Market forces predict grooming reciprocity in female baboons

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We argue that grooming is a commodity that female primates can trade, either for itself or in exchange for other services (*sensu* biological markets theory) and that the decision to do either will depend on the degree of competition within a social group. We test this using data from four chacma baboon troops, living in two populations that differ markedly in the degree of contest competition. As predicted by the predominance of grooming dyads in which females are closely ranked there was, in all four troops, a positive correlation between the time invested by one partner and that by the other. In addition, as predicted, the allocation of time was more closely matched in troops where grooming could not be exchanged for anything else. In troops where resource competition was high, we found in one of two troops a positive relationship between rank distance and the discrepancy in time allocation, with the lower ranking of the partners contributing more grooming.

Keywords: grooming; baboons; biological market; aggression; dominance; relationships

1. INTRODUCTION

Female chacma baboons (*Papio cynocephalus ursinus*) in the Drakensberg Mountains, South Africa, strive to maintain reciprocated grooming partnerships in the face of other demands on their time and, as with chacma baboons elsewhere, persist with these relationships in the complete absence of coalition formation (Ron *et al.* 1996; Henzi *et al.* 1997; J. B. Silk, personal communication). As such, they contradict the central predictions of the widely accepted grooming for support hypothesis, which states that females give grooming in the expectation of future coalitionary support during aggressive interactions on a tit-for-tat (reciprocal altruism) basis (Seyfarth 1977; Seyfarth & Cheney 1984; Harcourt 1988). The recent development of the biological markets theory (Noë & Hammerstein 1995) provides an alternative conception to models of reciprocal altruism, likening the formation of partnerships between animals to trade agreements involving the exchange of valuable commodities. The fact that Drakensberg baboon females adjust clique size in order to ensure within-bout reciprocation with their partners (Henzi *et al.* 1997) suggests that grooming may be traded as a commodity, rather than performed as an altruistic act and that the biological markets model may be a better predictor of female grooming patterns. Here we provide the first test of whether female baboons regard grooming as a tradeable commodity and show that variation in grooming patterns across populations may be linked to differences in the composition of the market-place. Both of these findings are necessary precursors to testing the predictions of the biological market theory itself.

If the intrinsic hygienic and hedonistic benefits of grooming (Keverne *et al.* 1989; Tanaka & Takefushi 1993) give it currency (Muroyama 1994), then it may be exchanged for itself (reciprocal traders) or in return for other goods (interchange traders). In primate groups, where animals have a range of potential partners from whom to choose, trading should be determined by their standing in the market-place and the goods which they can offer. This will be determined in large part by the extent to which dominance effects are important within a group. When, as in the Drakensberg Mountains (Henzi *et al.* 1992), resources cannot be monopolized, reciprocal traders will dominate since grooming can be traded only for itself. When resources are monopolizable and differences in resource holding potential (RHP) determine access to them, then grooming can be traded for other goods such as support during aggression, tolerance at feeding sites or, perhaps, direct access to the resource itself (de Waal 1997). Interchange traders are therefore predicted to appear, although reciprocal trading will still be found among individuals with a similar RHP.

If female chacma baboons use grooming as a commodity and dominance effects influence the nature of the relationship between two individuals, then the following predictions should hold for any single grooming interaction.

(i)   Prediction 1: time matching by individuals. If female baboons, which do not groom partners simultaneously, exchange grooming for itself, then equal amounts of grooming should be exchanged and immediate reciprocation would be the best way to avoid being cheated by grooming partners (Connor

1995). Reciprocal traders always make up a substantial proportion of any market, at least among female primates (Seyfarth 1977), i.e. most grooming occurs between closely ranked females. Therefore, the majority of dyads within any troop should time match grooming contributions within a reciprocated bout, regardless of overall aggression rates and levels of competition. This is not a trivial prediction, since the occurrence of reciprocated grooming has been regarded as a feature only of egalitarian groups (de Waal 1986; Cheney 1992).

(ii) Prediction 2: RHP and time matching. Although we should expect to find a positive correlation between the time contributions of grooming partners across all troops, the amount of variance explained should vary depending on the extent to which RHP is important. We therefore predict that in troops where RHP is low on average and dyads trade grooming exclusively for itself, the relationship between the time contributions of partners will explain more variance than in troops where individuals can trade grooming for other goods. In troops where interchange is possible, the more powerful individuals need only invest the time needed to initiate a sustained bout of grooming, with the result that time matching will be less consistent across dyads and the correlation will be weaker. We should therefore expect to find that in troops where rates of food-related aggression are high, the level of time matching between grooming partners will be lower than in troops where the effects of feeding competition are reduced.

(iii) Prediction 3: rank distance and time matching. Although data are not yet available to confirm Seyfarth & Cheney's (1984) prediction that individuals exchange grooming for commodities such as tolerance at feeding sites, it should be possible to look for indirect evidence that rank distance has an effect on the grooming relationships of dyads within a troop. Following prediction 2, if individuals trade grooming for other commodities, then time matching should become weaker as the rank distance between grooming partners increases, since distantly ranked animals are more likely to base their relationship on interchange rather than reciprocal grooming. The greater the power differential between two partners, the greater the market value of association, since females feeding in the vicinity of a higher ranking female will experience fewer displacements due to the reluctance of other animals to approach and risk aggression from the higher ranking female. By this, we do not mean that higher ranking females actively support lower ranking females, for which there is no evidence in chacma baboons; rather it is the risk of direct attack of non-tolerated animals by a higher ranking female that animals attempt to avoid. Higher ranking females may also maintain access to higher quality food patches relative to low-ranking females. The lower ranking female in a dyad should therefore be prepared to pay more in terms of grooming as power differentials increase.

Table 1. *Details of study troops*

troop	Drakensberg Mountains		De Hoop Nature Reserve	
	WA2	HT	ST	VT
size	18	36	19	44
number of females	6	12	7	12
number of males	3	7	1	2
% of time grooming	8	12	14	17
% of reciprocated bouts	31	51	40	40
median rank distance between grooming partners[a]	—	—	3	3

[a]Rank distances could not be determined for the Drakensberg Mountains.

We test these predictions using data from two populations of chacma baboons. After confirming that the study troops from these populations differ in the rate of food-related aggression and the strength of the dominance hierarchy, we go on to look at patterns of grooming between and within troops.

2. METHODS

The data come from two South African chacma baboon populations: the Drakensberg Mountains of Natal (study period 1993–1995) and the De Hoop Nature Reserve in the Western Cape (study period 1997–1998). Two mountain troops (WA2 and HT) were compared to two troops, matched for female cohort size, living in coastal scrub (ST and VT). Details of the study troops are given in table 1. The four troops were each followed on foot at a distance of 10–20 m throughout the day and female–female allogrooming interactions were recorded whenever we observed the initiation of a bout. For each bout, the identity of the participants was noted and the time spent grooming by each partner was recorded to the nearest second. In addition, all aggressive interactions were recorded, noting the identity of the participants, the outcome and, where possible, the context of the interaction. In the Drakensberg Mountains, visibility allowed us to record all agonism. At De Hoop Nature Reserve accurate estimates of relative dominance interactions were possible only from focal animal samples.

Henzi *et al.* (1997) showed that within-bout reciprocation is essential for the maintenance of grooming dyads over time, suggesting that there is something critically important about the capacity to respond to grooming immediately. Given this and the problem of determining *a priori* the period over which to measure responses to non-reciprocated bouts (minutes, hours or days), the analyses were based only on immediately reciprocated bouts, which occurred at approximately the same frequency in both populations (table 1). This constraint, given the finding of time matching below, means that the tests of predictions 2 and 3, which are about any single interaction, are actually conservative (increased probability of type II errors).

In order to control for over-representation of particular dyads within our data sets and consequent inflation of *n*, we extracted subsets of grooming bouts for each troop and performed statistical analyses on these alone. For each female, we extracted all
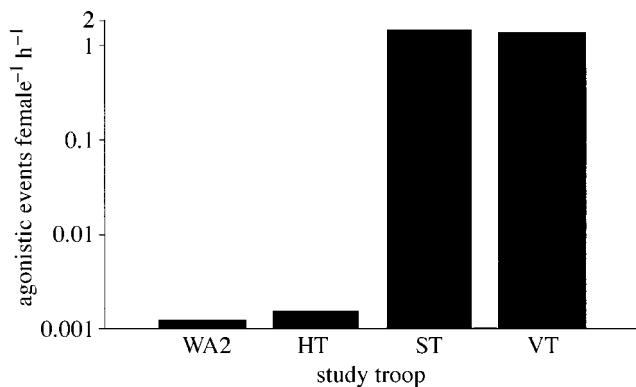
Figure 1. Rates of female–female agonism. Data come from 1587 h of observation in the Drakensberg Mountains and 44 h of focal animal sampling at De Hoop Nature Reserve.

grooming bouts in which she was designated as the initial groomer and from these selected at random a single grooming bout for each of the dyads of which she was a member. This gave us a maximum of $n(n-1)$ dyads per troop, where n is the number of adult females. However, as Henzi *et al.* (1997) showed, not all potential dyads will be represented due to constraints on an individuals' ability to groom all other troop members. Consequently, our sample sizes are all smaller than this maximum value.

To look at the effects of dominance on time matching, we calculated the rank distance between individuals in a dyad by subtracting the rank of the animal designated as the first groomer from the rank of the animal designated as the second groomer. We calculated the discrepancy between their time contributions to a grooming bout in the same way. Both rank distance and grooming discrepancy values can therefore have a positive or negative sign. All statistics were performed using the SPSS for Windows package and all tests were one-tailed since our predictions are directional.

3. RESULTS

(a) *Rates of aggression*

The rate of aggression among the De Hoop baboons was found to be two orders of magnitude higher than among the Drakensberg baboons (figure 1). While we were able to construct transitive, strongly linear, dominance hierarchies for ST and VT, the data were simply too few to allow us to do so for WA2 and HT, despite more than 600 and 900 h of observation, respectively.

(b) *Time matching*

In all four troops there was a significant positive correlation between the amount of time each participant spent grooming within a bout. However, the amount of variance explained was at least twice as large for the Drakensberg troops than for the De Hoop baboons (figure 2a–d) (Drakensberg: WA2, $R^2 = 0.588$, $n = 19$ dyads and $p < 0.001$, and HT, $R^2 = 0.331$, $n = 57$ and $p < 0.001$; De Hoop: ST, $R^2 = 0.163$, $n = 19$ and $p < 0.05$, and VT, $R^2 = 0.168$, $n = 40$ and $p < 0.01$). We tested for the leverage of individual points by determining their centred leverage values (SPSS 1998). Only one point in the four data sets, from HT, exceeded the proposed cut-off of 0.5. Excluding it increased the amount of explained variance to 46%. The slopes of both sets of matched cohorts were

significantly different ($t_{\text{WA2–ST}} = -3.2$, $v = 34$ and $p < 0.01$ and $t_{\text{HT–VT}} = 1.7$, $v = 92$ and $p < 0.05$; Zar 1974).

(c) *Rank distance effects*

In the absence of expressed dominance in the Drakensberg Mountains, rank distance effects could only be tested at De Hoop Nature Reserve. There was a significant relationship between rank distance and time discrepancy for VT (figure 3a) ($R^2 = 0.159$, $F_{1,38} = 7.167$ and $p = 0.01$), but not ST (figure 3b) ($R^2 = 0.003$, $F_{1,17} = 0.370$ and $p > 0.5$). No centred leverage values exceeded 0.5 and all were below 0.2.

4. DISCUSSION

Our data indicate that female baboons trade grooming as a commodity. While there is evidence that other primates do so too (Muroyama 1994; de Waal 1997), the time-matched grooming bouts displayed by our study troops provide the first evidence that grooming can be traded for itself and that the value of grooming as a commodity may be set by the local market. These data therefore suggest that biological market theory may provide a valid explanation of the behaviour of the Drakensberg females (and perhaps all primate species) and its predictions should therefore be subjected to more rigorous tests.

While the data are consistent with biological market theory, we cannot at present completely reject more traditional reciprocal altruism explanations. Indeed, the exchange of grooming in a time-matched fashion bears a superficial resemblance to the patterns predicted by a continuous reciprocal altruism model (Roberts & Sherratt 1998) in which players raise their investment when interacting with individuals who match or better the partner's last move. In this model, cooperation increases over the course of interactions between partners. At first glance, the time matching observed in our study troops appears to fit this pattern, with short bouts representing individuals just beginning a cooperative relationship and therefore investing relatively little, while longer bouts reflect established partnerships. However, with a little more consideration, it seems unlikely that such a strategy is operating. First, we cannot assume that the point at which we began collecting data was the point at which grooming partnerships established themselves. Second, the fact that all grooming dyads interspersed non-reciprocated bouts between reciprocated bouts throughout the study does not fit the model's predictions, since non-reciprocation amounts to defection. Third, the model implicitly assumes that longer bouts equate with higher levels of cooperation. We argue that duration is not in fact the issue; what matters is that the amount of grooming given is matched, since this is what determines whether or not an animal offers good value in the market-place. Finally, the Roberts & Sherratt (1998) model does not include any element of partner choice since it is concerned with dyadic interactions. It should be readily apparent that animals within a permanent social group have at least some choice regarding with whom they can interact, however limited this may be. A market-based model is therefore preferable to a dyadic reciprocal altruism set-up, since it represents a more realistic starting point from
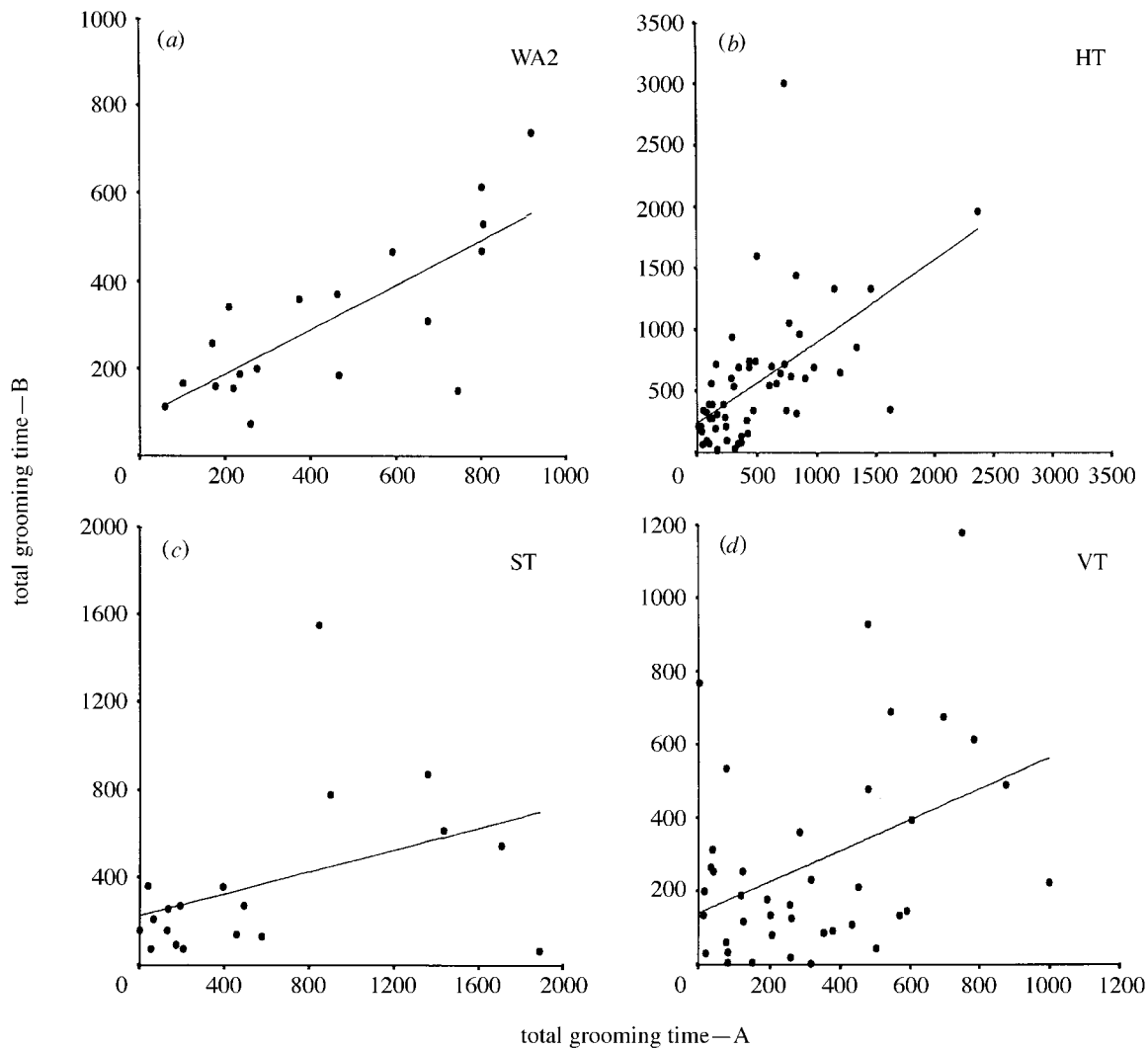
Figure 2. The degree of time matching within reciprocated grooming bouts.

which to model the interactions occurring within social groups.

Although it is clear that grooming is traded for itself in the absence of resource competition, it remains to be determined what is traded when differences in RHP are high. One obvious candidate is tolerance at a clumped food source (Seyfarth & Cheney 1984), although we have yet to explain the persistence of high levels of agonism in the De Hoop population despite interchange grooming. Two factors are relevant here. First, the agonism used in determining ranks combines all aggressive encounters, irrespective of intensity and it may be that increased tolerance, rather than being absolute, is simply mediated by an attenuation in aggressive force. Clearly, this needs resolution. Second, much of the aggression occurred among dyads that did not groom one another and for which we might therefore expect agonism.

It is pertinent to consider here the proposal of Hemelrijk & Luteijn (1998) that the degree of female grooming reciprocity should decrease with a decrease in the adult sex ratio, since competition for access to males will disrupt female relationships. Although our data would fit this scenario, we never saw female competition for access to males in either population (Weingrill 1998; L. Barrett, S. P. Henzi, T. Weingrill, J. E. Lycett and R. A. Hill,

unpublished data). Nor would we expect it in chacma baboons generally, since female receptivity is generally asynchronous and access to receptive females by males is strictly rank determined (Weingrill 1998; Henzi *et al.* 1999). At the same time, the two arguments are not incompatible. Hemelrijk & Luteijn (1998) did not consider why it is that we would expect a decline in reciprocity (measured as the frequency with which members of a dyad groom each other) rather than an overall depression of grooming rates. Nor did they factor in the actual cost of grooming or RHP. It may well be that females in species other than baboons are trading grooming for access to males. If this were so, we would predict time matching by closely ranked females would persist across a range of sex ratios while rank difference effects would become more marked as the number of males per female declines.

The absence of a relationship between rank distance and time discrepancy for ST suggests that there may be a group size effect on power differentials at De Hoop Nature Reserve. The small female cohort size may mean that power differential effects do not operate as powerfully as they do in VT. This would imply that rank distance may have an absolute effect on females' ability to interchange. In a small troop where rank distance can
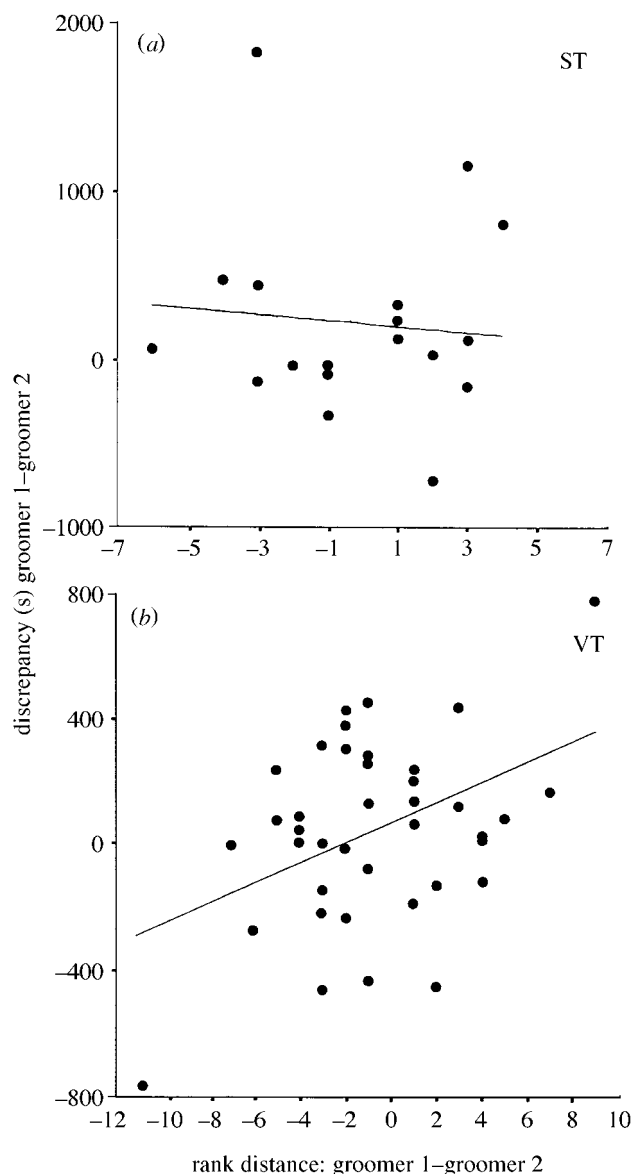
Figure 3. The relationship between rank distance and grooming reciprocity.

never be very high (a maximum of six in ST), the difference between the highest and lowest ranking female may still be insufficient to lead to an interchange relationship. In large troops, where greater rank distances exist (maximum of 11 in VT) and power differentials are increased, interchange becomes possible between high- and low-ranking animals. Some hint that this may be the case is given by the fact that the best fit to VT's data in figure 3 is given by a cubic regression ($y = 35.2 - 13.7x + 1.4x^2 + 0.9x^3$; $R^2 = 0.36$, $F_{1,36} = 6.64$ and $p < 0.001$), suggesting that the effects of rank are disproportionately manifest where rank differences are large. This is turn indicates that an ordinal ranking of individuals may be insufficient when attempting to analyse female social relationships in fine detail, requiring the resuscitation of measures such as cardinal ranks (Boyd & Silk 1983).

Alternatively, it may simply be that there is no rank distance effect in ST or that stochastic factors have obscured it. Three of the females were new mothers at the time of data collection and it has been shown that new infants are a source of attraction to other females

(Altmann 1980; Kenyatta 1995). This could have produced a distorted picture of grooming for ST. Four new mothers were also present in VT during the period of data collection, but the larger female cohort size may have lessened their overall impact on grooming patterns. The sample size for ST was too small to allow us to investigate the potential impact of mothers on patterns of grooming. More data are needed to resolve both this question and the complicating consequences of relatedness. Muroyama (1991), for example, demonstrated that within-bout reciprocity between female macaques is less likely when close kin groom. Should close kin rank adjacently (Dunbar 1988) then our data suggest that baboon females are operating on different principles. Even if they were not, it is unlikely that kinship is primarily responsible for the relationship between rank and reciprocity. For this to be the case, given that the lower correlation coefficients of the De Hoop troops were held to be due to the emergence of interchange trading, the Drakensberg females, if time matching was due to kinship, would have to be more closely related to one another, on average, than the De Hoop females. The opposite is probably more correct. With an interbirth interval of 38 months (Lycett *et al.* 1998), as opposed to 25 months at De Hoop Nature Reserve, Drakensberg females are less likely to have closely related adult female kin during the estimated seven or eight years of their adulthood.

The results of our study raise two issues. First, if females are able to interchange grooming for another commodity, does this arise as a consequence of low-ranking individuals competing for access to high-ranking females in order to gain tolerance (Seyfarth 1977)? Alternatively, do high-ranking individuals demand grooming from low-ranking individuals who must then cooperate or face increased aggression if they do not? Previous studies investigating the effects of dominance on grooming in cercopithecines have shown that grooming is directed up the hierarchy, although the manner in which this pattern is produced is rarely made clear, most authors assuming that low-ranking individuals compete for access to high-ranking animals because they are more 'attractive' (Dunbar 1988). However, if animals need grooming for its own sake and use it as a commodity, then it is just as likely that high-ranking females demand more grooming from other females, particularly if they have more favourable energy budgets and therefore more time available for socializing. We are currently investigating this in order to establish how large rank distance dyads come about and how they are sustained.

The second issue concerns the categorization of groups as 'despotic' or 'egalitarian' on the basis of group-level patterns of affiliation (van Schaik 1989; Cheney 1992). Although we do not deny that there may be species-typical differences in temperament, our results suggest that females within a single social group can vary in their patterns of grooming and can maintain both reciprocal (egalitarian) and interchange (despotic) relationships depending on the potential power difference between the members of a dyad. So-called egalitarian and despotic groups therefore appear to be distinguished by the ratio of reciprocal groomers to interchange groomers: in egalitarian societies where dominance gradients are shallow, reciprocal groomers predominate (possibly to the

exclusion of interchange groomers), whereas in despotic societies interchange groomers will be more prominent. Females in so-called egalitarian societies may therefore engage in reciprocal grooming relationships, not because they must unite against a common enemy (Rowell *et al.* 1991), but because they cannot trade grooming for anything else.

This means that if we are to understand fully the manner in which ecology influences social behaviour, a focus on the dynamics of social interactions, that is an understanding of the rules governing successive encounters between two individuals, is the appropriate level of analysis. Combining sets of interactions into gross categories of relationships in order to define a group or species (see, for example, Cheney 1992; Coussi-Korbel & Fragaszy 1995) will ultimately prove to be self-defeating, since such an approach cannot produce the fine distinctions needed to understand the complexities of an animal's social decision making within particular ecological circumstances.

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