LETTER

The relative roles of kinship and reciprocity in explaining primate altruism

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Abstract

Several hypotheses have been proposed to explain the evolution of altruistic behaviours. Their relative roles in explaining actual cases of animal altruism are, however, unclear. In particular, while kin selection is widely believed to have a pervasive influence on animal behaviour, reciprocity is generally thought to be rare. Despite this general agreement, there has been no direct test comparing the relative roles of kinship and reciprocity in explaining animal altruism. In this paper, we report on the results of such a test based on a meta-analysis of allogrooming in primates, grooming being probably the most common altruistic behaviour among mammals. In direct contrast to the prevailing view, reciprocity played a much larger role than kinship in explaining primate allogrooming. These results point to a more significant role of reciprocity in the evolution of animal altruism than is generally acknowledged.

Keywords

Altruism, grooming, kinship, primates, reciprocity.

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INTRODUCTION

Animals frequently engage in behaviours that benefit other individuals (Dugatkin 2002). Several hypotheses have been proposed to explain the evolution of such apparently altruistic behaviours, but the scientific debate has concentrated more on their theoretical plausibility than on their relative roles in explaining the evolution of actual cases of animal altruism (Nowak 2006). As a result, our understanding of the prevalence of the various evolutionary mechanisms that have been proposed is based more on an educated guess than on hard data. Despite this paucity of data, a general consensus can be identified in the literature. Of the two main mechanisms that have been proposed as explanations for the evolution of altruistic behaviours one, kin selection (Hamilton 1964), is widely believed to have a pervasive influence on animal behaviour (West *et al.* 2002), while the other, reciprocal altruism (Trivers 1971), is often considered to be of minor importance because the conditions for it to operate are believed to be rare (Hammerstein 2003; Stevens *et al.* 2005).

Besides ignoring the possible interactions between kin selection and reciprocity (Axelrod & Hamilton 1981), this view is based on two (often untold) assumptions. First, whenever an altruistic behaviour occurs among relatives its evolution is to be ascribed entirely to kin selection.

Second, the proximate mechanism supporting all cases of reciprocal altruism approximates what Brosnan & de Waal (2002) called 'calculated reciprocity', a mechanism that is likely to require cognitive capacities beyond those possessed by most animal species, including primates. In fact, both of these assumptions appear to be unwarranted (Chapais 2006; Schino & Aureli 2009), so that a more critical approach to defining the relative roles of kinship and reciprocity in explaining animal altruism seems to be needed.

One of the most widespread altruistic behaviours in animals is allogrooming (hereafter grooming), which provides immediate benefits to the recipient in terms of removal of ectoparasites (Zamma 2002) and reduction in tension/anxiety (Schino *et al.* 1988; Aureli *et al.* 1999; Engh *et al.* 2006) while implying costs for the actor in terms of reduced opportunities for other activities and decreased vigilance against predators and conspecifics (Maestripieri 1993; Cords 1995). Grooming is probably the most common altruistic behaviour among primates and, possibly, among other mammals and birds (Dunbar 1988; Mooring *et al.* 2004; Radford & Du Plessis 2006). In this paper, we took advantage of the widespread availability of grooming data of primates and used meta-analytical techniques to conduct what, to our knowledge, is the first quantitative test comparing the relative roles of kinship and reciprocity in

shaping how animals distribute their altruism among group members. In direct contrast to the prevailing view, reciprocity appeared to play a much larger role than kinship in explaining primate grooming.

MATERIALS AND METHODS

Data collection

We first extracted from the literature published matrices of grooming exchanged between group-living sexually mature female primates. To be included in our analyses, the published data had also to provide information on the kinship relations among the subjects. We supplemented

these published data with unpublished grooming matrices from our research teams and others kindly provided by colleagues.

The final database included 25 social groups belonging to 14 different species and nine genera. Data entered into the analyses are shown in Table 1. Only social groups comprising at least four adult females were considered. Information on the maternal kin relations among the subjects was derived from the original papers. For one of the study groups, kinship information was derived from genetic analyses, for all others from demographic records. In three groups dyads were classified simply as related or unrelated, in all others continuous degrees of maternal kinship were provided.

Table 1 Data entered in the meta-analyses

Species	Source/group	Group size (no. of adult females)	Grooming given and grooming received controlling kinship (semipartial r)	Grooming given and kinship controlling grooming received (semipartial r)
Ateles geoffroyi	Schaffner, Forshaw & Aureli (unpublished)/Apenheul[1]	6	0.0990	0.3519
Ateles geoffroyi	Schaffner & Aureli (unpublished)/Chester[2]	5	0.6186	0.0548
Cebus apella	Schino, Di Giuseppe & Visalberghi (unpublished)[3]	7	0.3020	0.2592
Cebus apella	Tiddi & Polizzi di Sorrentino (unpublished)[4]	9	0.3999	0.3076
Cebus olivaceus	O'Brien (1993)/Main Group	9	0.6608	0.1345
Colobus guereza	Grunau & Kuester (2001)	5	0.3059	−0.2665
Erithrocebus patas	Nakagawa (1992)	6	0.5418	0.1212
Lemur catta	Paoli & Palagi (unpublished)[5]	4	0.8525	−0.2683
Macaca arctoides	Butovskaya *et al.* (1994)	18	0.5454	0.0332
Macaca fascicularis	Aureli (unpublished)/group A[6]	9	0.0938	0.4981
Macaca fascicularis	Aureli (unpublished)/group B[7]	24	0.0600	0.2168
Macaca fascicularis	Butovskaya *et al.* (1995)/group H	7	0.5617	0.1245
Macaca fuscata	Aureli (unpublished)/Arnhem[8]	9	0.4045	0.2347
Macaca fuscata	Aureli (unpublished)/Artis[9]	6	0.1726	0.2548
Macaca fuscata	Mehlman & Chapais (1988)	6	0.3487	0.4308
Macaca fuscata	Takahashi & Furuichi 1998/Kinkazan A	14	0.5723	0.1245
Macaca fuscata	Takahashi & Furuichi (1998)/Yakushima M	7	0.4844	0.0632
Macaca fuscata	Ventura (1998)[10]	22	0.2750	0.3111
Macaca fuscata	Ventura *et al.* (2006)/Kw	20	0.8647	−0.0100
Macaca fuscata	Ventura *et al.* (2006)/Nina-A	8	0.2698	0.2837
Macaca mulatta	Sade (1972)	9	0.4559	0.1166
Macaca sylvanus	Aureli (unpublished)[11]	12	0.1879	0.3409
Mandrillus sphynx	Schino & Pellegrini (unpublished)[12]	6	0.5018	0.0707
Presbytis entellus	Borries *et al.* (1994)	13	0.4389	0.1054
Pan troglodytes	Aureli, Caws & Koyama (unpublished)[13]	15	0.6198	0.0539

For unpublished studies, details on the housing or location of the study group are provided below together with references to published studies that contain further information on the data collection procedures, when available: 1: Apenheul zoo, The Netherlands; 2: Chester zoo, UK (Schaffner & Aureli 2005); 3: ISTC-CNR primate centre, Italy (Schino *et al.* 2009); 4: Iguazù National Park, Argentina; 5: Pistoia zoo, Italy (Palagi *et al.* 2005); 6: Utrecht University, The Netherlands (Aureli *et al.* 1997); 7: Utrecht University, The Netherlands (Aureli *et al.* 1995); 8: Arnhem zoo, The Netherlands (Aureli *et al.* 1997); 9: Artis zoo, The Netherlands (Aureli *et al.* 1997); 10: Rome zoo, Italy (Schino *et al.* 2003); 11: Apenheul zoo, The Netherlands (Aureli *et al.* 1997); 12: Rome zoo, Italy (Schino & Pellegrini 2009); 13: Chester zoo, UK (Koyama *et al.* 2006).

Data analysis

For each social group, we entered in the analyses grooming given and received by each group member to/from each other group member, and their kinship. Based on within-subject regressions (Rabe-Hesketh & Skrondal 2008; van de Pol & Wright 2009), for each social group we calculated first bivariate correlation coefficients between grooming given and grooming received and between grooming given and kinship, and then semipartial correlation coefficients between grooming given and grooming received (controlling for kinship) and between grooming given and kinship (controlling for grooming received). Semipartial correlations provided us with estimates of the proportion of total variance in grooming distribution uniquely accounted for by reciprocity and by kinship removing the concomitant effect of the other variable, and thus of their relative roles in explaining grooming distribution within each social group.

Note that within-subject regressions estimate relationships between dependent and independent variables after data centring on each subject's mean scores. This procedure removes any effect due to interindividual differences in, for example, the general propensity to give or receive grooming (e.g. as a consequence of grooming given or received from anybody). As such, it allows testing for direct reciprocity excluding the influence of generalized reciprocity (Rutte & Taborsky 2007, 2008).

We obtained Fisher's Z transforms and their estimated variances from r values and sample sizes according to Rosenberg *et al.* (2000), and entered them into random-effect meta-analyses following Egger *et al.* (2001). Z values were then back transformed to r values for presentation. We also tested for publication bias following Egger *et al.* (1997), but as we did not detect any bias we are not reporting those tests.

Comparative analyses can be affected by the phylogenetic relationships between species. This is a problem that is especially relevant when correlations *between* species values are made in order to make inferences about correlated evolution. The problem of phylogenetic non-independence is less relevant when overall effect sizes are estimated (instead of relationships between effects) as in this study. However, in order to check for any effect of phylogenetic non-independence, we rerun all analyses using a single group (always the largest) per species or per genus (following Harvey & Pagel 1991). All analyses were run using Stata 10.1 (StataCorp 2007).

RESULTS

In order to provide results comparable to those reported in previous studies (Schino 2001; Schino & Aureli 2008), we first conducted separate meta-analyses of the effect of grooming received and kinship on grooming given without removing the effect of the other variable. Grooming given was significantly related to grooming received (weighed average $r = 0.709$, 95% confidence interval: 0.584–0.801, $z = 7.989$, $N = 25$, $P < 0.0001$). Similarly, grooming given was significantly related to kinship (weighed average $r = 0.493$, 95% confidence interval: 0.377–0.594, $z = 7.354$, $N = 25$, $P < 0.0001$). The effects of grooming received and kinship were not significantly different, as the confidence intervals yielded by the two meta-analyses overlapped. Similar results were obtained when analyses were rerun including only one group per species or per genus (see Appendix S1 in Supporting Information).

We then conducted meta-analyses based on the semipartial correlations between grooming received and grooming given and between kinship and grooming given while controlling the effect of the other variable (see Table 1 for the semipartial correlations of individual studies). A meta-analysis of grooming given in relation to grooming received while controlling for kinship revealed a weighed average semipartial r value of 0.453 (95% confidence interval: 0.319–0.568). This was significantly different from zero ($z = 6.106$, $N = 25$, $P < 0.0001$). Thus, after controlling kinship, reciprocity uniquely explained *c.* 20% ($r^2 = 0.205$) of the total variance in the distribution of grooming. In contrast, a meta-analysis of grooming given in relation to kinship while controlling for grooming received revealed a weighed average semipartial r value of only 0.178 (95% confidence interval: 0.114–0.240). This was again significantly different from zero ($z = 5.397$, $N = 25$, $P < 0.0001$), but accounted for only *c.* 3% ($r^2 = 0.032$) of the total variance in grooming distribution. Note that the two meta-analyses yielded 95% confidence intervals that did not overlap (Fig. 1). The effect of reciprocity was thus significantly larger than that of kinship. Similar results were obtained when analyses were rerun including only one group per species or per genus (see Appendix S1).

Given the paired nature of our data (two correlation coefficients for each social group), we also replicated the analyses above using t tests for paired data. Reciprocity had a larger effect than kinship both when bivariate correlations were compared ($t = 3.670$, d.f. $= 24$, $P = 0.0006$) and when semipartial correlations removing the effect of the other variable were compared ($t = 3.539$, d.f. $= 24$, $P = 0.0008$). Note, however, that these analyses, differently from the meta-analyses above, did not weigh data from the different studies in relation to their estimated variance.

DISCUSSION

Although theoretical models often suggest that interactions between different evolutionary mechanisms can favour the initial spread of altruistic behaviours (Axelrod & Hamilton 1981; Hamilton & Taborsky 2005), empirical data only allow
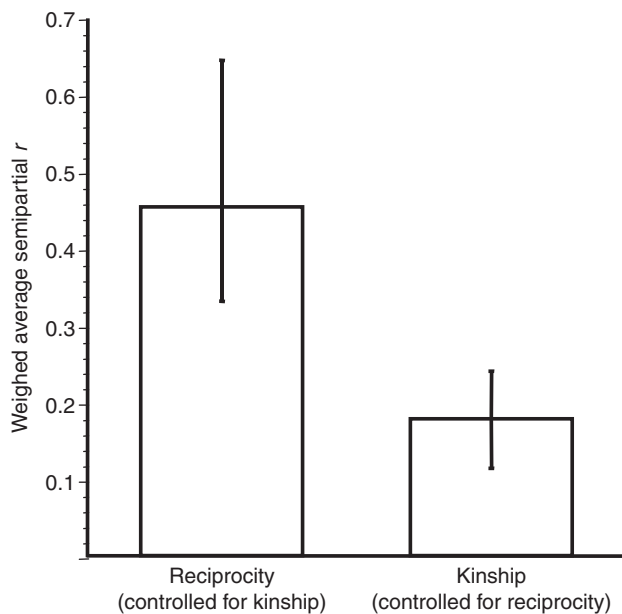
Figure 1 A comparison of the relative roles of reciprocity and kinship in explaining the distribution of primate grooming. The figure shows the weighed average semipartial r values (and their 95% confidence intervals) obtained from meta-analyses of the relation between grooming given and grooming received (controlling for kinship) and of the relation between grooming given and kinship (controlling for grooming received).

to examine how present-day animals distribute their altruistic behaviours in time or among group mates. In this study we, somewhat artificially, pitted the two leading theories explaining animal altruism against each other in order to obtain estimates of their relative roles in explaining primate grooming. Our results showed that reciprocity plays a much larger role than kinship in explaining how primates distribute their grooming among group members. To our knowledge, this is the first study that compares quantitatively the roles played by different evolutionary mechanisms in explaining animal altruism. The larger effect of reciprocity compared to kinship that we found is in direct contrast to the prevailing view that considers reciprocity as rare and unlikely to explain animal altruistic behaviours (Hammerstein 2003; Stevens *et al.* 2005).

Our data, however, did not allow us to test the role of generalized reciprocity (Rutte & Taborsky 2007) and group selection (Wilson & Wilson 2007) in the evolution of primate altruism. We had also to restrict our analysis to exchanges of grooming for other grooming, thus ignoring exchanges with rank-related benefits such as agonistic support (Schino 2007). This limitation, however, is likely to cause an underestimation of the role of reciprocity, and is thus unlikely to alter our general conclusions. Being based on meta-analyses of grooming distribution in 25 different primate groups, our results cannot be explained by the idiosyncratic behaviour of a few individuals. On the contrary, they likely reflect general behavioural patterns that are widespread across the primate order and possibly beyond.

The difficulties that in the last 40 years have plagued attempts to demonstrate actual cases of reciprocation may derive in part from the prominent role that models based on the Prisoner's Dilemma game have played in how reciprocity is conceived and tested (Noë 2006; Silk 2007). Models based on the Prisoner's Dilemma construe reciprocity as involving isolated dyads and thus concentrate on testing the temporal contingency between giving and receiving. As group-living animals usually have the possibility to interact with multiple partners, more recent theorizing has emphasized the role of partner choice in the evolution of animal social behaviour (Noë & Hammerstein 1995; Noë 2001). In this view, altruistic behaviours can evolve through a process of reciprocal partner choice in which animals maximize received benefits by directing their altruistic behaviour preferentially to those individuals that reciprocate most (Connor 1995; Sherratt & Roberts 1998; Schino & Aureli 2009).

The cognitive limitations of most animals, including primates, have been suggested to make reciprocation difficult and thus limit its evolvability (Stevens & Hauser 2005; Stevens *et al.* 2005). In addition to be rare, reciprocity is therefore also assumed to play a minor role in determining animal social preferences. In contrast to this reasoning, recent work has suggested that a proximate mechanism based on emotional bookkeeping can easily circumvent possible animal cognitive limitations and thus that proximate constraints are unlikely to have impeded the evolution of reciprocally altruistic behaviours (reviewed in Schino & Aureli 2009). The results reported here support this view and emphasize the role that reciprocity plays in determining primate social choices. By focusing exclusively on attempts to demonstrate the existence of a short-term temporal contingency between giving and receiving behavioural biologists may have been looking for the wrong kind of evidence. Primate social choices seem to be relatively indifferent to events in the immediate past, and seem to depend instead on long-term comparisons of benefits received by the various potential partners available (Schino *et al.* 2007, 2009; Melis *et al.* 2008; Gomes & Boesch 2009; Schino & Pellegrini 2009). Thus, while temporal contingencies between giving and receiving may play a relatively minor role in guiding animal reciprocity because of the associated cognitive constraints, reciprocal partner choice based on long-term social bonds may have a critical role in explaining the distribution of altruism among both primates (Schino & Aureli 2009) and non-primates (Smith *et al.* 2007; Romero & Aureli 2008).

Animals can maximize their inclusive fitness by directing their altruistic behaviours either to kin or to those individuals that reciprocate most (while a role for generalized reciprocity has also been proposed). Our results suggest that among primates reciprocity contributes to fitness maximization to a greater extent than previously thought. Further studies on other taxa and altruistic behaviours will be needed to evaluate the generality of this conclusion.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Additional results.

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