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Social scratch: Another custom in wild chimpanzees?

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ABSTRACT

Chimpanzees (*Pan troglodytes schweinfurthii*) in the Mahale Mountains National Park, Tanzania, scratch other individuals' bodies while they groom them. This behavioral pattern of "social scratch" is another example of locality-specific social behavior, or custom, as it is not found in the Gombe National Park, Tanzania, about 150 km north of Mahale, nor has it been reported from any other sites of chimpanzee study. Frequency of social scratch was correlated with frequency of social grooming, but not with frequency of self-scratch. Frequencies of social scratch per grooming bout among adult and adolescent males, and from lactating females to infants or juveniles, were high, and among males, higher-ranking males especially received more. These facts indicate some social function of the behavior. Social scratch was directed mostly to the dorsal side of the body. However, when lactating females social scratched to infants or juveniles, they scratched other body-parts. Social scratch was not lateralized to left or right. We present four hypotheses on the functional origin and on the learning process of this cultural behavioral pattern.

Key Words: Chimpanzees; Pan troglodytes schweinfurthii; social scratch; social groom; self-scratch; custom; culture.

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 Maestripieri 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, in press). 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 (first author)

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 (second author) and LFM (third

author)

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. 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 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 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 2. The 19 focal individuals averaged 0.31 ± 0.09 (mean±SE) social scratches per observation hour and 1.99 ± 0.57 social scratches per grooming hour. They received an average of 0.39 ± 0.13 social scratches per observation hour and 2.53 ± 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 1, r_s =0.36, p=0.09, N=24).

There was no sex difference in giving social scratch (SSg in Table 1, U=80, N[male]=12, N[female]=15, p=0.62; SS in Table 1, U=75.5, N[male]=12, N[female]=14, p=0.66) nor in receiving social scratch (SSr in Table 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 1, r_s =0.65, p<0.001, N=27) as well as in WCM and LFM's data (SS vs. GR in Table 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 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 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 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 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. 2) and lactating females to youngsters (LY in Fig. 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. 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 (χ^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 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 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. 3 and Fig. 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, χ^2 =44.57, *df*=3, *p*<0.01). The same tendency was seen in the parts where youngsters received social scratches (χ^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). 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.). Plooij (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 (te 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 Taï, 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 groomee'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.

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	Names	Year of birth	Rank of males	SG	GR	SC	SS	GRg(h)	SSg	SSg/GI	^R 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
Females	XT's inf.	1995						0.00	0	0.00	1.94	1	0.51
	LD's inf.	1996						0.00	0		0.10	0	0.00
	MJ's inf.	1996						0.00	0		0.31	18	57.24
	s 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
	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?		25	50	71	2	0.34	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	1988		10 14	2	40	0	1.26	0	0.00	4.14	12	2.90
	CS	1990 1990		21	0	40 59	0	0.29	0	0.00	4.14 1.61	2	1.24
	CS FU	1990		45	51	36	2	0.29	1	1.59	0.76	0	0.00
	PU PE	1991		43 6	3	50 11	2	0.85	0	0.00	2.16	0 14	6.48
	PE IV	1993		6 6	3 4	11 19	0	0.39	1	0.00 3.40	2.16 1.44	14 4	0.48 2.79
				U	4	19	0			5.40			
	SL's inf.	1994						0.00	0		0.39	0	0.00
	AA's inf.							0.00	0		0.04	0	0.00
	JN's inf.	1995						0.00	0		0.02	0	0.00
	WX's inf.							0.00	0		0.37	0	0.00
	TZ's inf.	1996		1588		2931		0.00	0		0.02	0	0.00

Table 1 Frequency of Scratching and Grooming by M Group.

	Names	SSg*	SSr*	obs.time(h)	SSg/obs.	SSr/obs	GR* time(h)	SSg/GR	SSr/GR
Males	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
	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
Females	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
	Total	104	149	320.72	0.31	0.39	40.88	1.99	2.53

Table 2. Observation Hours, Frequency of Social Scratching, and Duration of Grooming of Focal Targets ofMN (Data from Nov.1996-May 1997 shown here.).

* For abbreviations see Table 1.



Fig. 1 Typical Social Scratch (Photo by L. F. Marchant).

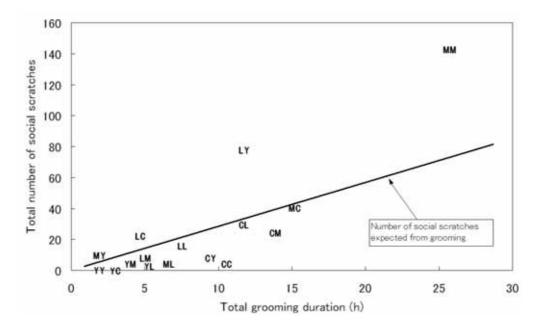
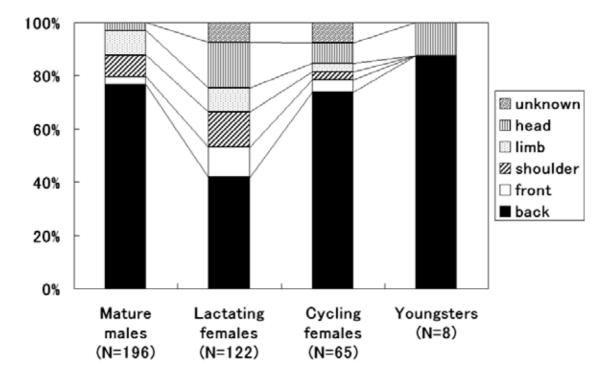
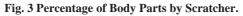


Fig. 2 Total Number of Social Scratches in each Combination of Age-Sex Classes Plotted against Total Duration of Grooming in the Combination.

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.





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].

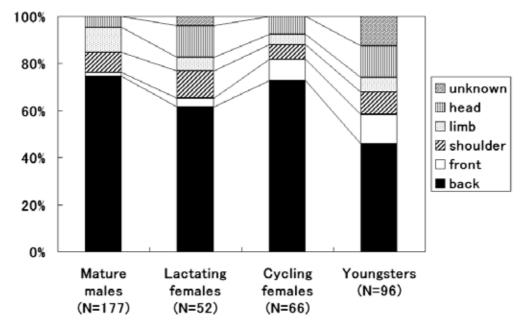
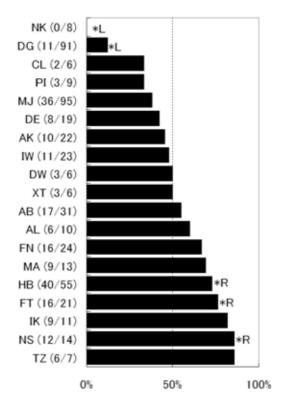


Fig. 4 Percentage of Body Parts by Recipient.





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.