the same time. In humans, mass (and often anonymous) individuals can be the targets of a behavior. The results of chimpanzees do not directly lead to understanding of the human gatherings, but it is possible that multiplying or overlapping of social interactions may serve to enlarge society and make it more complex in both species.

Grooming is not the only social interaction in chimpanzees, and the current result is only a small step toward connecting social behaviors to a society. However, the importance of overlaps of interactions for understanding sociality should be emphasized, because an overlap of interactions cannot be attributed to a single individual, but rather exists among individuals: one individual can groom another or perhaps can even demand to be groomed by another, but he cannot make 'gatherings' only through his own effort. A 'society' cannot simply be reduced to a behavior of a single individual or a relationship between individuals. Such an emergent characteristic of sociality might have evolved by expanding overlaps of interactions.

5.Summary

1. In chimpanzee grooming, 27 types of grooming cliques were observed and the largest one consisted of seven individuals.
2. The proportion of multi-interaction-grooming cliques was more than 25% in chimpanzees, whereas it was less than 10% in other primate species.
3. Overlap of grooming interactions (e.g. grooming and being groomed simultaneously or being groomed by multiple individuals) accounted for about 20% of individual grooming. The maximum number of interactions for one individual at one time was four.

4. Grooming clusters of two to 23 individuals were observed. Although the clusters of two individuals were most frequent as events, clusters of three or more members accounted for about 70% of total duration.
5. Adult males groom longer than any other age–sex classes in relatively small (size = 2–4) clusters, whereas the duration of female grooming was as long as that of males in clusters with more than five individuals.
6. The overlap of interactions is important for understanding the evolution of sociality.

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Table 1 Hours of observation and grooming of focal individuals

Names	Sex	Year of birth	Rank/status	Kin	Hours of total observation	Hours of grooming[a]	Groom/ observation (%)
Kalunde	m	1963[b]	2		29.6	9.5	32.0
Nsaba	m	1973	1		15.7	3.6	23.0
Fanana	m	1978[b]	3		30.9	4.8	15.6
Hanby	m	1980	5		20.7	3.1	14.7
Dogura[c]	m	1981[b]	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[b]	Adolescent	ys	13.8	1.0	7.3
Darwin	m	1988	Juvenile		33.2	2.8	8.3
Gwekulo	f	1962[b]	Cycling		25.8	5.5	21.2
Fatuma	f	1963[b]	Lactating	so, da	22.8	4.3	18.9
Ikocha	f	1965[b]	Lactating	so, da	26.2	4.2	15.9
Nkonbo	f	1970[b]	Cycling		28.0	3.3	11.8
Pinky	f	1972[b]	Cycling	so	26.8	2.9	10.9
Christina	f	1975[b]	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, ys	21.0	1.8	8.5

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

[a] Only grooming during their focal follow is shown here.

[b] Estimated.

[c] Although Dogura was still 15 years old, he was fourth-ranking (third-ranking in 1997), overtaking some older males, and was the most important coalition partner for the beta male. Therefore, I treated the age as adult.

Table 2 Frequencies of mutual and polyadic grooming among various species of primates

Species	Clique [2]	Clique [3]	Clique [4]	Clique [5]–[27]	Observation units	Source
(A) Primate species with no quantitave data						
Ateles geoffroyi	‘Never’	–	‘Sometimes’	–		Ahumada, 1992
Cebus apella	–	–	‘Often’	–		Parr et al., 1997
Cercopithecus mitis	‘Never’	–	‘Very rare’	–		Rowell et al., 1991
Macaca fuscata	–	+	+	–		Furuya, 1957
Macaca mulatta	+	–	–	–		Boccia, 1983
	–	‘Sometimes’	+	+		Sade, 1965
Macaca nemestrina	‘Occasional’	–	–	–		Kaufman and Rosenblum, 1966
Macaca radiata	‘Occasional’	–	–	–		Kaufman and Rosenblum, 1966
	–	–	+	+		Simonds, 1965
Semnopithecus entellus	‘Rare’		‘Common’[a]	–		Borries et al., 1994
	–	–	+	+		McKenna, 1978
Trachypithecus cristatus	–	+	‘At times’	+		Bernstein, 1968
Pan paniscus	–		‘Sometimes’[a]	–		Kuroda, 1980
	‘Rare’	+	+	+		Kano, 1998
(B) Primate species with quantitave data						
Macaca assamensis	0.8%(45/5397)	–	7.1%(385/5397)	0.1%(5/5397)[b]	Episodes[c]	Cooper and Bernstein, 2000
Macaca mulatta	–	1.1%(17/1488)	3.9%(58/1488)	0.1%(2/1488)[d]	Episodes[c]	Matheson and Bernstein, 2000
Homo sapiens (/Gui bushman)	–	0.5%(1/184)	7.1%(13/184)	–	Interactions	Sugawara, 1984
Pan troglodytes	10.4%(10.7/103.4)	7.5%(7.7/103.4)	4.0%(4.1/103.4)	4.5%(4.7/103.4)	Hours	This study

For clique types, see Fig. 1. Single quotation marks indicate authors’ description of frequencies without data; +, description without any information on frequency; –, no description in the article.

[a] Triadic grooming but no information on types.

[b] Clique [10].

[c] Although these ‘episodes’ are not defined in the original articles, if the average duration of multi-interactional episodes was shorter than that of single-interactional episodes (which is very likely), then the proportion with episodes shown here would be overestimated. Thus, if we could use duration as a common measure, this tendency (more multi-interactional-cliques in chimpanzees than in other species) would likely be emphasized.

[d] Cliques [9] and [10].

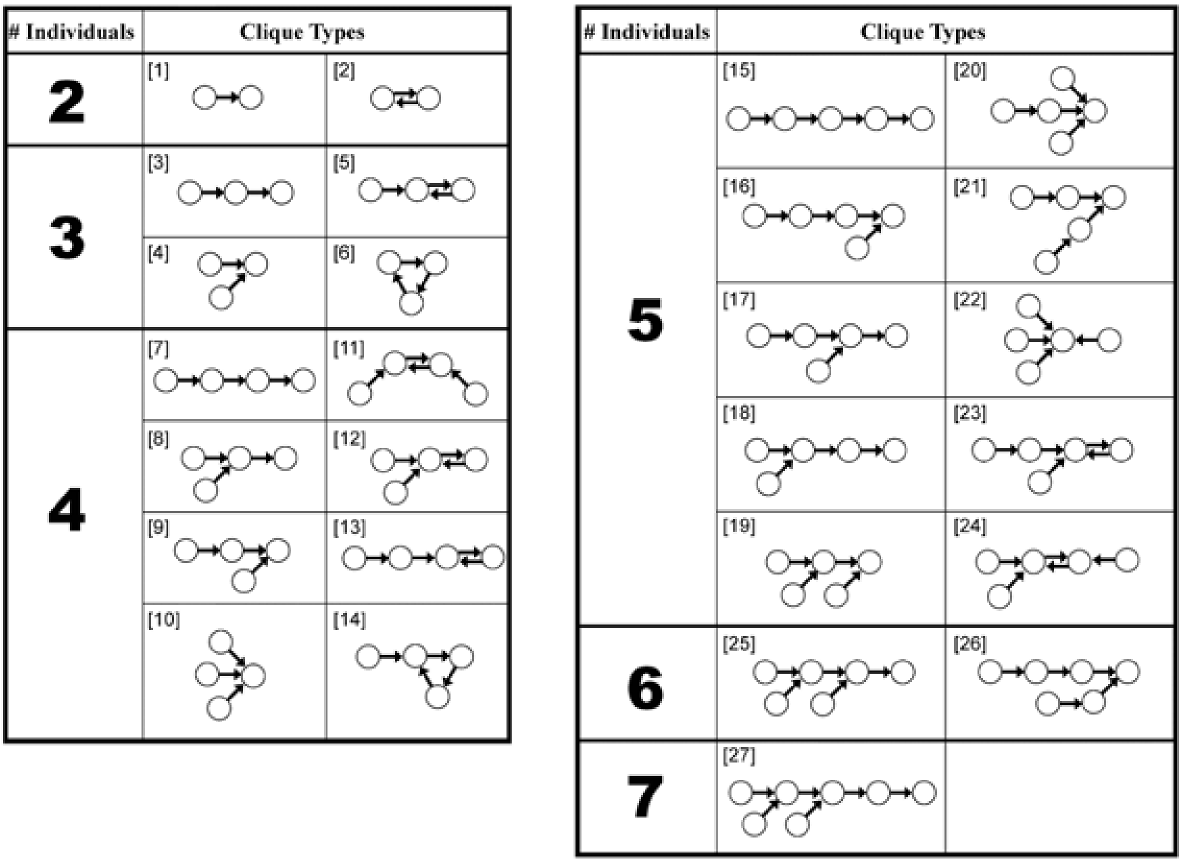

Fig. 1. Types of grooming cliques observed in the study. Circles in the figure indicate individuals, and arrows indicate the flows of grooming interactions.

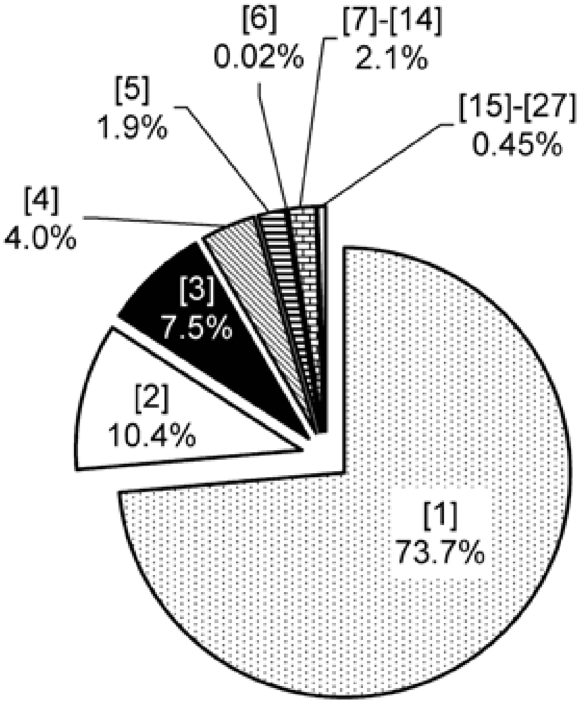

Fig. 2. Proportion of relative duration of each grooming clique type observed during study (for grooming clique types, see Fig. 1).

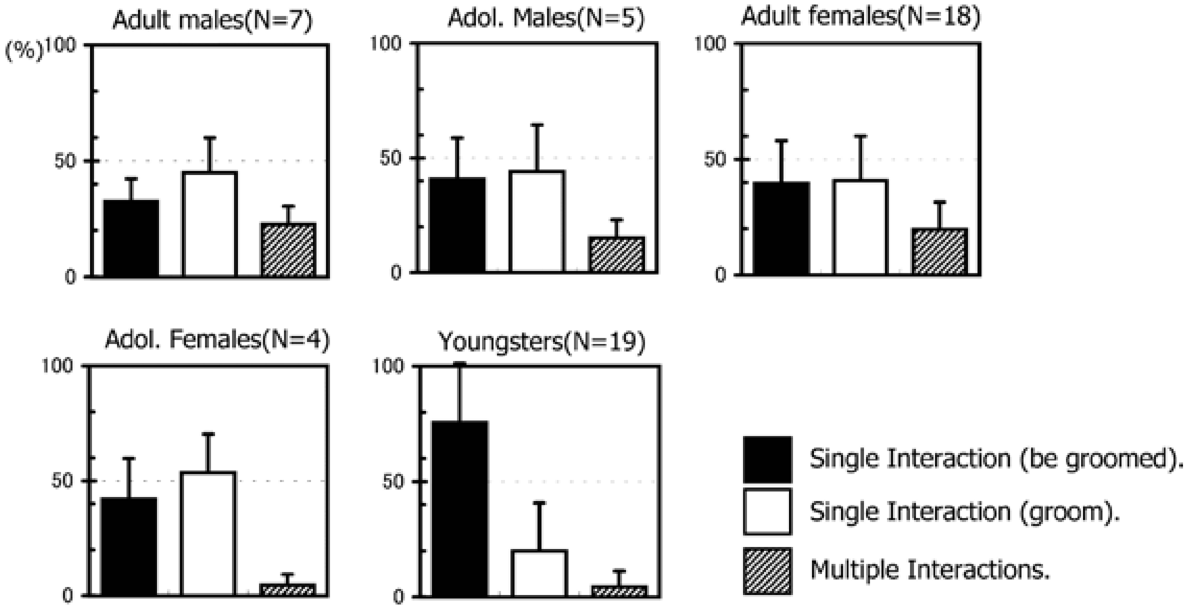

Fig. 3. Age–sex differences in proportion of single/multiple interactions. Bars indicate mean relative duration of individuals in each age–sex class, where partner(s) of the interaction(s) can be individual(s) of any age–sex class. Number of individuals in each class is shown in parentheses. Error bars represent standard deviations.

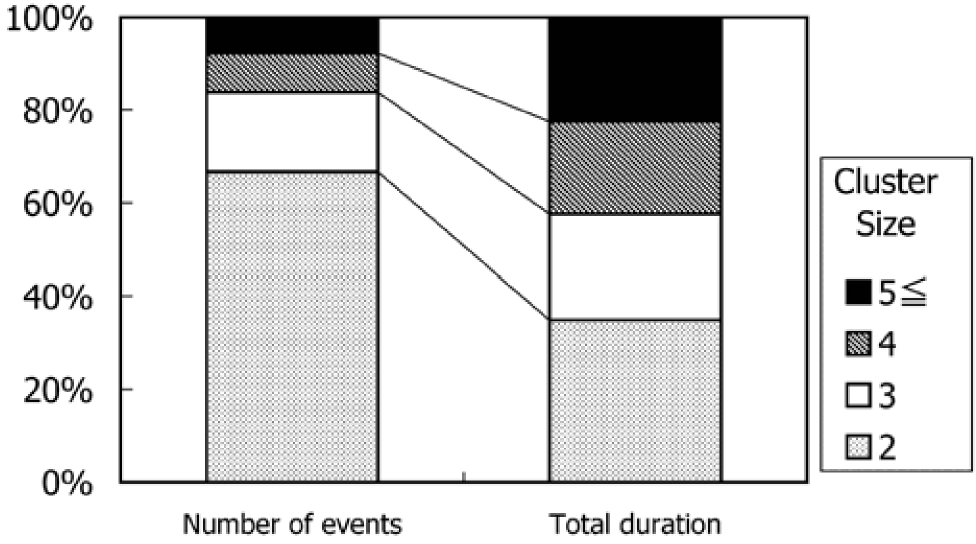

Fig. 4. Proportion of each size of grooming cluster with the number of events (left) and relative duration (right).

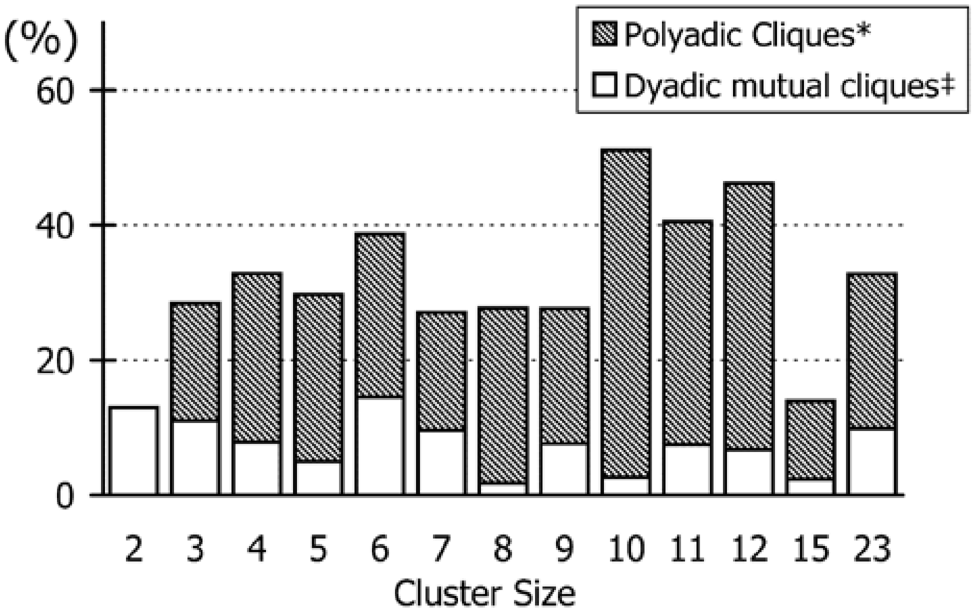

Fig. 5. Proportion of multi-interaction-cliques in different sizes of grooming clusters. Total does not reach 100% because single-interaction-cliques (namely clique [1] in Fig. 1) are not shown in this figure.
***Corresponds to cliques [3]–[27] in Fig. 1.**
‡Corresponds to clique [2] in Fig. 1.

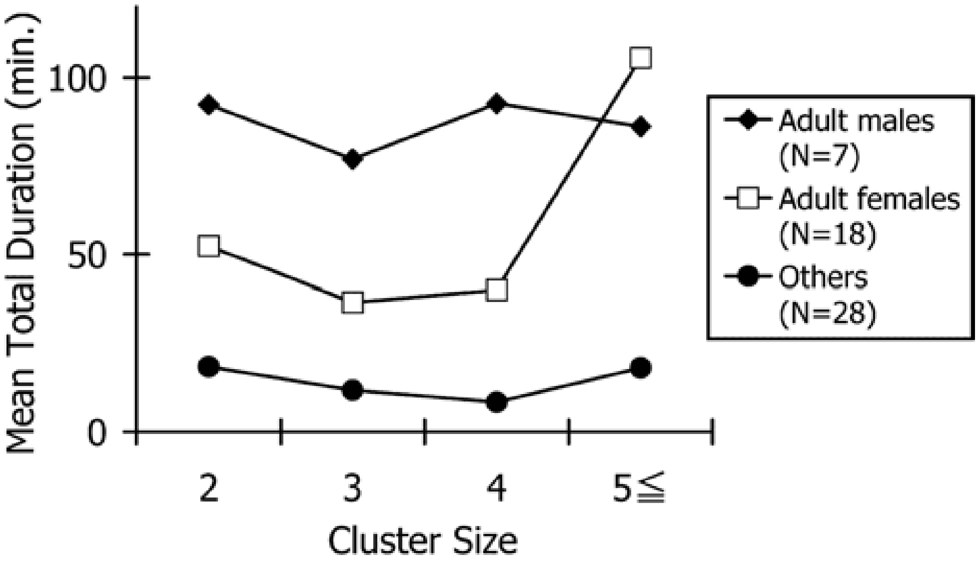

Fig. 6. Age–sex differences in grooming in different sizes of grooming clusters. Although data-points in the figure represent mean total grooming duration of each age–sex class, individual data were used for ANOVA test (Number of individuals in each class is indicated in the figure). Adolescents and youngsters in Fig. 3 were combined into ‘others’ as they showed similar tendencies. Only data on giving grooming are shown here (data on receiving grooming showed similar tendencies).