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Grooming reciprocation among female primates: a meta-analysis

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The theory of reciprocal altruism offers an explanation for the evolution of altruistic behaviours among unrelated animals. Among primates, grooming is one of the most common altruistic behaviours. Primates have been suggested to exchange grooming both for itself and for rank-related benefits. While previous meta-analyses have shown that they direct their grooming up the hierarchy and exchange it for agonistic support, no comprehensive evaluation of grooming reciprocation has been made. Here we report on a meta-analysis of grooming reciprocation among female primates based on 48 social groups belonging to 22 different species and 12 genera. The results of this meta-analysis showed that female primates groom preferentially those group mates that groom them most. To the extent allowed by the availability of kinship data, this result holds true when controlling for maternal kinship. These results, together with previous findings, suggest that primates are indeed able to exchange grooming both for itself and for different rank-related benefits.

Keywords: reciprocation; altruism; grooming; primates

1. INTRODUCTION

Altruistic behaviours, that is those that benefit the recipient at some cost to the donor, defied evolutionary explanations until the formulation of kin selection theory (Fisher 1930; Haldane 1932; Hamilton 1964) and reciprocal altruism theory (Trivers 1971), that provided evolutionary explanations of altruism among related and unrelated animals, respectively.

However, while evidence for kin selection in favouring altruism among relatives is robust (Griffin & West 2002), evidence for reciprocal altruism is much weaker. Relatively few examples of reciprocal altruism have been published, and these have often been difficult to replicate (Packer 1977; Wilkinson 1984; Milinski 1987; Bercovitch 1988; Dugatkin 1988).

Allogrooming (grooming, hereafter) is possibly the most common primate affiliative behaviour and is also observed in non-primates (e.g. Wilkinson 1986; Mooring *et al.* 2004). It is generally considered to be altruistic, in that it provides benefits to the recipient in terms of removal of ectoparasites, release of beta-endorphines and reduction of tension (Schino *et al.* 1988; Keverne *et al.* 1989; Aureli *et al.* 1999; Zamma 2002). Its costs, however, are less clear (Dunbar & Sharman 1984; Maestripieri 1993). The study of grooming has had a pivotal role in our understanding of the evolution of reciprocal altruism (e.g. Seyfarth & Cheney 1984).

Demonstrating reciprocal altruism requires showing the existence of a contingency between giving and receiving (Olendorf *et al.* 2004). Traditionally, this has been interpreted as a (relatively) short-term temporal contingency. For example, both Seyfarth & Cheney (1984) and Hemelrijk (1994) showed that previous grooming may increase the probability of agonistic support, and both Barrett *et al.* (1999) and Manson *et al.* (2004) showed that monkeys time-match grooming given and received during each grooming session.

Group living animals, however, do not make their behavioural decisions exclusively in the context of short-term dyadic interactions, because a further level of complexity is added by the possibility of exerting partner choice, that is of deciding which partner to interact with (Noë & Hammerstein 1995; Noë 2001). While classical reciprocal altruism theory (Trivers 1971) interpreted partner choice mostly in terms of detection of cheaters, more recent biological market approaches emphasized the varying balance between giving and receiving that is due to economic forces such as fluctuating demand/offer ratios (e.g. Henzi & Barrett 2002; Slater *et al.* 2007). Within this framework, it becomes important to test how animals distribute their altruistic behaviours (e.g. grooming) among their group mates, that is to investigate their quantitative partner choices.

Grooming offers a unique possibility in this respect, as it is commonly and easily observed. Indeed, data on the distribution of grooming are frequently published, and correlations between giving and receiving have been reported, suggesting the maintenance of a long-term balance (e.g. Silk *et al.* 2006). We thus capitalized on the availability of published grooming data and used modern meta-analytical techniques to test whether female primates reciprocate the overall amount of grooming they receive, that is whether they exert partner choice by grooming preferentially those individuals that groom them most.

2. MATERIAL AND METHODS

(a) *Data collection and analysis*

Data inserted into analyses are derived from published or unpublished matrices of grooming exchanged between adult females. Details of the data collection procedure and data entered into analyses are shown in the electronic supplementary material. Data available for analysis include 48 social groups belonging to 22 different species and 12 genera.

For each grooming matrix, we calculated the row-wise matrix correlation between grooming given and grooming received (i.e. between the grooming matrix and its transposition) using the software MATMAN v. 1.1 (Noldus Information Technology 2003). When information about maternal kinship was available, we also calculated partial row-wise matrix correlations between grooming given and received, controlling for the effect of maternal kinship. For each social group, we thus obtained one or two (if kinship data were available) r values (table 1 in the electronic supplementary material).

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Data entered into the meta-analyses were Fisher's Z-transforms and their estimated variances were obtained from r values and sample sizes according to Rosenberg *et al.* (2000). We conducted random effect meta-analyses following Egger *et al.* (2001). Meta-analyses are potentially affected by publication bias, that is, by the tendency of non-significant results to remain unpublished. We tested for publication bias following Egger *et al.* (1997).

All analyses were run using Stata v. 9.2 (Sterne *et al.* 2001). We present weighted average r values as measures of effect size and their 95% CI.

3. RESULTS

A meta-analysis of grooming reciprocation yielded a weighted average r significantly greater than 0 ($r=0.583$, 95% CI$=0.472$–0.676, $N=48$, $z=8.505$, $p<0.001$). Egger's test did not detect any significant publication bias in this sample (intercept$=0.782$, $t=0.55$, n.s.). Limiting the analysis to macaques (the only set with enough data for a single-genus analysis) did not change the results (weighted average $r=0.602$, 95% CI$=0.451$–0.719, $N=22$, $z=6.482$, $p<0.001$; Egger's test: intercept$=1.694$, $t=0.75$, n.s.).

The analyses above were rerun using data on grooming reciprocation that controlled the influence of maternal kinship. As expected, weighted average r was considerably reduced, but it remained significantly greater than 0 ($r=0.468$, 95% CI$=0.287$–0.616, $N=22$, $z=4.700$, $p<0.001$). Egger's test did not detect any significant publication bias in this sample (intercept$=1.255$, $t=0.57$, n.s.). Limiting the analysis to macaques did not change the results (weighted average $r=0.358$, 95% CI$=0.155$–0.532, $N=13$, $z=3.366$, $p<0.001$; Egger's test: intercept$=1.224$, $t=0.44$, n.s.).

4. DISCUSSION

Using a large data sample from a variety of species, this study shows female primates reciprocate the amount of grooming received, that is that they groom preferentially those individuals that groom them most. The application of meta-analytical techniques allowed us to highlight a general pattern that seems to be widespread across the primate order. It is also interesting to note that recent evidence points to similar exchanges of altruistic behaviours in other taxa. For example, group living coatis (*Nasua nasua*) support preferentially during fights those individuals that support them most (Romero & Aureli in press).

Kin selection is known to potentially influence grooming relationships. Indeed, a previous meta-analysis had shown that primates groom preferentially their maternal kin (Schino 2001). However, to the extent that we were able to control for kinship (see the electronic supplementary material), grooming reciprocation as observed in this study was not simply due to the influence of maternal kinship and is thus to be ascribed to the exchange of mutual benefits (*sensu* West *et al.* 2007). Obviously, while our results provide general support for reciprocal altruism theory, they tell us nothing about possible short-term alteration of long-term grooming balances caused by fluctuating market forces.

Also, this meta-analysis could only reveal the general pattern of grooming reciprocation and could not delve into the proximate mechanisms involved. Thus, while it is clear that female primates prefer to groom those individuals that groom them most, little is still known about how they make their choices, and about the time-frame of their decisions. While some authors have argued that short-term temporal contingencies govern primate decision making (e.g. Henzi & Barrett 1999), recent evidence show that robust correlations between giving and receiving are evident even in the absence of short-term contingencies (Schino *et al.* 2007). The maintenance of long-term balances in the face of possible short-term fluctuation in reciprocation is clearly an aspect that will need further research.

Schino (2001, 2007) used meta-analytical techniques to show that female primates tend to direct their grooming up the hierarchy in order to exchange it for agonistic support (and possibly other rank-related benefits). Not all grooming, however, is directed up the hierarchy to be exchanged for rank-related benefits. As shown by our results, grooming is also exchanged for other grooming. The combined results of the present and previous meta-analyses thus suggest that primates overall are able to exchange grooming both for itself and for different rank-related benefits. These results provide the basis for investigations of the trade-off between these two processes, and of the proximate mechanisms underlying primate decision making in the context of reciprocal exchanges. Understanding the mechanisms (computational, emotional or otherwise) underlying the capacity to keep track and make decisions about the exchange of multiple currencies will be a challenge for the ingenuity of animal behaviourists.

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