

## RESEARCH ARTICLE

# Reciprocation and Interchange in Wild Japanese Macaques: Grooming, Cofeeding, and Agonistic Support

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Social primates spend a significant proportion of their time exchanging grooming with their group companions. Although grooming is mainly exchanged in kind, given its hygienic and tension-reducing functions, it is still debated whether grooming also provides some social benefits, such as preferential access to resources (e.g., food or mating partners). In this study we analyzed grooming distribution among wild female Japanese macaques living in two groups on Yakushima. We tested the tendency of monkeys to reciprocate the amount of grooming received, and to direct their grooming up the hierarchy. Then we analyzed the relation of grooming to three of its possible benefits: reduced aggression, increased tolerance over food, and agonistic support against a male aggressor. The data were analyzed by means of row-wise matrix correlations. Grooming was highly reciprocated (i.e., exchanged in kind) and directed up the hierarchy in both the study groups. No significant relationship was found between grooming and aggression. Conversely, grooming favored tolerance over food, since it was positively correlated with presence on the same food patch, close proximity, and close approaches (both within 1 m) during feeding. Grooming was also positively related to agonistic support against adult males, although this relationship became nonsignificant when we controlled for kinship. Although these results are not definitive, they suggest that monkeys may derive various social benefits from grooming. This conclusion is supported by the fact that in various primate species animals tend to prefer high-ranking individuals as grooming partners. *Am. J. Primatol.* 68:1138–1149, 2006. © 2006 Wiley-Liss, Inc.

**Key words:** aggression; coalition; grooming exchange; *Macaca fuscata yakui*; social behavior; tolerance

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## INTRODUCTION

Allogrooming (hereafter “grooming”) is possibly the most common affiliative behavior exhibited by Cercopithecine monkeys. The benefits of receiving grooming range from the removal of ectoparasites [Tanaka & Takefushi, 1993; Zamma, 2002] to the reduction of tension, possibly through the release of  $\beta$ -endorphins [Keverne et al., 1989; Schino et al., 1988]. Given the costs associated with grooming (in terms of reduced time for other activities or for vigilance [Cords, 1995; Maestripieri, 1993]), its evolution is generally thought to be based on a combination of kin selection and reciprocal altruism. In recent years, principles derived from the biological market theory [Noë & Hammerstein, 1994, 1995] have been successfully applied to the study of the within-group distribution of grooming [Barrett et al., 1999; Henzi & Barrett, 2002].

Investigating the benefits that are returned in exchange for grooming has been a central issue for primatologists [Dunbar, 1991; Seyfarth, 1977]. While earlier theoretical and empirical investigations focused mostly on the possibility of an interchange of grooming with different “currencies” (e.g., agonistic support), more recent reviews have emphasized its reciprocation (i.e., the exchange of grooming given with grooming received [Henzi & Barrett, 1999]). Indeed, evidence for grooming reciprocation [Barrett et al., 1999; Furuichi, 1984; Leinfelder et al., 2001; Muroyama, 1991] is more persistent in the various studies than evidence for an interchange with different benefits, such as access to infants [Henzi & Barrett, 2002; Muroyama, 1994], preferential mating [Hemelrijk et al., 1999], or agonistic support [Hemelrijk & Ek, 1991; Seyfarth, 1980] (see Henzi and Barrett [1999] for a critical review).

Challenging this poverty of evidence for such interchange is the widespread observation that Cercopithecine monkeys tend to direct their grooming up the hierarchy (see Schino [2001] for a recent meta-analysis). This observation suggests that grooming may indeed be exchanged for rank-related benefits. In this paper we first test whether wild female Japanese macaques (*Macaca fuscata yakui*) reciprocate the total amount of grooming exchanged, and whether they tend to direct their grooming up the hierarchy. We then examine the relationship between grooming and, respectively, aggression, presence on the same food patch, cofeeding, and coalition formation in order to evaluate the possibility of interchange between grooming and other socially positive behaviors. If grooming is exchanged for other currencies, we expect, respectively, a negative correlation between grooming given and aggression received, and a positive correlation between grooming given and tolerated cofeeding and/or coalition formation at the dyadic level.

## MATERIALS AND METHODS

### Subjects and Study Area

The subjects of this study were the female members of two wild groups of Japanese macaques living in Yakushima Island (31°N, 131°E), Japan. The two groups (Nina A and Kw) numbered 25 and 55 monkeys, respectively, including eight and 20 sexually active females ( $\geq 4$  years old), respectively, that were the focus of this study. While maturation of primates in the wild can be delayed compared to that in captive or provisioned groups, both of the two 4-year-old females in this study were observed to be in estrus and engage in sexual activity with adult males. Nonetheless, as a precaution all relevant analyses were run with and without these two individuals to check for a possible age effect. Since no

statistical differences were found, these two females were included in the data set. The two groups inhabited non-overlapping home ranges (at 0–200 m a.s.l.) that were approximately 1 km far apart and characterized by similar vegetation (a warm temperate/subtropical broad-leaved forest; see Agetsuma and Nakagawa [1998] for details on the habitat characteristics of Yakushima).

Monkeys in each group were arranged in a linear hierarchy on the basis of the direction of dyadic submissive behavior. At least one submissive behavior was observed for each dyad ( $3.4 \pm 2.2$  submissive events per dyad; mean  $\pm$  SE) and this was always unidirectional, so the females could be organized into a linear hierarchy. Kinship relations were known for Nina A but not for Kw females. Mother–offspring, sibling, and grandmother–grandoffspring dyads were considered as kin, and all other individuals were considered nonkin.

### Data Collection

Data on Nina A females were collected between June 2001 and May 2002, while data on Kw females were collected between January and May 2002. The monkeys were followed from 0700 to 1800 hr. A total of 207.7 hr of observation were obtained for Nina A females ( $25.9 \pm 1.7$  hr per female, range = 18.7–17.5 hr), and 139.8 hr were obtained for Kw females ( $7.0 \pm 1.7$  hr, range = 7.5–4.8 hr).

During 10-min focal animal observations, the observer (R.V. or B.M.) recorded the duration of all grooming interactions involving the focal animal and the time she spent in proximity with one or more females (see Table I for a description of the behavioral categories recorded). Moreover, all of the aggressive interactions and approaches given or received by the focal animal to or from the other group females were recorded during focal observations. Dyadic agonistic interactions with a clear-cut result were also collected ad libitum to construct the hierarchy for the females in the two groups. For each study animal an attempt was made to distribute focal observations evenly throughout the day. When for a given time of the day we had a similar amount of hours for each study animal, we selected at random the monkey to be subjected to a focal session, independently from its activity. The data collection began when interobserver reliability (using the kappa coefficient [Martin & Bateson, 1993]) was over 95%. Data on agonistic support and presence on the same food patch were recorded ad libitum because of their rarity. A food patch was defined as a discrete area in which individuals were

**TABLE I. Definitions of the Behavioral Categories Recorded**

Behavior	Definition
Grooming	A monkey picks through and/or slowly brushes aside the fur of another individual with one or both hands
Feeding	A monkey is gnawing, searching for food or is picking up food items
Aggressive behavior	A monkey threatens (i.e., directs an open mouth display), chases, bites, or slaps another individual
Proximity	The distance between two monkeys is $\leq 1$ m
Approach	A monkey reduces the distance from another individual from $> 1$ m to $\leq 1$ m
Agonistic support	A monkey intervenes in an ongoing agonistic interaction between two or more individuals, helping one of the opponents

able to collect food continuously as they moved within it [Whitten, 1988]. The food patches were mostly single trees, except for eight observations in which the canopy of two trees of the same species was so closely interconnected that it could not be distinguished. In those cases we considered the two tree canopies as forming a single food patch. We used cofeeding as a measure of tolerance over food. Cofeeding between two monkeys was defined as the time the monkeys spent feeding within 1 m of each other.

## Data Analysis

Data were analyzed by means of row-wise matrix correlations (the Kr test). Row-wise matrix correlations allow one to avoid the problem of non-independence of the different dyads in a social group, and at the same time to take into account interindividual differences in absolute rates of behavior [Hemelrijk, 1990a,b]. A row-wise matrix correlation thus tests whether each individual in a social group directs its social interactions (e.g., grooming) toward group mates in relation to the behavior received. We were particularly interested in rank-related exchanges of grooming with other social behaviors. Therefore, in addition to analyzing entire matrices, we also reanalyzed data while focusing on the grooming directed from lower- to higher-ranking monkeys. To do so, we deleted from the matrices all grooming directed from higher- to lower-ranking monkeys and partialled out the now-empty cells using the procedure recommended by Hemelrijk [1990a]. This procedure involves the creation of a “dummy matrix” containing missing/nonmissing values for each dyad. The dummy matrix is then inserted as control variable in a partial correlation test. Similarly, the effects of kin relations between subjects are controlled by creating a “kinship matrix” that contains kin/nonkin values for each dyad, and inserting such matrix into partial correlation tests.

For the analysis of presence on the same food patch, we divided the number of times a female was foraging on the same patch with another female by the total number of times she was observed on a patch with other females. When we analyzed agonistic support, we divided the number of supports received by each female by the total number of aggression received by that female in order to control for the possibility that agonistic support was simply more likely to occur the more frequently a female received aggression. For each analysis, we report the results relative to the two study groups separately, and (since they constituted two independent tests of the same hypothesis) the combined *P*-value obtained using Fisher’s technique [Sokal & Rohlf, 1981]. All probabilities are two-tailed.

Grooming in Japanese macaques has been reported to undergo significant fluctuations in relation to the seasonal sexual activity [e.g., D’Amato et al., 1982]. Given that data collection on one of our study groups (Nina A) encompassed both the mating and birth seasons, we tested for possible seasonal differences in grooming distribution before proceeding with further analyses. We constructed separate matrices containing grooming scores relative to the mating and nonmating seasons. The two matrices were significantly correlated ( $\tau_{rw} = 0.715$ ,  $P < 0.001$ ). Moreover, running the analyses shown in the next section for the mating and nonmating seasons separately did not change our results (for the sake of brevity, these data are not presented). For Nina A we therefore lumped data collected throughout the year. Kw data were collected only during the nonmating season.

## RESULTS

### Grooming Reciprocation and Distribution

Table II shows the grooming scores for the two study groups. Females in both study groups reciprocated the total amount of grooming received, as shown by significant correlations between the matrices of grooming given and received (Kr test; Nina A:  $\tau_{rw} = 0.507$ ,  $P < 0.0005$ ; Kw:  $\tau_{rw} = 0.741$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 34.069$ ,  $df = 4$ ,  $P < 0.001$ ). In Nina A group the correlation remained significant when the effect of kinship was partialled out ( $\tau_{rw,xy,z} = 0.425$ ,  $P = 0.001$ ). Kinship relations were unknown in the Kw group.

Females in both groups tended to direct their grooming up the hierarchy, as shown by significant negative correlations between the matrix of grooming given and that of the ranks of the recipients (Nina A:  $\tau_{rw} = -0.262$ ,  $P < 0.05$ ; Kw:  $\tau_{rw} = -0.105$ ,  $P < 0.05$ ; Fisher's combined test:  $\chi^2 = 13.193$ ,  $df = 4$ ,  $P < 0.02$ ). Controlling for the effect of kinship for Nina A females did not affect significance ( $\tau_{rw,xy,z} = -0.261$ ,  $P < 0.05$ ).

### Grooming and Overall Aggression

Female Japanese macaques did not direct their aggression in inverse relation to the grooming they received from group mates (Nina A:  $\tau_{rw} = 0.128$ , N.S.; Kw:  $\tau_{rw} = 0.069$ , NS; Fisher's combined test:  $\chi^2 = 9.210$ ,  $df = 4$ , NS). Controlling for the effect of kinship did not alter the result (Nina A:  $\tau_{rw,xy,z} = 0.058$ , N.S.).

Since aggression by Japanese macaques is mostly directed down the hierarchy, we re-ran the analysis considering only aggression directed to and grooming received from low-rankers (i.e., excluding dyads below the diagonal). The matrix correlations were again nonsignificant or became significantly positive (Nina A:  $\tau_{rw} = -0.055$ , N.S.; Kw:  $\tau_{rw} = 0.178$ ,  $P < 0.05$ ; Fisher's combined test:  $\chi^2 = 7.993$ ,  $df = 4$ , NS). For Nina A females this result did not change when we controlled for the effect of kinship ( $\tau_{rw,xy,z} = 0.480$ , NS).

### Grooming, Presence on the Same Food Patch, and Cofeeding

In the Kw group, females spent more time feeding in the same food patch with those females from which they received more grooming ( $\tau_{rw} = 0.269$ ,  $P < 0.0001$ ). In contrast, in the Nina A group this relation was not significant ( $\tau_{rw} = 0.158$ , N.S.). The combined test was significant ( $\chi^2 = 22.149$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for the effect of kinship in Nina A group did not alter the result ( $\tau_{rw,xy,z} = 0.145$ , N.S.).

When we analyzed the relation between cofeeding (i.e., feeding within 1 m of each other) and grooming, the results were similar (Nina A:  $\tau_{rw} = 0.171$ , NS; Kw:  $\tau_{rw} = 0.384$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 18.993$ ,  $df = 4$ ,  $P < 0.001$ ; partial correlation controlling kinship in Nina A:  $\tau_{rw,xy,z} = 0.107$ , N.S.). The distribution of cofeeding in the two study groups is shown in Table III.

Significant positive correlations were found between grooming received and the rate of close approaches (within 1 m) received while feeding (Nina A:  $\tau_{rw} = 0.237$ ,  $P < 0.05$ ; Kw:  $\tau_{rw} = 0.306$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 25.183$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for the effect of kinship in Nina A group made the relation nonsignificant ( $\tau_{rw,xy,z} = 0.121$ , N.S.).

Since one of our aims was to test the relationship between grooming and access to food patches that could potentially be monopolized by high-ranking individuals, we re-ran the analysis considering only grooming directed from low-

TABLE II. Matrices of Grooming Given (% of Observation Time) Among Females in Nina A (a) and Kw (b) Group

Monkey	Sya	Shi	Han	Ram	Hot	Htu	Yam	Yri
<b>a. Nina A Group</b>								
Sya		1.65	3.26	0.50	0.34	0	1.03	0.49
Shi	6.85		9.19	2.90	0.60	0	0.94	0.19
Han	1.79	5.81		0.95	0.14	0.11	0.41	0.09
Ram	1.87	6.14	6.81		6.79	2.95	4.03	0.66
Hot	3.21	1.20	2.21	7.28		10.34*	1.79	0.35
Htu	0.41	0.18	0.63	3.47	7.54*		0.12	1.22
Yam	3.55	2.54	5.31	1.52	0.85	0.05		56.25*
Yri	1.27	0.75	0.84	0.07	0	0.41	11.22*	
<b>b. Kw Group</b>								
Ani		0.03	2.40	0	0	0	0	0
Ann	2.67	0	0	5.02	1.70	0.12	0	0
Bla	0	0	0.65	5.23	0	0	0	0
Chi	0	0	0.77	1.89	0	0	5.37	0
Cho	0	0	1.60	0	0	0	7.41	0
Dor	0	0.68	0.72	0	0.89	0.57	0	0
Eli	1.48	0	12.65	0	2.75	1.76	0.57	0.85
Elz	0.24	0	5.26	0	0	0	1.12	0
Fum	11.80	5.47	4.14	0	0.09	0	0	0
Hnn	0	0	0.34	0	5.09	0	0	0
Jun	0.20	0	0.35	0	2.05	0	2.35	0
Kik	0	2.36	0.14	0	0	10.54	0	1.80
Liv	0.11	0.15	0.07	2.09	0	0	0	0
Miy	0	0	0.51	0	5.78	0	0.07	1.26
Nob	0	0	0.20	0	0	0	0	0
Oli	0.30	1.19	2.78	0	0.84	0.24	5.19	3.72
Raf	0	0	0.12	0	2.23	0	0	0
Sar	0	0	1.32	0	1.13	0.20	0	0
Zaz	0	0.09	0.02	0	2.11	1.17	0	1.18
Zin	0	0	0.57	0	3.67	1.96	0	0.92
			0.24	0	2.93	1.03	0	4.66

\*Close kin females in Nina A group.

**TABLE III. Matrices of Female Co-Feeding (% of Observation Time Spent in Proximity, i.e., ≤ 1 m, During Foraging) in Nina A (a) and Kw (b) Group**

Monkey	Sya	Shi	Han	Ram	Hot	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Yri
<b>a. Nina A Group</b>													
Sya		0.619	0.589	0.000	0.030	0	0.000	0.000	0	0.020	0	0	0.005
Shi	1.520		0.139	0.336	0.000	0	0.000	0.000	0	0.113	0	0	0.031
Han	0.406	0.447		0.053	0.038	0	0.000	0.000	0	0.800	0	0	0.344
Ram	0.442	0.260	0.021		0.004	0	0.000	0.107	0	0.012	0	0	0.000
Hot	0.263	0.029	0.315	0.000		0.182*	0.067*	0.174	0	0.052	0	0	0.012
Htu	0.064	0.000	0.031	0.012	0.010	0	0.107	0.052	0	0.132	0	0	0.132
Yam	0.226	0.051	0.076	0.000	0.003	0	0.004	0.045*	0	0.052	0	0	0.369*
Yri	0.112	0.000	0.000	0.031	0.003	0	0.004	0.045*	0	0.052	0	0	0.369*
<b>b. Kw Group</b>													
Ani	0	0	0	0	0	0	0	0	0	0	0	0	0
Ann	0.497	0	0	0	0	0	0	0	0	0	0	0	0
Bla	0	0	0	0.091	0	0	0.156	0	0	0	0	0	0
Chi	0	0	0	0	0	0	0	0	0	0	0	0	0
Cho	0	0	0	0	0	0	0	0	0	0	0.840	0	0
Dor	0	0	0	0	0	0.263	0	0	0	0	0	0	0
Eli	0	0	0	0	0	0.068	0	0.064	0	0	0	0	0.195
Elz	0	0	0.088	0	0.107	0	0	0	0	0	0	0	0
Fum	0.004	0.060	0	0	0	0	0.039	0	0	0	0	0	0
Hnn	0	0.056	0.584	0	0	0	0.052	0	0.037	0	0	0	0.117
Jun	0	0	0	0	0	0	0	0	0	0.510	0.325	0	0
Kik	0	0.200	0	0	0	0	0	1.145	0	0	0.028	0.131	0.331
Liv	0	0	0	0	0	0.575	0	0	0.113	0.008	0.041	0.234	0
Miy	0	0	0	0	0	0	0	0	0	0	0	0	0
Nob	0	0	0	0.078	0	0	0	0	0	0.331	0.325	0	0
Oli	0	0.515	0	0	0.008	0	0	0	0	0.020	0.008	0.031	0
Raf	0	0	0	0	0	0	0.062	0.919	0	0	0	0	0
Sar	0	0	0	0	0	0.181	0.062	0.022	0	0	0	0	0
Zaz	0.058	0	0	0	0	0	0	0	0	0	0	0	0.232
Zin	0	0	0	0	0.361	0	0	0	0	0	0	0	0.252

\*Close kin females in Nina A group.

to high-rankers (i.e., again excluding dyads below the diagonal). The resulting correlations between grooming received from low-rankers and feeding in the same food patch were significantly positive in both groups (Nina A:  $\tau_{rw} = 0.400$ ,  $P < 0.05$ ; Kw:  $\tau_{rw} = 0.396$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 24.761$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for kinship in Nina A did not alter the significance of the relation ( $\tau_{rw,xy,z} = 0.403$ ,  $P < 0.05$ ). Similarly, grooming received from low-rankers was significantly correlated with cofeeding within 1 m in both study groups (Nina A:  $\tau_{rw} = 0.378$ ,  $P < 0.05$ ; Kw:  $\tau_{rw} = 0.423$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 21.806$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for kinship in Nina A did not alter the significance of the relation ( $\tau_{rw,xy,z} = 0.419$ ,  $P < 0.01$ ).

Finally, grooming received from low-rankers was significantly correlated with close approaches received in both study groups (Nina A:  $\tau_{rw} = 0.518$ ,  $P < 0.01$ ; Kw:  $\tau_{rw} = 0.361$ ,  $P < 0.001$ ; Fisher's combined test:  $\chi^2 = 24.185$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for kinship in Nina A did not alter the significance of the relation ( $\tau_{rw,xy,z} = 0.490$ ,  $P < 0.01$ ).

It is worth noting that no aggression was ever recorded when two females were feeding in close proximity or following a close approach while feeding.

### Grooming and Agonistic Support

Coalitions (see Table I for our definition of agonistic support) among females were formed almost exclusively in response to attacks by mature males (89.8% of all coalitions observed: 26/26 in Nina A and 18/23 in Kw). We therefore decided to analyze only coalitions formed in response to attacks received by mature males. Table IV reports their distribution in the two study groups.

A significant positive matrix correlation was found between agonistic support given against male aggressors and grooming received from other females in both study groups (Nina A:  $\tau_{rw} = 0.254$ ,  $P < 0.05$ ; Kw:  $\tau_{rw} = 0.288$ ,  $P < 0.0001$ ; Fisher's combined test:  $\chi^2 = 24.879$ ,  $df = 4$ ,  $P < 0.001$ ). Controlling for the effect of kinship in Nina A removed the significance of the correlation ( $\tau_{rw,xy,z} = 0.070$ , N.S.).

When analyzes were restricted to grooming directed from low- to high-rankers (i.e., excluding dyads below the diagonal), correlations in Nina A became nonsignificant, while the other results were similar (Nina A:  $\tau_{rw} = 0.170$ , N.S.; Kw:  $\tau_{rw} = 0.224$ ,  $P < 0.02$ ; Fisher's combined test:  $\chi^2 = 12.175$ ,  $df = 4$ ,  $P < 0.02$ ; controlling for kinship in Nina A:  $\tau_{rw,xy,z} = 0.121$ , N.S.).

## DISCUSSION

The wild Japanese macaques we studied distributed their grooming in conformance with two main rules: they groomed most those individuals from which they received more grooming and/or those that ranked higher than themselves. The first of these results adds to the growing body of evidence showing the importance of grooming reciprocation among individuals (see the Introduction for references). The second, a common feature of primate grooming [Schino, 2001], suggests the possibility of an interchange of grooming with rank-related benefits. In the second part of our study, we therefore examined the relation between grooming and a few candidates for interchange.

Similarly to what has been reported in other primate populations (e.g., *Macaca radiata* [Silk, 1982], *Cebus capucinus* [Perry, 1996], and *Macaca fuscata* [Schino et al., 2005]), in the wild Japanese macaques grooming exchange was not negatively related to frequency of aggression received. In one of the study groups

**TABLE IV. Matrices of Female Agonistic Support (i.e., % of Aggression Received by Males followed by Support) in Nina A (a) and Kw (b) Group**

Monkey	Sya	Shi	Han	Ram	Hot	Liv	Miy	Nob	Oli	Raf	Sar	Zaz	Zin	Yri
<b>a. Nina A Group</b>														
Sya		3.6	12.1	0	0	0	0	0	0	0	0	0	0	3.0
Shi			21.2	0	0	0	0	0	0	0	0	0	0	0
Han	6.3	0		0	0	0	0	0	0	0	0	0	0	0
Ram	0	0	0		0	0	0	0	0	0	0	0	0	0
Hot	0	0	0	0		0	0	0	0	0	0	0	0	0
Htu	0	0	0	0	0*		11.8*	0	0	0	0	0	0	0
Yam	0	3.6	0	0	0	0	0	0	0	0	0	0	0	15.2*
Yri	0	0	0	0	0	0	0	0	0	2.5*	0	0	0	0
<b>b. Kw Group</b>														
Ani	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ann	50.0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chi	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cho	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Dor	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eli	0	0	50.0	0	0	0	0	0	0	0	0	0	0	0
Elz	0	0	50.0	0	0	0	0	0	0	0	0	0	0	0
Fum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hnn	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Jun	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Kik	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Liv	0	0	0	50.0	0	0	0	0	0	0	0	0	0	100.0
Miy	0	0	100.0	0	0	0	0	0	0	0	0	0	0	0
Nob	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oli	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raf	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sar	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zaz	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zin	0	0	0	33.0	0	0	0	0	0	0	0	0	0	100.0

\*Close kin females in Nina A group.

the correlation between grooming and aggression was even significantly positive, which might suggest that high-ranking females “extort” grooming by the threat of force (see Schino et al. [2005] for a more thorough analysis and discussion about the relation between grooming and aggression). During feeding, however, monkeys appeared to be more willing to tolerate the proximity of those group mates that groomed them the most. Since no aggression was ever recorded during feeding, the monkeys apparently were able to assess correctly which individuals would tolerate their presence. However, it is impossible to say whether this assessment was based on a previous experience of tolerance or grooming. It is also worth noting that the relationships between grooming and cofeeding become tighter when the analysis was restricted to the grooming directed from lower- to higher-ranking animals, which suggests that monkeys may indeed use grooming to “buy” the tolerance of higher-ranking group mates at feeding sites [Mayagoitia et al., 1993; de Waal, 1997; Barrett et al., 2002].

A significant relationship also emerged between the amount of grooming received by a monkey and its willingness to intervene in an ongoing aggression in support of its grooming partners. Previous research in this area yielded inconsistent results (see Henzi and Barrett [1999] for a review). In our study groups such coalitions almost invariably involved two females siding against an attacking adult male. Since females are always lower-ranking than adult males, it is not clear whether high-ranking females make better allies in this context. Indeed, when analyses were restricted to support by higher-rankers (and grooming by lower-rankers), the observed relations weakened. Thus, while these results indicate a positive relation between grooming and coalitionary support, they may not explain the tendency of monkeys to direct their grooming up the hierarchy. Also, kinship is known to have a profound influence on macaque social behavior [Furuichi, 1983; Gouzoules & Gouzoules, 1986], and indeed controlling for kinship weakened the observed relations between grooming and coalitions in one of the study groups. More complete data on kinship relations in multiple social groups are needed before we can reach a better understanding of the independent effect of grooming on coalition formation in Japanese macaques.

A few of our analyses yielded different results in the two study groups. While it is not possible at this time to speculate about the factors that may underlie such discrepancies, these results emphasize the danger of generalizing from data obtained from a single social group. More research is needed to assess whether such differences reflect true intraspecific variability or just the vagaries of statistical sampling.

While correlational data such as ours cannot be used to investigate direct causal relations, they do provide suggestive evidence of covariation. To summarize, the wild Japanese macaques in Yakushima appeared to exchange grooming received both with the same “currency” (other grooming) and with different currencies (tolerance at feeding sites and coalitionary support against adult males). In particular, we suggest that the need to exchange grooming for tolerance at feeding sites may be the main factor underlying the tendency of Japanese macaques in Yakushima to direct their grooming up the hierarchy.

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