

Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons

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(Accepted: 8 January 2009)

Summary

The scarcity of evidence for contingent reciprocity has led to a growing interest in how market forces shape the distribution of exchanges in animal groups. In a biological market, supply and demand determines the value of an exchange, and individuals choose to trade with the partner offering the highest value. Partners maximize their immediate benefits without the need to monitor the balance of their exchange over time. Applied to grooming exchanges in primate groups, a market model predicts that females will primarily balance the amount of grooming they trade within single bouts, particularly when all partners offer similar value. If some partners can offer other benefits, like reduced aggression, females may exchange grooming for those benefits. In such cases, grooming will not be evenly balanced within bouts. Here, we examine the patterning of grooming in a group of free-ranging olive baboons (*Papio anubis*). In contrast to predictions derived from a biological market model, two-thirds of all grooming bouts in this group were completely one-sided and females did not consistently provide more grooming to higher-ranking partners. Grooming was more evenly balanced across multiple bouts than within single bouts, suggesting that females are not constrained to complete exchanges within single transactions.

Keywords: baboons, biological market model, grooming, rank, reciprocity.

Introduction

Biological market models provide a way to generate cooperation among un-related individuals without contingent reciprocity. In the biological marketplace, individuals attempt to maximize their benefits in each transaction, and

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select the partner offering the highest value (Nöe & Hammerstein, 1994; Henzi & Barrett, 1999). When the demand for a partner or commodity is greater than the supply, buyers compete for access to the preferred partner by raising the price they are willing to pay (Nöe & Hammerstein, 1994). Simultaneous exchanges, binding offers, or expulsion from the market place make cheating impossible or unprofitable (Connor, 1995; Nöe & Hammerstein, 1995; Henzi & Barrett, 1999). Although most exchanges will occur over short time-scales, when individuals interact repeatedly and commodity values can be measured incrementally, individuals may select partners based on long-term monitoring and balancing of trade (Nöe & Hammerstein, 1994).

Biological market models have been invoked to explain a number of different types of behaviour in several species. For example, large client fish with many cleaner fish partners to choose from receive better service and get bitten by cleaners less often than client fish with limited choice (Bshary, 2001). The balanced exchange of eggs between pairs of hermaphroditic hamlet fish (*Hypoplectrus nigricans*), once considered to be an example of contingent reciprocity (Fischer, 1988), may actually be stable because individuals have limited opportunities to find additional partners in the widely dispersed population and cannot benefit from defection (Connor, 1992; Nöe, 2001). When a pair of male baboons (*Papio anubis*) forms a coalition and steals a fertile female from her consort partner, the higher-ranking coalition partner is more likely to subsequently monopolize the female. The higher-ranking partner is 'paid' in mating opportunities for the greater value he brings to the coalition (Nöe, 1990, 1992).

Recently, Henzi & Barrett (1999) have used a biological market model to examine cooperative exchanges among female primates. They argue that grooming is a valuable commodity, and predict that females will mainly trade grooming in kind. Individuals will exchange similar amounts of grooming within single bouts, both to avoid being cheated (Henzi & Barrett, 1999) and because they lack the cognitive capacity to monitor exchanges with multiple partners over extended periods of time (Barrett & Henzi, 2002). In some situations, grooming may be exchanged for other commodities, such as access to infants (Henzi & Barrett, 2002) or tolerance from higher-ranking females (Henzi & Barrett, 1999). However, if cognitive limitations restrict their ability to keep track of the balance of trade, exchanges will be limited to goods and services that are provided within a limited time frame.

Studies of grooming behaviour in primates provide some support for predictions derived from a biological market model. Female baboons (*Papio cynocephalus*) and blue monkeys (*Cercopithecus mitis*) exchange similar amounts of grooming within bouts (Henzi & Barrett, 1999; Barrett et al., 2002; Payne et al., 2003; Pazol & Cords, 2005), but Japanese macaques (*Macaca fuscata*) do not (Schino et al., 2003). In white-faced capuchins (*Cebus capucinus*) and bonnet macaques (*Macaca radiata*), the amount of grooming provided by one partner is correlated with the amount of grooming received from the other partner during a bout, but partner contributions are not evenly balanced and the majority of grooming bouts are completely one-sided (Manson et al., 2004).

There is also some evidence that females trade grooming for access to valuable commodities, such as food, support, and access to infants. Young infants are highly attractive to female primates (Silk, 1999), and female baboons and patas monkeys (*Erythrocebus patas*) preferentially groom mothers of young infants in exchange for a chance to greet, touch, and handle their infants (Muroyama, 1994; Henzi & Barrett, 2002). Experimental evidence indicates that chimpanzees (*Pan troglodytes*) trade grooming for access to desirable food resources (de Waal, 1997), and vervets (*Cercopithecus aethiops*) and long-tailed macaques (*Macaca fascicularis*) trade grooming for support from higher-ranking females (Seyfarth & Cheney, 1984; Hemelrijk, 1994).

In some groups, including some groups of bonnet macaques (*Macaca radiata*), baboons (*Papio cynocephalus ursinus*), and white-faced capuchins (*Cebus capucinus*), lower-ranking females provide more grooming to higher-ranking partners than they receive in return (Henzi & Barrett, 1999; Schino, 2001; Barrett et al., 2002; Manson et al., 2004). This might indicate that females trade grooming for support, tolerance, or access to resources from higher-ranking partners, but dominance rank does not influence the distribution of grooming in all groups with well-established dominance hierarchies. Rank does not affect the distribution of grooming in some groups of blue monkeys (*Cercopithecus mitis stuhlmanni* and *C. m. erythrarchus*), hamadryas baboons (*Papio hamadryas*), and Japanese macaques (*Macaca fuscata*) (Leinfelder et al., 2001; Payne et al., 2003; Schino et al., 2003; Pazol & Cords, 2005). There are even groups in which higher-ranking partners give more grooming than they receive (wedge-capped capuchins, *Cebus olivaceus* (O'Brien, 1993); brown capuchins, *Cebus apella* (O'Brien, 1993; Parr et al., 1997)).

The variable effects of rank on grooming contributions might reflect flexible responses to local market conditions. Barrett and her colleagues have speculated that species (or groups) that experience strong within-group competition may establish more hierarchical relationships and trade grooming for tolerance or access to resources. Species (or groups) that experience strong between-group competition may groom equitably with all group members to facilitate cooperative resource defense against other groups (but see Cheney, 1992; Henzi & Barrett, 1999; Barrett & Henzi, 2001; Payne et al., 2003; Pazol & Cords, 2005). It is also possible that local levels of feeding competition affect grooming exchanges, regardless of the strength of between-group competition. Individuals experiencing intense competition in groups with steep rank gradients may profit from trading grooming for tolerance while feeding (Henzi & Barrett, 1999; Barrett & Henzi, 2001; Payne et al., 2003; Pazol & Cords, 2005). Presumably these transactions must be completed within a short time window if primates are unable to monitor the balance of trade over extended time periods. Barrett and her colleagues have shown that grooming among female baboons is less balanced when rates of aggression are high than when rates of aggression are lower (Barrett et al., 1999, 2002), but they have not demonstrated that females who increase their grooming contributions actually obtain services or resources from their grooming partners. Blue monkeys do not alter their grooming in response to changes in the level resource competition (Payne et al., 2003; Pazol & Cords, 2005).

The goal of this study is to examine the time frame of grooming exchanges among adult female baboons, and consider whether the distribution of grooming is consistent with predictions derived from the biological market model. The biological market model of grooming predicts that individuals will primarily balance exchanges within bouts, so the balance of grooming within bouts will be greater than or equal to the balance of grooming summed across multiple bouts. Unequal exchanges within single bouts may be the product of interruptions, defections on the trade, or trade for another commodity (Henzi & Barrett, 1999), and will generate imperfect balance over many interactions. If partners perfectly time-match grooming within bouts, then short-term balance will also generate long-term balance in grooming contributions. However, evidence that grooming is more evenly balanced across bouts than within bouts is not compatible with the view that individual behaviour is based solely on short-term interests negotiated within a biological market.

Methods

Study site and animals

The study was conducted on a troop of 60 olive baboons (*Papio anubis*) that range in the Ndorobo Reserve and Chololo ranch on the Laikipia Plateau of central Kenya. The study troop (NBO) resulted from the fusion of a local group (STT) monitored since 1985 (Barton et al., 1992; Strum, 2005), and members of a group (WBY/MLK) translocated from Gilgil to Chololo in 1984 (Strum, 2005). Although the dominance hierarchy in the fused group was initially unstable, social relationships and traveling patterns stabilized by September 2001, and the troop was officially named NBO (Strum, In Prep.). Data on maternal kinship, dominance ranks, births, and deaths were provided by S.C. Strum. During the study period, the adult females included one pair of maternal sisters, one mother-daughter dyad, and one aunt and niece dyad. The data presented here were collected during three 5- to 6-month field seasons spanning an 18-month period between June 2003 and December 2004.

Data collection

All data were collected by R.E.F. All 16 adult females in the troop were observed during 30-min focal follows. A total of 1610 focal samples (805 hours) were collected, and each female was observed for an average of 50.5 ± 3.4 h (11.5–58.2 h). R.E.F. recorded the initiation and termination of all grooming interactions to the nearest second. If the focal female was grooming or being groomed at the end of a focal sample, the sample continued until the bout ended. Bouts were considered to be over if grooming stopped for more than 2 min.

Analyses

Following Barrett et al. (1999), grooming bouts were composed of one or more 'episodes' in which one partner grooms the other. By definition, episodes are unilateral interactions, while grooming bouts may be bilateral if partners exchange roles. Previous analyses defined a bout as a series of episodes separated by less than 10-s pauses (Barrett et al., 1999; Manson et al., 2004). However, females in this troop frequently resumed grooming after pauses of more than 10 s (Frank, 2007). As a more generous test of

the within-bout time-matching hypothesis, we analyzed bouts defined as a sequence of episodes separated by pauses of less than 2 min. Only 4% of all pauses during grooming by the same dyad lasted more than 2 min, while 30% of all pauses lasted more than 10 s (Frank, 2007).

A biological market model predicts that the balance of grooming within bouts will fluctuate with supply and demand for different partners and the value they can offer under different circumstances. However, it is problematic to classify bouts according to the situation in which they occur or the value they may hold for a particular dyad. Unilateral and unbalanced bouts may be instances of lower-ranking females grooming a higher-ranking partner in exchange for benefits in another currency, or they may be instances of intentional cheating or interruptions by third parties. Bouts between a new mother and a female without an infant may be a trade of grooming for access to the infant, or have little to do with the infant. Since it is not possible to determine what bouts should be considered good-faith attempts at balanced grooming exchange between partners of equal value we have conservatively included all observed bouts of grooming in our analyses.

We performed all analyses in STATA 9.0, using all bouts of grooming, whether or not partners traded roles during the bout. One of the two partners in a dyad was randomly assigned as 'first partner' and the other as 'second partner'. All durations were normalized by taking the square root of the seconds spent grooming. To measure the extent of grooming reciprocity within bouts, we performed an Ordinary Least Squares regression testing the effect of the first partner's grooming contribution on the second partner's grooming contribution. Dyads often groomed on more than one occasion, so to control for unequal representation in the data set, we clustered the data by dyad, and weighted their bouts by the number of times they groomed. To measure the extent of grooming reciprocity across bouts, we summed each partner's total contribution, and performed an Ordinary Least Squares regression testing the effect of the first partner's contribution on the second partner's contribution, weighted by the number of bouts each dyad performed. We used a Wald's Post-estimation test to compare the parameters of the across-bout model to the null hypothesis that it would be equally as balanced as the within-bout model. To determine whether lower-ranking females contributed more grooming to higher-ranking partners as the rank distance between them increased, we performed a negative binomial regression of absolute rank distance on the lower-ranking partner's grooming contribution, and controlled

for the total length of the grooming bout for single bouts or the total amount of grooming exchanged in each dyad for summed grooming. Grooming durations for this analysis were not transformed since the negative binomial regression treats the dependent variable as a count of events occurring out of a total possible number of events.

Results

The time-scale of reciprocation

We observed 435 bouts of grooming between 87 different dyads. Females alternated roles during 149 (34%) of these bouts, averaging 1.66 ± 1.17 role reversals per bout, with a maximum of 8 reversals. The lower-ranking partner performed the grooming in 51% of the unilateral bouts and contributed 54% of the grooming exchanged within bilateral bouts. On average, bouts lasted 323.15 ± 18.56 s.

Within a single bout, the shortest period in which balancing could occur, the amount of grooming given by one partner in a dyad was significantly related to the amount of grooming her partner gave in return ($N = 435$, $F_{1,86} = 33.32$, $p < 0.0001$, $r^2 = 0.09$, $\beta = 0.32 \pm 0.05$ (95% CI: 0.207, 0.425); Figure 1), but grooming was not evenly balanced within bouts. Perfectly balanced within-bout grooming would generate a slope of 1.0, but the observed slope (0.32) is considerably lower, and indicates that one partner often gives more than another in single bouts.

Discrepancies in the balance of short-term exchanges are reduced as the time scale is extended. The total grooming contributions of each partner in a dyad were summed across bouts for the entire study period (15 months). Again, the amount of grooming provided by one female is significantly related to the amount of grooming provided by her partner ($N = 87$, $F_{1,85} = 179.65$, $p < 0.0001$, $r^2 = 0.68$, $\beta = 0.77 \pm 0.06$ (95% CI: 0.656, 0.885); Figure 2). However, the slope of this regression is significantly higher than the slope of the regression for single bouts (Wald test: slope = 0.32, $F_{1,85} = 62.49$, $p < 0.0001$), which indicates that grooming is more evenly balanced across bouts than within bouts.

The distribution of grooming within dyads

The study group contained only three pairs of close maternal kin. On average, these three dyads groomed more frequently (kin $N = 55$ bouts, mean \pm

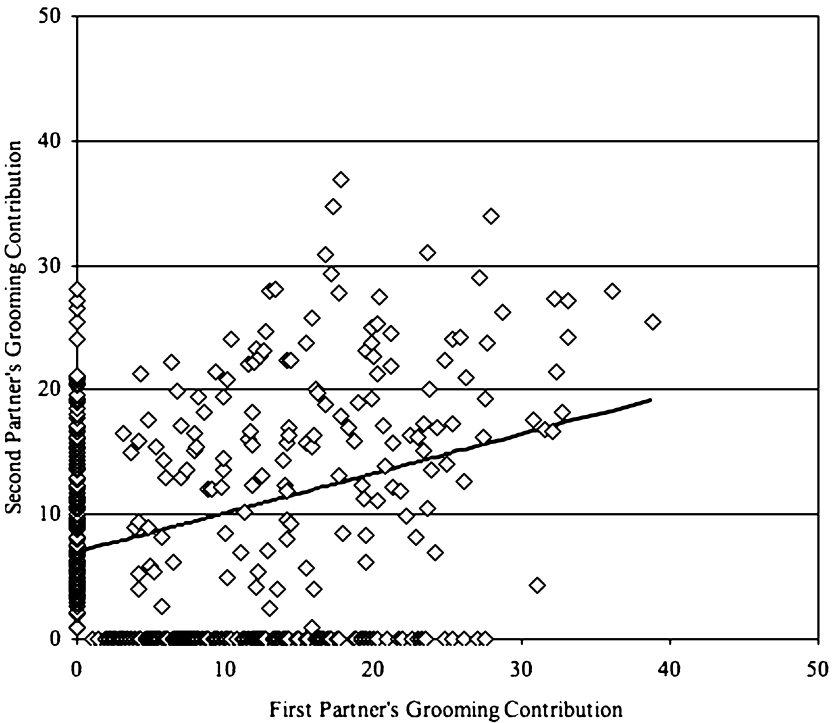


Figure 1. Grooming reciprocity within single bouts. The amount of grooming given by one female in a dyad is significantly related to the amount returned by her partner within a single bout, but partners often do not balance their grooming contributions within a bout. Grooming durations were square-root transformed to normalize the distribution. $N = 435$ bouts involving 87 dyads.

$SEM(\mu) = 27.07 \pm 1.68$ bouts per dyad; non-kin $N = 380$ bouts, $\mu = 13.24 \pm 0.67$ bouts per dyad), and for longer periods of time within a single bout (kin $\mu = 393.96 \pm 60.90$ s; non-kin: $\mu = 313.64 \pm 19.35$ s) than pairs of unrelated females. The relationship between the amount of grooming given and received within a bout by the initiating partner remains significant when the effects of kinship are held constant ($N = 435$, $F_{3,86} = 82.94$, $p < 0.0001$, $r^2 = 0.10$). Nonkin are slightly more balanced in their grooming contributions than kin, but the slope for kin is not significantly different than that of nonkin (non-kin $\beta = 0.324 \pm 0.75$, $p = 0.001$; kin $\beta = 0.295 \pm 0.078$, $p = 0.19$). When grooming contributions are summed across bouts, unrelated females balance their grooming more evenly than related females, and this difference is significant ($N = 87$, $F_{3,83} = 73.0$, $p <$

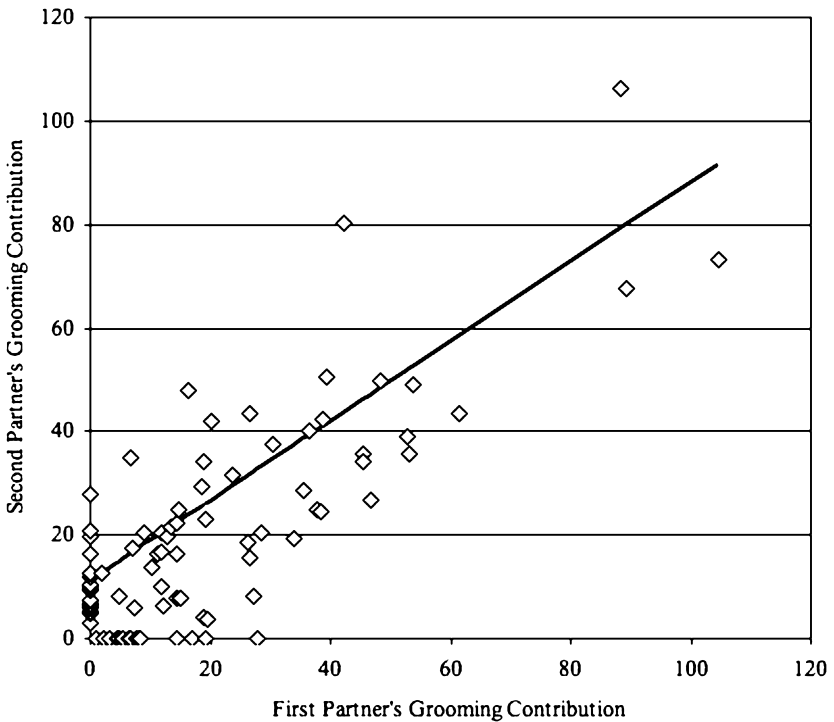


Figure 2. Grooming reciprocity across bouts. The total amount of grooming given by one female in a dyad is significantly related to the amount given by her partner across all of their bouts, and is significantly more balanced than grooming within single bouts. Grooming durations were square-root transformed. $N = 87$ dyads.

$0.0001, r^2 = 0.73$; non-kin $\beta = 0.911 \pm 0.066, p < 0.001$; kin $\beta = 0.520 \pm 0.156, p = 0.014$).

If lower-ranking females trade grooming for valuable commodities offered by higher-ranking partners, then the amount of grooming given should increase as rank distance between two partners increases, reflecting the increasingly higher value of those partners. However, the amount of grooming given by the lower-ranking partner in a single bout, controlling for total bout length, did not consistently increase as the rank distance between partners increased ($N = 435$ bouts, Wald $\chi^2(1) = 0.01, p = 0.943, \alpha = 3.98, \beta = 0.002 \pm 0.02, p = 0.943$). When grooming was summed across the study period, again rank distance did not consistently effect the proportion of grooming contributed by the lower-ranking partner ($N = 87$ dyads, Wald $\chi^2(1) = 0.01, p = 0.912, \alpha = 3.02, \beta = -0.004 \pm 0.034, p = 0.912$).

Discussion

Female baboons in this study balance their grooming exchanges over many interactions, even though they do not always trade roles or balance grooming within single bouts. The data presented here suggest that females are not limited to short-term trades and may be able to track the balance of their grooming exchanges across bouts. These findings are consistent with recent evidence demonstrating that female baboons in Amboseli maintain grooming relationships with preferred partners over extended periods of time (Silk et al., 2006a), and that females with strong social bonds have more equitable grooming relationships (Silk et al., 2006b). Recent studies of chimpanzees (Gomes et al., 2009) and capuchins (Schino et al., 2009) have also demonstrated greater balance in grooming over multiple interactions than within single bouts.

It is not entirely clear what processes underlie the formation and maintenance of grooming relationships in this group. It is possible that some form of contingent reciprocity explains the patterning of grooming, although observational studies like this one do not provide direct evidence for contingency. Long-term exchanges may also play a role in biological markets. When commodities have incremental value and the costs of cheating and benefits gained from repeat interactions with trading partners outweigh the benefits of short-term cheating, it may be profitable for partners to extend exchanges over time (Nöe & Hammerstein, 1994, 1995). While Barrett and her colleagues have expressed doubt that primates are capable of implementing such strategies (Barrett & Henzi, 2002), the results presented here strongly suggest that baboons are able to keep track of exchanges in at least one currency over substantial periods of time.

The finding that grooming is often unbalanced over short time periods corresponds to results from other studies. In one of the South African baboon groups that Barrett and her colleagues studied, only 30% of all grooming bouts involved within-bout role reversals, while 85% of all grooming bouts involved role reversals in another group (Henzi & Barrett, 1999, 2002; Barrett et al., 2000, 2002). The frequencies of within-bout role reversals are relatively low in bonnet macaques (5–7%) and white-faced capuchins (12–27%) (Manson et al., 2004), and Japanese macaques (28%) (Schino et al., 2003). Such imbalances must mean that females exchange grooming for other goods or services, keep track of grooming over long time periods, or tolerate a very high rate of cheating.

In this group of baboons, some exchanges do involve multiple currencies. Females use grooming to gain access to infants (Frank, 2007). Females also adjust their grooming contributions in relation to the risk of being harassed by their partner while feeding (Frank, 2007). However, there does not seem to be a simple relationship between the rank of females and their value as exchange partners. The amount of grooming contributed by lower-ranking partners in these situations did not increase with rank distance or reflect the provision of benefits in other currencies.

The data presented here indicate that females balance grooming over time scales much longer than single bouts. This suggests that female primates may be able to track benefits given and received in one currency over considerable periods of time. Despite disagreement on the commodities being traded and the time-scale over which individuals calculate their trade relationships (Barrett & Henzi, 2002), it is plausible that both market forces and long-term contingent relationships factor into the decisions that individuals make, which generate observed patterns of social interaction. Individuals in stable social groups can choose to interact with a variety of partners who differ in value, and partner choice may play an important role in the dynamics of social life (Barrett et al., 1999). However, this does not necessarily preclude the possibility that animals develop long term social bonds based on contingent cooperation or nepotism. To fully understand the dynamics of cooperative relationships in primates and other social mammals, we need to consider both short-term opportunities for market-based exchanges and long-term prospects for contingent reciprocity.

Acknowledgements

This study was funded by the Leakey Foundation and the UCLA Department of Anthropology. Permission to work in Kenya was provided by the Office of the President, in connection with Shirley Strum and the Uaso Ngiri Baboon Project. Research protocols were approved by the UCLA Animal Research Committee. We thank Shirley Strum, Joseph Manson, Peter Henzi and two anonymous reviewers for their comments on earlier drafts of this paper and the Statistical Consulting Group at UCLA for their advice on the analyses presented here.

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