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Support for being groomed in long-tailed macaques, *Macaca fascicularis*

CHARLOTTE K. HEMELRIJK*
Ethologie und Wildforschung, Zoologisches Institut, Universität Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland

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Grooming and support in fights among primates are thought to be altruistic (Seyfarth & Cheney 1984). According to the theory of reciprocal altruism, such acts can be maintained by natural selection among non-relatives only if an actor receives an altruistic act in return (Trivers 1971). Indications for reciprocation and exchange of grooming and support in fights among primates come mainly from observations on spontaneous behaviour (e.g. Packer 1977; de Waal & Luttrell 1988; Hemelrijk & Ek 1991). These studies, however, are not conclusive, since (1) they are contradicted by other studies (Silk 1982; Bercovitch 1988; Noë 1990); (2) they may easily be side-effects of correlations with other variables (e.g. dominance rank, see Hemelrijk 1990b) and (3) they do not show whether giving is contingent on receiving in time.

Furthermore, in the only experimental study in which a causal relationship between receiving and subsequent giving (i.e. being groomed and support) has been claimed (Seyfarth & Cheney 1984), actual support was not recorded. Seyfarth & Cheney (1984), using female vervet monkeys, *Cercopithecus aethiops*, tape-recorded a certain vocalization (which was assumed to solicit support) used by animal A in a fight and played these recordings back near animal B, either after B was groomed by A or after a period when no grooming had occurred. They found that B looked up to the speaker (from which the groomer's vocalization was played back) for longer if it had recently been groomed by A. From this, Seyfarth & Cheney concluded that being groomed in the recent past by an unrelated individual increases the likelihood that the groomee subsequently helps its benefactor in a fight. It is not known, however, if looking up is a correlate of 'support'.

Seyfarth & Cheney also omitted to check whether B's active grooming of A, instead of her being groomed by A, also stimulates B's subsequent attention to A's scream. In other words, any recent grooming interaction between B and A, irrespective of its direction, may have heightened B's attention to the scream of A. Because of this, Seyfarth & Cheney's results may not be relevant to the theory of reciprocal altruism.

Therefore, I studied interchange of support for being groomed by giving individual long-tailed macaques the opportunity to support others under three conditions: after being groomed by the other, after grooming the other and without prior grooming. The results provide direct evidence that after being groomed recently by another a monkey is more likely to support its groomer than without prior grooming.

The experiments were performed at the field station Bockengut (University of Zürich) with macaques from a colony of 36–40 individuals housed in a 1050 m^2 indoor/outdoor enclosure. The colony was formed in 1983 by removing several matrilines from a long-established colony at the Basel Zoo.

To guide the social behaviour of the test individuals and to exclude disturbances by other group members, triads of individuals were separated from the rest of the group and kept temporarily in smaller indoor and outdoor cages. Experiments took place in an indoor cage, one triad at a time. Each triad partook in an experiment only once a day and not more than four times a week. After the experiments, triads were reunited with the rest of the group.

To elicit grooming, one of the individuals (A or B) of the experimental triad was lured into a small passage cage with a morsel of food, and a sticky mixture of seeds and syrup was dropped on its back. After this, it was reunited with the other two and I watched for 10 min to see who groomed whom. During the next 10-min period, aggressive

*Present address: Insitüt für Informatik, Universität Zürich-Irchel, Winterthurerstrasse 190, 8057 Zürich, Switzerland.

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interactions were provoked with the help of an assistant by feeding individual C, the lowest ranking individual of the triad, popcorn, biscuits and nuts (long-tailed macaques hardly ever attack higher ranking individuals). To stimulate the two higher ranking individuals to fight for food with C, they were occasionally fed tidbits as well. These aggressive interactions did not terminate previous grooming interactions. We noted whether one individual was attacked by a second monkey (by being confronted with a threat face, or being lunged at or pursued) and whether the third monkey subsequently supported by attacking one of the combatants in the fight. Most interactions consisted only of threat and chasing; none resulted in physical injury.

Whenever it was established that the third member (B) had been watching the aggressive interaction between the other two, this was counted as an opportunity for intervention. Conflicts, opportunities to support and support were noted only if both observers agreed. Since the second observer did not know whether grooming had occurred in the first 10 min, she performed her observations blind. Members of a dyad AB were not kin and to meet the requirements of statistical analysis, neither was included in another dyad.

From April 1992 to July 1993, about 400 experiments were performed on about 80 different triads. Experiments on each new triad were continued when in the first three experimental sessions it had shown at least once all of the following three activities: (1) grooming between A and B; (2) an aggressive interaction between A and C; (3) an aggressive intervention by B in an aggressive interaction between A and C. The experiments were terminated when: (1) A and B no longer groomed one another, but groomed C; (2) it appeared impossible to provoke aggression in three subsequent experimental trials; or (3) the winter set in and the animals had to be allowed free access to the indoor cages. It appeared impossible to induce aggression in males (eight trials) and therefore I confined myself to mature females (3·5 years and older). Only for seven triads could data be collected on all three conditions (being groomed, grooming and no recent grooming).

Grooming could have occurred in the waiting cage before the experiment began and therefore might have stimulated support in the experiment, even if it was recorded as a non-grooming condition; to check this possibility, the second observer recorded grooming in the 10 min preceding the syrup treatment. Such unintended situations did not occur: even when animals had groomed each other in the pretest period, the interval between pretest-grooming and the opportunity to support was longer than that in any 'real' grooming condition (where grooming occurred in the first 10 min of the experiment).

Although grooming induced by the syrup-and-seeds treatment involved a higher percentage of licking than non-stimulated grooming, grooming continued after the syrup was removed and occurred frequently when no syrup was administered. Therefore, the results are not considered to be a consequence of abnormal grooming behaviour.

The results concern aggressor support only, since victim support did not occur. (It also occurred less often than aggressor support in the complete group.) In agreement with Seyfarth & Cheney (1984) the percentage of support (i.e. the frequency with which B supported A relative to the total number of opportunities B had to support A) differed significantly between the three conditions (Friedman test, $\chi^2_r=9{\cdot}5$, $P=0{\cdot}008$; Fig. 1). Females supported others significantly more often after being groomed by them in the recent past than without prior grooming (multi-comparison test based on the Friedman rank sums, difference between both rank sums (RSdiff)=11, $P=0{\cdot}008$ one-tailed). In addition, the tendency to support others was not increased by any grooming interaction (irrespective of its direction), since after having groomed A (instead of being groomed by her), B did not support A relatively more often than without foregoing grooming (RSdiff=4, NS).

It is unknown whether grooming and support are altruistic acts in terms of inclusive fitness (Dunbar 1988). The results, although confirming reciprocation, should therefore not be considered solid proof for the theory of reciprocal altruism. Futhermore, to study whether a Tit-for-Tat-like mechanism (Axelrod & Hamilton 1981) might operate, one would need to know whether received support also leads to increased grooming (or another kind of beneficial act) of the supporter by the receiver of support.

In the same period observational data were collected on the group as a whole in the outside enclosure. Unfortunately, these could not be

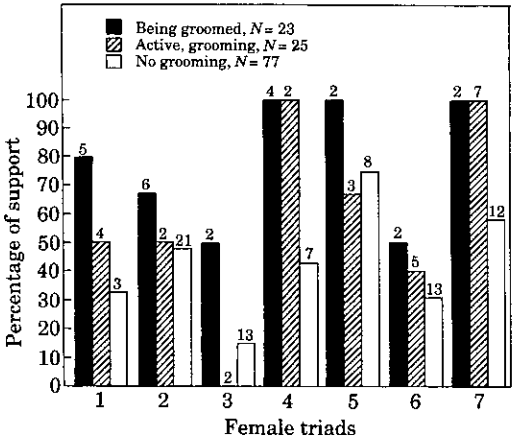

Figure 1. Percentage of support (i.e. the frequency with which B supported A relative to the total number of opportunities B had to support A) in seven triads for the three conditions. The numbers above the bars indicate the number of experimental trials. The number of experiments varied between the three conditions almost significantly (Friedman test, $\chi^2_r = 5{\cdot}6$, $P = 0{\cdot}06$). Because the non-grooming condition prevailed, the corresponding percentage of support may have been more reliable than that measured for the other conditions; however, individual comparisons of the number of experiments between the three conditions revealed no significant differences (multi-comparison test).

compared with the experimental data, since: (1) in the complete group no support was observed among the pairs used in the experiments; (2) although support appeared to be significantly correlated (*Kr* test, see Hemelrijk 1990a, b) with received grooming after partialling out received support, grooming, dominance rank and kin relations, it was impossible to partial out the variables simultaneously.

From a cognitive point of view, one would be inclined to assume that individuals who exchange acts must remember the identity of the groomer. This, however, is not proven by these experiments nor by those of Seyfarth & Cheney, since the alternative possibility that being groomed increases the tendency to support whomsoever is not refuted. To test this, additional experiments must be performed with quartets, in which B has the opportunity to support C against A, as was the case in my experiments, but now after (active or passive) grooming with the fourth partner D or without preceding grooming with D or A.

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