



Female baboons do not raise the stakes but they give as good as they get

LOUISE BARRETT*†, S. PETER HENZI*, TONY WEINGRILL*, JOHN E. LYCETT*† & RUSSELL A. HILL†

*Behavioural Ecology Research Group, University of Natal

†Evolutionary Psychology and Behavioural Ecology Research Group, School of Biological Sciences, University of Liverpool

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We used data from four chacma baboon, *Papio cynocephalus ursinus*, troops, living in two populations, to test the raise the stakes (RTS) strategy of reciprocity. Female baboons did not raise the stakes either within or across grooming bouts. Instead they time-matched grooming contributions and divided grooming into short episodes. In addition, analysis of the grooming behaviour of frequently versus infrequently grooming dyads did not reveal differences in grooming patterns predicted by the RTS strategy. We suggest time constraints preclude the escalation of grooming bout length as required by RTS; the data were more consistent with a strategy of give as good as you get. However, this strategy could not explain all the patterns observed, and we conclude that biological market theory represents a more appropriate framework for investigating female grooming dynamics than dyadic games based on the iterated prisoner's dilemma. We suggest that competitive altruism among individuals acts as a market force influencing an individual's value as a grooming partner.

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The theory of reciprocal altruism and the iterated prisoner's dilemma (IPD) have received widespread attention as explanations for the occurrence of altruism between unrelated individuals. Despite the theoretical value of these ideas, they have proved difficult to test in real biological systems. This is a consequence of the problems involved in quantifying precisely the costs and benefits of particular actions, especially when these are in different currencies (e.g. Seyfarth & Cheney 1988), as well as difficulty in determining the exact nature of the payoff matrix (Milinski 1987; Godin & Davis 1995; Milinski et al. 1997).

In recent years, two approaches have been used in an attempt to circumvent these problems. First, a number of authors have proposed alternative models of reciprocity and cooperation that do not rely on the prisoner's dilemma (e.g. parcelling, pseudoreciprocity: Connor 1995a, b; biological markets: Noë & Hammerstein 1995). The alternative tack has been to modify the IPD game by allowing more realistic assumptions to govern individual

players' actions and permit the development of more flexible strategies, with the aim of deriving predictions that are easier to test empirically.

In the most recent of such models, Roberts & Sherratt (1998) allowed individuals to 'test the water' before embarking on a full-blown cooperative relationship as a means of avoiding defection and exploitation. In this view, cooperation need not take place in an all-or-none fashion, but can build up gradually over the course of a series of interactions, allowing individuals to gain 'confidence' or 'trust' in their partners. Roberts & Sherratt (1998) formulated a strategy called 'raise the stakes' (RTS) which reflected these considerations. An individual playing RTS will increase its investment in a cooperative interaction if its partner matches or betters the individual's own last move. In this way, cooperation gradually increases over time if both players use RTS.

Both Roberts & Sherratt (1998) and Keller & Reeve (1998) have stated that raise the stakes represents an advance on previous formulations of the IPD since it makes predictions that can be tested easily, especially since 'several systems exist in which changes in the level of investment between partners can be followed over time'. More explicitly, Keller & Reeve (1998) suggested that primate grooming patterns represent an example of a system where RTS could apply.

Correspondence: L. Barrett, Evolutionary Psychology and Behavioural Ecology Research Group, School of Biological Sciences, University of Liverpool, Liverpool L69 3BX, U.K. (email: louiseb@liverpool.ac.uk). S. P. Henzi and A. Weingrill are at the Behavioural Ecology Research Group, University of Natal, Durban 4041, South Africa.

We have shown that female baboons exchange grooming in a 'time-matched' fashion, resulting in a positive correlation at group level between the times each individual spends grooming within a reciprocated bout (Barrett *et al.* 1999). We interpreted this as an instance of commodity trading within a biological market (Noë & Hammerstein 1995): female baboons trade grooming for its own intrinsic benefits and they time-match as a consequence of the need to offer good value in the market place. We considered a biological market the most appropriate model since it assumes that there is both partner choice and competition between individuals for the best partners. These assumptions mean that biological markets are more realistic than dyadic models and more applicable to animals living in temporally stable social groups.

Although a biological market therefore seems to be the most appropriate model for our study troops, our data also appear to conform to the RTS strategy. According to RTS, the short grooming bouts we observed represent individuals just beginning a cooperative relationship, and therefore investing relatively little, while longer bouts reflect established partnerships. Given this, and the fact that proponents of RTS suggest that primate grooming is an appropriate system for testing this strategy (Keller & Reeve 1998), it seems worthwhile to test RTS as an alternative explanation for the grooming patterns we observed in our study groups.

However, there are two problems with RTS, one conceptual and one practical, that reduce its applicability to real biological systems, especially those of female primates. The conceptual problem is that within social groups, relationships among adult females are not initiated at a single, definitive moment. Individuals interact and groom with others from a very young age, and these relationships are necessarily one-sided since young animals lack the skill and coordination to groom effectively. The nature of these interactions changes dynamically through time (see e.g. Muroyama 1995), but there is no point at which individuals can suddenly choose to initiate a completely new relationship and use RTS to establish whether cooperation is likely to be forthcoming. By the time that individuals have reached an age where they can control when and with whom they interact, they are already firmly enmeshed in a complex web of relationships. A model of relationship formation that makes no allowance for this effect is not applicable to permanently social animals, except in cases where animals immigrate into new troops, which is the exception rather than the rule for female baboons (Henzi *et al.*, *in press*).

Even if this conceptual problem can be circumvented, there will always be the practical problem when one embarks on a study of animals with established relationships, it is impossible to know the stage that the animals have reached and therefore what patterns of grooming one should predict. In our own case, we cannot assume that the point at which we began collecting data was also the point at which grooming partnerships were established.

These two issues combined mean that, as with other formulations of the IPD, RTS is still difficult to test

empirically on those systems where cooperative strategies are most frequently observed and where they have the greatest biological impact. However, in the case of female baboons, it is possible to capture the essential nature of the Roberts–Sherratt argument if it is recast in terms of the frequency with which individuals interact. Infrequent groomers can be expected to show different patterns of grooming to frequent partners according to RTS since, although they have established a relationship, their level of uncertainty about their partners should be greater than among frequent groomers. Such individuals may use RTS to reduce the risk of being cheated by an unfamiliar partner. This reinterpretation of the RTS strategy therefore sits within our conception of biological markets as an overall framework to explain patterns of grooming and partner choice among females, since we are hypothesizing that RTS comes into operation only after partner choice has been made and only if the selected partner is unfamiliar. We assume that market forces determine the likelihood that individuals will have to select an unfamiliar partner over a familiar one.

In this paper, we first test whether RTS, as defined by Roberts & Sherratt (1988), is used by female baboons in their grooming interactions. Having shown that this is not the case, we then go on to investigate whether a modified form of RTS can be applied to at least some aspects of grooming among primates. We do this by testing our prediction that unfamiliar partners should show evidence of RTS while familiar partners should not.

PREDICTIONS

Raising the Stakes

As female baboons engage in reciprocated grooming bouts (i.e. individuals groom each other sequentially, although never simultaneously, during the course of a bout), the RTS model could operate in two ways. First, individuals could gradually increase the total time spent grooming with a particular partner over the course of several grooming bouts. Alternatively, individuals could escalate grooming within bouts, gradually increasing the length of their individual contributions (hereafter referred to as grooming 'episodes') in response to either their partner's previous contribution (the most strict interpretation of RTS) or in response to their own previous contribution given that their partner provided at least some grooming in return (a less strict interpretation of the model).

We therefore test the following predictions: (1) dyads will show an increase in the total length of grooming bouts over time (contributions of both participants summed); and (2) there will be an increase in grooming episode length over the course of a bout (which may or may not be associated with an increase in overall bout length over time).

This latter prediction can be manifest in two ways. If individuals respond to their partner's previous episode then there should be a consistent increase in episode length over the course of a bout. If individuals respond to their own previous episode, then there should be a

consistent increase in their own contributions over the course of the bout, but not necessarily a consistent increase between adjacent episodes. In addition, for both forms of RTS we can predict that (3) there will be a decline in the frequency of nonreciprocated bouts over time since nonreciprocation amounts to defection and should be observed less frequently over time if dyads are playing RTS.

Frequent versus Infrequent Groomers

According to the RTS model, individuals with an established relationship and who interact frequently are expected to have already gone through a phase of 'testing the water' and should have reached a plateau at which they are investing an equal amount in the relationship. By contrast, individuals who groom each other infrequently may fail to reach this plateau and their greater levels of uncertainty regarding the trustworthiness of their partner should lead to shorter and more variable levels of investment than among frequent groomers. We therefore predict that (4) the total length of undisturbed grooming bouts should be longer for frequent groomers and (5) the first episode of a grooming bout should be both longer and less variable among frequent than infrequent groomers.

This latter prediction is the more important since the first episode of a reciprocated grooming bout may signal how much the groomer is willing to invest initially. Infrequent groomers should therefore be more tentative at this initial stage and less willing to embark on lengthy first episodes. As this prediction is built on the assumption that individuals use their initial grooming investment to signal their willingness to continue, we also test (6) whether initial grooming episodes are correlated with the resulting length of the grooming interaction, and whether this differs between frequent and infrequent groomers.

METHODS

The data came from two South African chacma baboon, *Papio cynocephalus ursinus*, populations: the Drakensberg Mountains of Natal (study period 1993–1995) and De Hoop Nature Reserve in the Western Cape (study period 1997–1998). Two mountain troops (HT: 12 adult females; WA2: six adult females) were compared with two troops, matched for female cohort size, living in coastal scrub (VT: 12 adult females; ST: seven adult females). Rates of aggression were approximately three times as high at De Hoop than in the Drakensberg. Females at De Hoop could therefore be placed in a strong linear dominance hierarchy while the Drakensberg females showed such a low rate of aggression that ranking was not possible. Further details are given in Barrett et al. (1999). 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. This involved one animal approaching another and grooming it or, alternatively, the

approaching animal presenting a body part (e.g. shoulder, flank) to the other individual who then groomed the presenting individual. Only if we witnessed either of these events did we begin timing. No data were collected if the bout was already underway when it came to our attention. For each bout, the identity of the participants was noted, and the time spent grooming by each partner was recorded to the nearest second.

Henzi et al. (1997) have shown 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 bouts that are not immediately reciprocated (min, h or days), analyses are based only on bouts in which both individuals participated. These occur at approximately the same frequency in both populations (Barrett et al. 1999).

Within-Dyad Raise the Stakes

Two sets of data were extracted from the full data sets for each of the four troops.

(1) To test whether females increased investment in their grooming relationships over time, we extracted data from nine dyads for which we had data on five or more reciprocated grooming bouts (Table 1). Each troop contributed at least one dyad to the overall sample. To avoid pseudoreplication, we performed statistical analyses for each dyad separately and then combined the results using Fisher's procedure for independent probabilities (see Sokal & Rohlf 1981). We also extracted the sequence of reciprocated and nonreciprocated bouts across time in order to determine whether nonreciprocated bouts declined over time.

(2) To test whether females raised the stakes in the short term within reciprocated bouts, we extracted all grooming bouts in which more than three intrabout grooming episodes were recorded for each troop. To control for overrepresentation of particular dyads within these data sets and consequent inflation of N , we followed the method of Barrett et al. (1999). For each female, we extracted all 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. Data were then partitioned according to the number of intrabout grooming episodes that occurred. We could not perform statistical analyses where there were fewer than five dyads per group (but these are shown in the results to illustrate trends). This led to the exclusion of all data for ST and for two episode groupings for WA2.

We used sign tests to determine whether there was any statistically significant tendency for episode lengths to increase across a bout for both each dyad as a whole and for each individual's contributions within a dyad. We designated a plus sign to a consistent increase in episode length across bouts, no matter how small. Episodes that were the same length as the previous episode were treated

Table 1. Spearman rank correlations between date and bout length and individual contributions to grooming bouts (groomer 1 and groomer 2) for individual dyads

Dyad (troop)	N	Bout length versus order of occurrence		Groomer 1 versus groomer 2	
		r_s	P	r_s	P
A (VT)	7	-0.429	0.169	0.536	0.108
B (VT)	6	0.371	0.234	0.771	0.036
C (VT)	23	-0.094	0.335	0.584	0.002
D (VT)	16	-0.044	0.436	0.428	0.049
E (ST)	8	-0.381	0.176	0.659	0.038
F (HT)	6	0.143	0.394	0.829	0.021
G (HT)	5	-0.300	0.312	0.500	0.196
H (WA2)	10	-0.406	0.122	0.455	0.093
I (WA2)	6	-0.429	0.198	0.143	0.394

N: Number of bouts. Data were included in the analyses only if there were five or more reciprocated grooming bouts per dyad.

as an increase, since an RTS player escalates if its contribution is matched or bettered (Roberts & Sherratt 1998). A minus sign was given to bouts in which no consistent increase was observed (i.e. episodes decreased compared to the previous episode). A nonparametric two-way ANOVA was used to test for significance in the lengths of episodes across reciprocated bouts.

Frequent versus Infrequent Groomers

To investigate differences between frequent and infrequent groomers, we used the method outlined above to extract one reciprocated grooming bout per dyad (regardless of the number of episodes it contained) and then partitioned the data set according to whether the dyad groomed frequently or infrequently. We obtained these latter data by calculating the proportion of each female's total grooming time that was allocated to all other females. For WA2 and HT, total observed grooming time was used since all bouts were recorded, while for VT and ST, percentages were calculated from scan records. Frequently grooming dyads were those who spent more than 5% of their time grooming while infrequently grooming dyads were those who spent less than 5% of their time grooming (following Dunbar 1984). Only data for HT and VT could be used for these analyses as all females in WA2 and ST were classed as frequent groomers under this criterion. Mann-Whitney tests and Spearman rank correlation were used to test predictions concerning differences between the two classes. Unless specified, all tests are one tailed, as our predictions are directional.

RESULTS

Raising the Stakes Across Grooming Bouts

Contrary to prediction, there was a negative relationship between order of occurrence and grooming bout length for seven of nine dyads: a result significantly unlikely to occur by chance (Table 1; Fisher's test for combined probabilities: $\chi^2_{18}=26.0$, $P<0.05$). However, for

all dyads, there was a positive correlation between the times each partner spent grooming within a bout. Again, this result is significantly unlikely to occur by chance alone (Table 1: $\chi^2_{18}=5.1$, $P<0.001$). Nonreciprocated and reciprocated bouts occurred randomly through time for all dyads, and nonreciprocation did not influence subsequent cooperation (runs tests for individual dyads: $-0.545<Z<0.160$, $0.182<P<1.000$; $\chi^2_{18}=5.1$, $P=0.99$).

Raising the Stakes Within Grooming Bouts

Response to partner's previous episode

For each set of reciprocated bouts, there was no consistent or significant increase in episode length in any of the three study troops for which data were analysed (Table 2). The only significant results were in the opposite direction to that predicted. In addition, differences between episode lengths across bouts were not significant (Table 2).

Response to own previous episode

For both groomers in each set of reciprocated bouts, there was no consistent or significant increase in episode length in response to an individual's own previous episode (Table 3). Again, the only significant results were in the opposite direction to that predicted.

Frequent versus infrequent groomers

There was no significant difference between the initial episode lengths for frequent and infrequent groomers in either VT or HT (Mann-Whitney U test: HT: $U=313$, $N_1=17$, $N_2=40$, $P=0.637$; VT: $U=158$, $N_1=26$, $N_2=14$, $P=0.510$; Fig. 1). However, in HT, frequent groomers had significantly longer grooming bouts than infrequent groomers ($U=145$, $N_1=17$, $N_2=40$, $P<0.001$; Fig. 1). This effect was not found in VT ($U=153$, $N_1=26$, $N_2=14$, $P=0.424$; Fig. 1). There was also no significant correlation between the length of the initial episode in a bout and the subsequent length of the bout for either frequent

Table 2. Results of sign tests and ANOVA to test for raising the stakes within individual grooming bouts

Troop	Number of episodes per bout (no. of dyads)	Increase across bout		Sign test <i>P</i>	Friedman ANOVA		
		Yes	No		χ^2	<i>df</i>	<i>P</i>
VT	3 (23)	4	19	0.01	0.261	2	0.900
	4 (9)	2	7	0.09	5.563	3	0.137
	5 (8)	1	7	0.04	5.60	4	0.231
ST	3 (3)	1	2				
	4 (3)	0	3				
	5 (2)	0	2				
WA2	3 (8)	3	5	0.36	2.25	2	0.325
	4 (3)	0	3				
	5 (3)	0	3				
HT	3 (10)	4	6	0.38	1.44	2	0.486
	4 (11)	2	9	0.09	6.82	3	0.090
	5 (6)	0	6	0.02	3.07	4	0.547
	6 (5)	1	4	0.19	10.9	5	0.060
	7 (5)	0	5	0.03	8.14	6	0.228

Data were analysed only if there were five or more dyads represented for each category of grooming bout. However, all available data are shown in the table to indicate trends. Sign tests were used to determine whether there was any consistent increase in episode length within bouts. ANOVA was used to determine whether there was any significant difference in episode length across bouts.

Table 3. Sign tests for each individual groomer's response to its own previous episode

Troop	Number of episodes per bout (no. of dyads)	Groomer 1: increase across bout		Sign test <i>P</i> two-tailed	Groomer 2: increase across bout		Sign test <i>P</i> two-tailed
		Yes	No		Yes	No	
VT	3 (23)	11	12	1.00			
	4 (9)	8	1	0.07	4	5	1.00
	5 (8)	0	8	0.04	6	2	0.29
ST	3 (3)	2	0				
	4 (3)	1	2				
	5 (2)	1	2				
WA2	3 (8)	5	3	0.36			
	4 (3)	0	3		1	2	
	5 (3)	1	2		3	0	
HT	3 (10)	6	4	0.38			
	4 (11)	7	4	0.55	5	6	1.00
	5 (6)	1	5	0.21	4	2	0.69
	6 (5)	3	2	1.00	4	1	0.19
	7 (5)	0	5	0.03	0	5	0.03

Data were analysed only if there were five or more dyads represented for each category of grooming bout. However, all available data are shown in the table to indicate trends.

or infrequent groomers in both troops (HT: frequent groomers: $r_s = -0.182$, $N=40$, $P=0.130$; infrequent groomers: $r_s = -0.020$, $N=17$, $P=0.424$. VT: frequent: $r_s = -0.108$, $N=14$, $P=0.357$; infrequent: $r_s=0.319$, $N=26$, $P=0.056$). There was, however, a significant positive correlation between overall partner contributions to a grooming bout (time matching) for both frequent and infrequent groomers in HT (frequent: $r_s=0.620$, $N=40$, $P=0.0001$; infrequent: $r_s=0.460$, $N=17$, $P=0.032$), and for infrequent groomers only in VT (frequent: $r_s=0.044$, $N=14$, $P=0.441$; infrequent: $r_s=0.361$, $N=26$, $P=0.035$).

This latter effect was not related to rank differences between the two classes of groomer (rank distance, $\bar{X} \pm SD$; frequent groomers: 3.3 ± 2.3 ; infrequent groomers: 2.7 ± 2.4 ; $U=146.5$, $N_1=26$, $N_2=14$, $P=0.318$).

DISCUSSION

Female baboons in our study troops showed no tendency to raise the stakes either within or across grooming bouts in either the strict (respond to partner's previous episode) or less stringent (respond to own previous episode) sense.

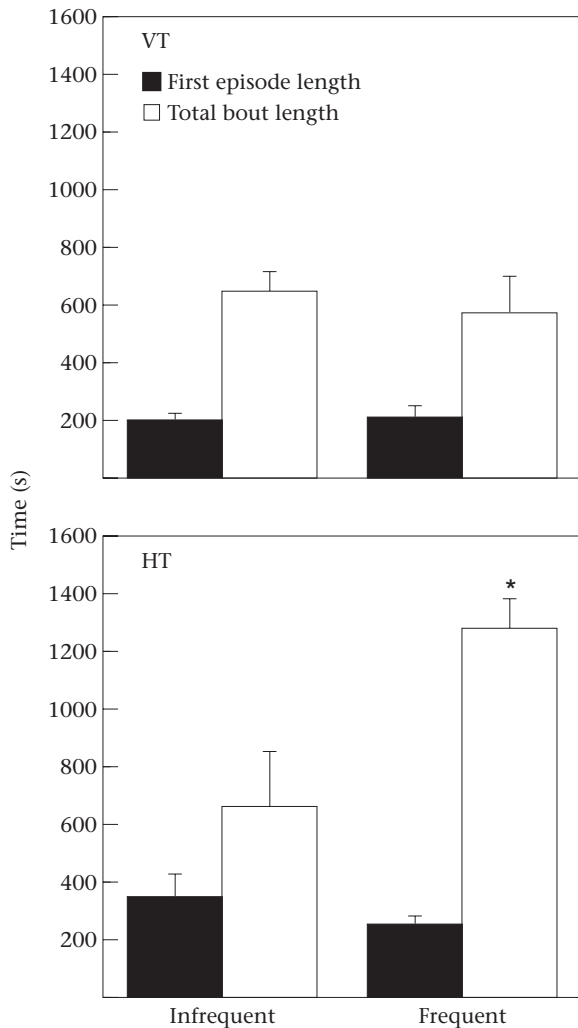


Figure 1. Comparison of initial episode length and total bout length ($\bar{X} \pm \text{SE}$) for frequent and infrequent groomers in troops VT and HT. * $P < 0.05$.

Instead, females tended to match their partner's contribution within a bout, regardless of previous levels of cooperation, resulting in a positive correlation between the times spent grooming within a bout. While RTS assumes implicitly that longer bouts equal a higher level of cooperation, our data suggest that duration is not, in fact, the issue; what matters is that the amount of grooming given is matched, independently of previous interactions. We therefore argue that short and long bouts represent an equivalent level of cooperation, and that factors other than an attempt to build up trust within a partnership determine grooming bout length.

Although there was no evidence that females were raising the stakes, the data did show some support for one of the alternative strategies, give as good as you get (GGG), which was pitted against RTS in Roberts & Sherratt's (1998) computer tournaments. A player using GGG matches its partner's previous contribution but does not escalate investment. The 'passivity' of GGG meant that it did not do as well as RTS, since the latter was actively able to increase the level of cooperation.

However, under conditions where escalation of cooperation was constrained, GGG was observed to reach an equilibrium with RTS. In real life, animals are likely to be constrained in their ability to escalate grooming bouts over protracted periods; both our study populations, for example, are strongly time constrained (Henzi et al. 1997; L. Barrett & P. Henzi, unpublished data), which probably explains why individuals matched but did not escalate grooming time. This time constraint would also explain why grooming bout lengths vary so widely between dyads.

Although GGG seems superficially appropriate, female baboons 'give as good as they get' only in the sense that, overall within a bout, grooming time between partners was matched. This was achieved by dividing grooming bouts up into a series of short episodes that did not differ significantly in length. This may occur because each female decides to invest a constant amount of time in each episode regardless of the amount that her partner invests. If females do not respond to the variability in their partner's grooming time, then according to Roberts & Sherratt's (1998) definition, strictly speaking they are not giving as good as they get. However, if females were deciding, independently of each other, to invest a fixed amount of time in a grooming bout, then we would expect females to have different 'set points' regarding the amount of grooming to invest. If so, episode lengths should differ much more substantially between females and the overall level of time matching should be much poorer. The fact that for all dyads examined, individuals tended to match grooming time and did not differ significantly from their partner's episode lengths through either escalation or 'short changing' suggests that females are, in fact, responsive to their partner's investment, even if this does not correspond exactly to the GGG strategy.

In any case, we should not expect either GGG or RTS to explain all aspects of a real-life situation since they are simplified strategies designed for a computer simulation. For example, female baboons continued to engage in nonreciprocated bouts, even though both RTS and GGG predict that these should decrease over time. We believe that this occurs because grooming can be traded for different things with different partners. That is, grooming acts as a commodity within a biological market. Female baboons use grooming to buy access to infants (P. Henzi & L. Barrett, unpublished data). To handle young infants that are not their own, females must first groom the mother and 'buy' her tolerance. We found that all grooming bouts associated with infant handling were nonreciprocated and the length of the grooming bout was dependent on the rank difference between the mother and the groomer: the lower the ranking of the handler compared to the mother, the longer the grooming bout. The exchange value of grooming was also influenced by whether the handler could offer other commodities in exchange for handling. Neither RTS nor GGG can recognize these more complex grooming exchanges.

A comparison of frequent versus infrequent groomers also provided only limited support for the RTS strategy.

There was no difference between initial episode lengths among frequent and infrequent groomers for both troops suggesting that, even when individuals do not interact regularly, the boundaries of the relationship are set and agreed upon by both parties. There was also no evidence that initial episode lengths acted as a signal of the amount of effort that individuals were willing to invest in a grooming bout, which again does not support the RTS strategy.

The only data that were in line with a strategy of RTS was the finding that, in HT, frequent groomers had significantly longer grooming bouts than infrequent groomers. While this could be interpreted as evidence for greater certainty and willingness to interact on the part of females, a more likely explanation involves variation in female clique size (the number of females a given female grooms within the group: see Henzi et al. 1997). Henzi et al. (1997) showed that, within HT, time constraints prevented females from grooming all other group members and females therefore reduced clique size and concentrated effort on fewer partners. This in turn allowed them to spend more time grooming those individuals. This effect alone could account for the difference in total bout length between frequent groomers for HT versus VT: although both troops contained 12 adult females, mean clique size was seven in HT, but 10 in VT, that is, individuals groomed virtually all members of the female cohort which, given overall time budget constraints, would necessarily reduce grooming time per dyad.

Our results show that RTS cannot explain patterns of grooming in our study troops, in either its original or modified form. As we have already pointed out, it is the nature of the social system that renders RTS inapplicable to primates. Consequently, a more valuable approach would be for theoreticians to recognize this fact and tackle these systems in all their complexity, using models such as biological markets as their basis, rather than continuing to assume that, because grooming is dyadic, a dyadic model will suffice to explain patterns of reciprocity within social groups. This bias towards dyadic models seems to occur because theoreticians continue to model systems that are tractable, rather than those that apply to the real world. However, RTS may find application in situations where groups of unfamiliar individuals are convened, as is often the case in captivity, in species in which females transfer to other groups at adulthood and among animals that form semipermanent groups. Under these conditions, where animals are strangers to each other, RTS may indeed be the most effective means of establishing relationships. Testing the RTS strategy under these conditions should therefore be illuminating.

A proposal by Roberts (1998) suggests agreement with our view concerning permanently social groups. He argued that, in such groups, the wider context in which cooperation takes place needs to be considered. Whenever there is competition for social partners, individuals may compete to be 'altruistic'. Thus, when individuals groom, they are not only interacting with each other, but also actively competing against the whole population of

potential partners. Consequently, individuals may forego the benefits of cheating within the narrow context of a grooming pair in order to maintain an altruistic 'reputation' that has benefits in the wider context. In essence, this is the biological markets argument: individuals compete for those who offer value in the market place, and good reciprocators preferentially interact with each other because competition and partner choice enable exploitative partners to be ostracized. The 'competitive altruism' of Roberts (1998) represents a 'market force' determining an individual's standing in the market place (Noë & Hammerstein 1995; Barrett et al. 1999). We therefore agree with Roberts (1998, page 428) that 'reciprocity is just one way of getting a return on investment in altruism . . . Other mechanisms deserve attention'. The concepts of biological markets and competitive altruism offer the most promising directions to take the analysis of complex social behaviour. Future work should focus on integrating these ideas to produce a comprehensive model of individual social interaction.

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References

- Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999. Market forces predict grooming reciprocity in female baboons. *Proceedings of the Royal Society of London, Series B*, **266**, 665–670.
- Connor, R. 1995a. Altruists among non-relatives: alternative to the Prisoner's dilemma. *Trends in Ecology and Evolution*, **10**, 84–86.
- Connor, R. 1995b. Impala allogrooming and the parcelling model of reciprocity. *Animal Behaviour*, **49**, 528–530.
- Dunbar, R. I. M. 1984. *Reproductive Decisions: an Economic Analysis of Gelada Baboon Social Strategies*. Princeton, New Jersey: Princeton University Press.
- Godin, J.-G. G. & Davis, S. A. 1995. Who dares benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. *Proceedings of the Royal Society of London, Series B*, **259**, 193–200.
- Henzi, S. P., Lycett, J. E. & Weingrill, T. 1997. Cohort size and the allocation of social effort by female mountain baboons. *Animal Behaviour*, **54**, 1235–1243.
- Henzi, S. P., Barrett, L., Weingrill, T., Dixon, P. M. & Hill, R. A. In press. Ruths amid the alien corn: the role of males in the translocation of female chacma baboons. *South African Journal of Science*.
- Keller, L. & Reeve, H. K. 1998. Familiarity breeds cooperation. *Nature*, **394**, 121–122.
- Milinski, M. 1987. Tit-for-Tat and the evolution of cooperation in sticklebacks. *Nature*, **325**, 433–435.
- Milinski, M., Luthi, J. H., Egger, R. & Parker, G. A. 1997. Cooperation under predation risk: experiments on costs and benefits. *Proceedings of the Royal Society of London, Series B*, **264**, 831–837.

- Muroyama, Y.** 1995. Developmental changes in mother-offspring grooming in Japanese macaques. *American Journal of Primatology*, **37**, 57–64.
- Noë, R. & Hammerstein, P.** 1995. Biological markets. *Trends in Evolution and Ecology*, **10**, 336–340.
- Roberts, G.** 1998. Competitive altruism: from reciprocity to the handicap principle. *Proceedings of the Royal Society of London, Series B*, **265**, 427–431.
- Roberts, G. & Sherratt, T.** 1998. Development of co-operative relationships through increasing investment. *Nature*, **394**, 175–179.
- Seyfarth, R. M. & Cheney, D. L.** 1988. Empirical tests of reciprocity theory: problems in assessment. *Ethology and Sociobiology*, **9**, 181–187.
- Sokal, R. R. & Rohlf, F. J.** 1981. *Biometry*. New York: W. H. Freeman.