

Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons (*Papio anubis*)

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(Accepted: 4 November 2008)

Summary

In a biological market, individuals seek to maximize their benefits by trading social commodities with the partner offering the highest value. When demand for a partner or commodity is greater than supply, individuals compete for access to the preferred partner by raising the price they are willing to pay. In primates, this model has been used to explain the pattern of grooming between mothers of new infants and other individuals who attempt to handle those infants. Here we describe the pattern of interactions with mothers of newborn infants in a group of wild olive baboons (*Papio anubis*) in Laikipia, Kenya. Females in this group provide a greater share of grooming within bouts when their partners have young infants than when they do not have young infants. Females groom mothers longer when they handle her infant than when they do not. However, females do not compete for access to infants by raising their grooming offers to mothers as the availability of infants declines. The change in relative grooming contributions results from mothers decreasing their grooming rather than non-mothers increasing their contributions. These results suggest that females do trade across currencies, but market pricing does not always explain the pattern of exchange.

Keywords: biological market, grooming, infant handling, exchange.

Introduction

When unrelated individuals cooperate, it is usually assumed that contingent reciprocity underlies the pattern of their exchanges. Recently, a biological

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markets approach has been applied to the analysis of cooperative behaviors. This approach treats interactions as transactions in a marketplace in which individuals play the roles of buyers and sellers who negotiate the 'price' of commodities (Noë & Hammerstein, 1994). Buyers assess the value of each seller's offer, and choose to trade with the highest bidder. 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 (Noë & Hammerstein, 1994). The biological markets approach has been applied to a variety of biological problems, including cleaning behavior among reef fish (Bshary, 2001; Bshary & Schaffer, 2002), association choices among hyenas (Smith et al., 2007), and the exchange of grooming for access to other females' infants (Henzi & Barrett, 2002). Here, we examine how market forces affect the exchange of grooming with mothers of young infants in a group of free-ranging olive baboons.

Grooming is an important social currency in Old World primate groups (Dunbar, 1991). Females devote considerable amounts of time to social grooming, and selectively groom kin and reciprocating partners (Seyfarth & Cheney, 1984; Perry, 1996; Silk et al., 1999; Barrett & Henzi, 2001; Schino, 2001). Grooming serves hygienic functions (Dunbar, 1991; Reichard & Sommer, 1994; Perez & Baro, 1999) and also provides beneficial physiological effects for recipients (Boccia, 1987). In some species, females trade grooming for support in agonistic encounters (Seyfarth, 1977; Seyfarth & Cheney, 1984; Hemelrijk, 1994; Schino, 2007), and may use grooming as a currency in negotiating access to infants (references below).

Newborn primates are extremely attractive to group members, particularly adolescent and adult females (Altmann, 1980; Maestripieri, 1994a; Silk et al., 1996, 2003; Manson, 1999; Silk, 1999). In some species, such as Asian colobines, infants are frequently held and carried by other group members (Nicholson, 1987; Stanford, 1992). In other species, including baboons and macaques, mothers are much more restrictive of their infants (Altmann, 1980; Nicholson, 1987). Nonetheless, female baboons and macaques persistently attempt to touch, nuzzle, inspect, and greet young infants (Altmann, 1980; Cheney & Seyfarth, 1997; Silk, 1999; Bentley-Condit et al., 2001; Henzi & Barrett, 2002; Silk et al., 2003). Mothers rarely initiate handling bouts, perhaps because handling may be dangerous to infants (Nicholson, 1987), and avoid rough or persistent handlers (Silk et al., 2003). Females of-

ten groom mothers of young infants (Seyfarth, 1977; Altmann, 1980; Nicholson, 1987; Matsumura, 1997; Manson, 1999; Manson et al., 1999; Silk et al., 2003), which may facilitate their access to infants (Altmann, 1980; Muroyama, 1994; Henzi & Barrett, 2002).

Although females' interest in newborns is well established, there is continuing debate about the function of infant handling (Silk, 1999; Silk et al., 2003). In species, like baboons, in which mothers are reluctant to allow their infants to be handled, infant handling may be a form of subtle harassment (Nicholson, 1987; Maestripieri, 1994b, 1999; Silk, 1999), a mechanism for testing the strength of social bonds (Manson, 1999), or a by-product of selection for good maternal care (Paul & Kuester, 1996; Silk, 1999). While infant handling seems to be beneficial to actors in some way, handling may have negative or neutral impacts on the mother and her infant.

Henzi & Barrett (2002) examined how market forces influence grooming toward mothers in a group of free-ranging chacma baboons in South Africa. They assumed that infants are a scarce and valuable commodity, and that mothers could control the market for access to their infants. They found that non-mothers were more likely to initiate bouts with mothers than vice versa, non-mothers were rarely groomed by mothers, and mothers were more tolerant of other females' efforts to handle their infants if they were groomed first (Henzi & Barrett, 2002). Within dyads, the proportion of grooming provided by one female was higher when her partner had an infant than when her partner did not (Barrett & Henzi, 2002). Two factors affected the price that females paid for access to infants. First, females groomed higher-ranking mothers longer than lower-ranking mothers. Second, females groomed lower-ranking mothers longer as the number of infants available declined (Henzi & Barrett, 2002). Henzi & Barrett observed that infant handling interactions were usually brief, and the duration and intensity of handling interactions were not affected by the duration of grooming that preceded them. A similar pattern of grooming was found between mothers and non-mothers among female long-tailed macaques (*Macaca fascicularis*) (Gumert, 2007).

Like chacma baboons, female olive baboons exchange grooming with many partners and attempt to interact with mothers and their young infants (Strum, 2001). However, the females in this population do not trade equal

amounts of grooming within single bouts and do not provide more grooming to higher-ranking partners than they receive (Frank, 2007). Grooming between two partners is more evenly balanced over many interactions than within bouts, suggesting that females monitor their exchanges over extended periods of time (Frank, 2007). Chimpanzees (Gomes et al., 2009) and Japanese macaques (Schino et al., 2003) also do not reciprocate evenly within bouts and balance their grooming exchanges more evenly over extended periods of time.

Given these differences in the patterning of grooming exchanges, we examine the biological market for infants in a population of free-ranging olive baboons in Kenya. Following Henzi & Barrett (2002), we focus on the dynamics of grooming interactions among females, rather than the details of handling interactions. This assumes that acts of infant handling are of equal value, as demonstrated by Henzi & Barrett (2002), so that market forces will only affect the length of grooming bouts and the proportion of grooming given by the non-mother to the mother within each dyad. If females trade grooming for access to infants, then females will selectively groom mothers with young infants and groom them for longer when they handle an infant than when they do not. Females without infants will also initiate grooming with mothers of young infants and receive relatively little grooming in return. Since the act of infant handling may be costly to mothers, females should first offer grooming and then handle the infant (Muroyama, 1994). Grooming bouts between non-mothers will be more evenly balanced than bouts between mothers and non-mothers, and the relative and absolute grooming contributions within dyads will change when one partner has an infant. The amount of grooming given to a particular mother will also reflect the current market value of that female and her infant. Thus, females will groom higher ranking mothers more than lower ranking mothers, be less likely to handle infants of higher ranking mothers than lower ranking mothers, and do so more gently. If potential handlers must compete for access to infants then bouts with mothers should be longer than bouts with non-mothers and increase in length as the number of infants declines.

Methods

Study site and animals

Data on the grooming interactions of all adult females in a troop of 60 olive baboons (*P. anubis*) that range in the Ndorbo Reserve and on Chololo Ranch

in the Laikipia Plateau of central Kenya were collected during three 5–6-month-long field seasons spanning an 18-month period from June 2003 to December 2004. 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 aunt–niece dyad, and one mother–daughter dyad.

Infant baboons less than 3 months old have a distinctive natal coat, and receive more attention from other members of the troop than older infants (Altmann, 1980; Silk, 1999; Henzi & Barrett, 2002; Silk et al., 2003). For the purposes of these analyses, when females have infants less than 3 months of age they are categorized as ‘mothers’, and at all other times they are categorized as ‘non-mothers’. Four females had infants less than 3 months old at the beginning of the study, 11 gave birth during the study, and one did not have a young infant at any time during the study period. Thus, all but one of the 16 adult females in the group was observed when she had an infant less than 3 months old (mother) and when she did not have an infant less than 3 months old (non-mother).

Data collection

All adult females were the subjects of 30-min focal follows (Altmann, 1974), totaling 805 h of focal data. During focal observations, the beginning and end of all grooming episodes were recorded to the nearest second and data collection continued until all grooming had stopped for at least two minutes. This sometimes extended beyond the scheduled end of the focal sample. Infant handling was defined as touching, pushing, pulling, or hitting an infant. Only touching was considered ‘gentle’ handling. The other three types of contact with the infant were considered ‘rough’. Females who handled an infant within 2 min before the onset or after the end of grooming were considered to have handled an infant as part of their grooming bout.

Analyses

Following Barrett et al. (2000), grooming bouts consist of a series of one or more ‘episodes’ in which one partner grooms the other. By definition, episodes are unilateral interactions, while grooming bouts are bilateral if partners exchange roles. Grooming bouts were defined as a sequence of episodes separated by pauses of less than 2 min. We refer to bouts in which

only one member of the dyad groomed as 'unilateral bouts', and bouts in which both partners contributed grooming as 'bilateral bouts'. For each grooming bout, we extracted the following information: (a) identity of the female who initiated the bout (initiator, hereafter), (b) identity of the female who was the original recipient (target, hereafter), (c) the total amount of grooming performed by the initiator and by the target, (d) maternal status of the initiator and target, (e) rank of the initiator and target and, if applicable, (f) whether the non-mother handled the infant of the mother, (g) whether handling preceded or followed the first episode of grooming, and (h) whether the handling was rough or gentle. Dominance ranks were assessed on a monthly basis using daily ad libitum observations of avoidance and aggression between females. The female dominance hierarchy remained stable throughout the study.

For pair-wise comparisons of two variables, we used the nonparametric Wilcoxon matched-pairs signed-rank test. To determine the effects of rank distance and the number of available mothers on grooming contributions, and to assess how the amount of grooming given by one female affected the amount of grooming given by her partner, we used Ordinary Least Squares Regression, following statistical methods first presented by Manson et al. (2004). The analysis of dyadic grooming data is problematic because bouts involving the same dyad are not independent. However, in these regressions, data were clustered by initiator-target dyads and weighted by their frequency within the sample (Manson et al., 2004). The distribution of duration variables was non-normal, so all analyses were based on the value of the square root of grooming duration. Statistical tests were performed using STATA 9.0 (2007). Reported test statistics are two-tailed. Preliminary analyses showed that maternal kinship did not affect the pattern of any of the results, and is not considered in the analyses reported below.

Results

The effect of infants on the distribution of grooming among females

Females preferentially groom mothers of young infants

Adult females participated in 435 grooming bouts. Of these, 178 involved a dyad composed of one mother and one non-mother and 14 involved two

mothers. Thus, 192 bouts involved at least one mother of a young infant. To determine whether females selectively groom mothers, we compared the proportion of grooming bouts involving mothers on a given day to the proportion of females with infants in the group on the same day. On average, $\mu \pm \text{SE} = 0.41 \pm 0.03$ of all grooming bouts each day involved a mother with a young infant, but just 0.15 ± 0.01 of the adult females in the troop had a young infant on a given day. The proportion of bouts involving mothers was consistently higher than expected based on their availability (Wilcoxon Signed-Rank Test: $z = 6.638$, $p < 0.0001$, $N = 152$ days).

Non-mothers usually initiate grooming with mothers

When mothers and non-mothers groomed, non-mothers were almost always responsible for initiating the grooming bouts. Non-mothers initiated 91% ($N = 192$) of all bouts involving mothers with young infants. For each female we calculated the proportion of grooming bouts she initiated when grooming with mothers and the proportion of grooming bouts she initiated when grooming with non-mothers. Non-mothers were more likely to be the initiators of grooming bouts with mothers ($\mu = 0.78 \pm 0.07$) than with other non-mothers ($\mu = 0.48 \pm 0.06$; $z = 3.18$, $p < 0.002$, $N = 15$). Thirteen of the 15 females who groomed with both mothers and non-mothers followed this pattern.

Mothers engage in fewer bilateral grooming bouts than non-mothers

Grooming was bilateral in 20% of bouts involving a mother and a non-mother ($N = 178$ bouts), and 45% of the bouts involving two non-mothers ($N = 243$ bouts). To determine whether this difference was consistent across females, we calculated the proportion of bouts that each non-mother initiated that were bilateral, first with partners who were mothers and then with partners who were not mothers. Females were significantly less likely to groom bilaterally with mothers ($\mu = 0.21 \pm 0.05$) than with non-mothers ($\mu = 0.45 \pm 0.05$; $z = -2.38$, $p < 0.02$, $N = 13$; 3 non-mothers did not groom with both mothers and non-mothers).

Grooming bouts with mothers are shorter because they tend to be unilateral

On average, bouts with mothers were shorter than bouts with non-mothers (mothers $\mu = 242.6 \pm 37.8$ s, non-mothers $\mu = 375.4 \pm 35.3$ s; $z =$

Table 1. Bout type but not maternal status affects the length of a grooming bout.

	Sum of squares	df	<i>F</i>	<i>p</i>
Maternal status	143 378.6	1	1.57	0.21
Type bout	19 103 557.9	1	209.64	0.0001
Maternal status × Type bout	62 929.4	1	0.69	0.41
Model	25 258 737.1	3	92.4	0.0001
Residual	37 999 098.7	417		
Total	63 257 835.8	420		

Maternal status indicates whether one partner was a mother (1) or not (0). Type bout indicates whether the bout was unilateral (0) or bilateral (1). The dependent variable was total bout length. Only the type of bout significantly affects total bout length.

2.27, $p < 0.02$, $N = 13$). This may be due to the fact that bilateral grooming bouts are typically longer than unilateral grooming bouts (bilateral: $\mu = 665.17 \pm 459.59$ s vs. unilateral $\mu = 145.95 \pm 163.33$ s), and females' reproductive status influences the likelihood that grooming will be bilateral. A multivariate analysis indicates that the type of bout (bilateral/unilateral) affects total bout length, but maternal status does not (Table 1).

Two non-mothers balance their grooming more evenly than a mother and a non-mother

To examine the balance of grooming exchanged between females during individual bouts, we regressed the amount of grooming given by the initiating female against the amount of grooming she received from her partner. Maternal status was included as a dichotomous variable. If the slope of the regression is less than 1, the initiating female provides more grooming to her partner than she gets in return. The amount of grooming given by the initiating female affects the amount of grooming a target gives in return ($F_{3,127} = 20.25$, $p < 0.0001$, $R^2 = 0.26$, $N = 421$). This relationship held true for dyads in which neither female had an infant ($t = 6.79$, $p < 0.0001$) and dyads in which one of the females had an infant ($t = 2.46$, $p < 0.02$). However, the slope describing the relationship between grooming given and returned by two non-mothers ($\beta = 0.616 \pm 0.091$) is significantly higher than the slope describing the relationship between grooming given and returned between a mother and a non-mother ($\beta = 0.227 \pm 0.092$; $F_{1,127} = 8.97$, $p <$

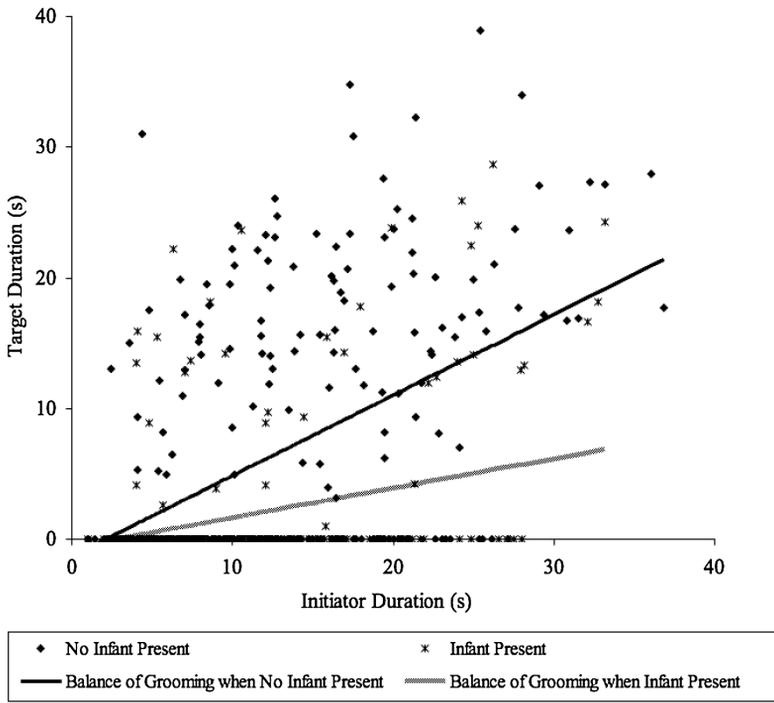


Figure 1. Grooming between two non-mothers is significantly more balanced than grooming between a mother and a non-mother. Grooming durations are the square root of the seconds spent grooming by each partner. Both unilateral and bilateral bouts are shown here.

0.005; Figure 1), indicating that grooming is more evenly balanced between two non-mothers than between non-mothers and mothers.

Non-mothers do not groom more, mothers groom less

If females invest more time in grooming mothers because they have young infants, then we would expect females' grooming interactions with particular partners to be affected by the presence of an infant. In 39 dyads, we were able to compare the proportion of a dyad's total grooming that one female directed toward another female during all their interactions when her partner did or did not have a young infant. In 36 of these cases, females were responsible for a larger proportion of grooming when the partner was a mother ($\mu = 0.90 \pm 0.03$) than when she was a non-mother ($\mu = 0.47 \pm 0.06$; $z = -4.785$, $p < 0.0001$, $N = 39$; Figure 2). We calculated the average duration a female groomed her partner during all bouts when her partner was a mother

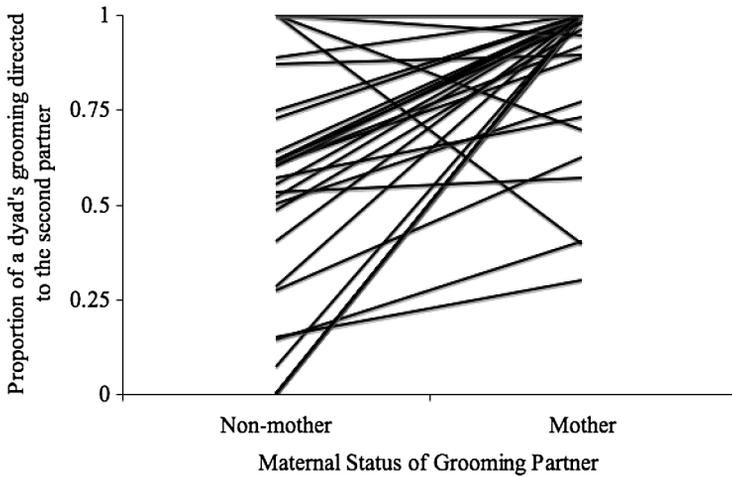


Figure 2. Within dyads, females contribute a larger proportion of the grooming when their partner has an infant than when the same partner does not. Grooming contributions here are summed across all relevant bouts and the focus of the analysis is on the alphabetically first partner and her grooming contribution to the alphabetically second partner in each dyad, when the second partner does and does not have an infant.

and when her partner was a non-mother. Females do not consistently groom their partner longer during a bout when she is a mother than when she is not (mothers $\mu = 159.1 \pm 19.16$ s; non-mothers $\mu = 176.2 \pm 29.2$ s). Half of the females spent more time grooming their partner when she was a mother than when she was not a mother, and half showed the opposite pattern (Wilcoxon Signed-Rank Test: $z = 0.181$, $p = 0.86$, $N = 39$). We also calculated the average duration a female groomed her non-mother partner during all bouts when the female was a mother and when she was a non-mother. Females significantly decrease the amount of grooming they give a partner when they have an infant compared to when they do not (female is a non-mother: $\mu = 157.9 \pm 23.6$; female is a mother: $\mu = 34.7 \pm 11.9$; $z = 4.469$, $p < 0.0001$, $N = 39$).

The effects of market forces on grooming between mothers and non-mothers

Females do not give more grooming to higher-ranking mothers

To determine whether relative rank influenced the amount of grooming that mothers received from non-mothers, we regressed the rank distance between

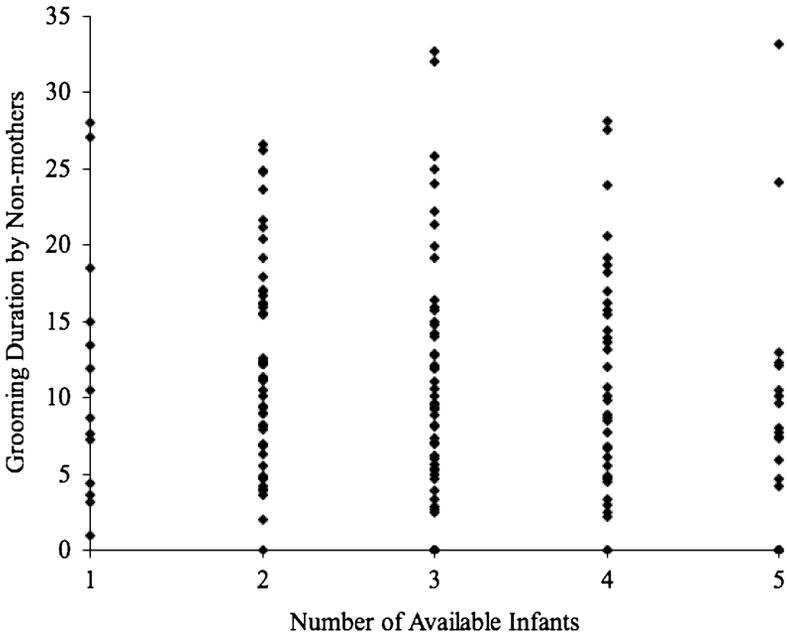


Figure 3. Non-mothers do not increase the grooming they give to mothers as the supply of infants declines in either all bouts or bilateral bouts. All bouts of grooming are shown here and the duration of bouts by non-mothers is the square root of seconds spent grooming her partner.

each mother and non-mother against the amount of grooming the same non-mother provided to her partner during each of their bouts. The rank distance between partners had no impact on the amount of grooming provided by non-mothers to mothers ($F_{1,77} = 0.15$, $R^2 = 0$, $p = 0.70$, $N = 178$).

Females do not give more grooming to mothers when infants are scarce

Infants are expected to be a more valuable commodity when they are scarce. However, the number of young infants present in the group (range 1–5) did not significantly affect the amount of grooming provided by non-mothers to mothers ($F_{1,77} = 1.87$, $R^2 = 0.02$, $p = 0.18$, $N = 178$; Figure 3).

Mothers do not calibrate their grooming reciprocation based on the demand for their infant

Another way in that market forces might affect the balance of trade is by reducing the amount of grooming mothers provide in return as demand for

their infant increases. However, in bilateral bouts, mothers did not reduce the amount of grooming they gave to non-mothers as the number of infants declined ($F_{1,22} = 0$, $R^2 = 0$, $p = 0.98$, $N = 36$).

The role of infant handling in the grooming market

Grooming does not always precede infant handling, regardless of rank

We observed 178 grooming bouts involving one non-mother and one mother of a young infant. Non-mothers groomed the mother and then handled her infant 30% ($N = 54$) of the time, handled the infant and then groomed the mother 34% ($N = 60$) of the time, and did not handle the infant during their grooming interaction 36% ($N = 64$) of the time. For each female, we compared her average rank distance (mother rank – non-mother rank) from all the mothers she groomed when she handled infants during a grooming bout versus when she did not (no handling: $\mu = -1.5 \pm 1.2$; handling $\mu = -1.6 \pm 1.2$), when she groomed before handling versus when she handled before grooming (handle first $\mu = -1.7 \pm 1.2$; groom first: $\mu = -0.9 \pm 1.3$), and when she handled gently versus when she handled roughly (gentle: $\mu = -1.3 \pm 1.0$; rough: $\mu = -1.4 \pm 1.0$). Rank distance between the mother and non-mother did not differ between bouts in which the non-mother handled the infant or did not handle the infant ($z = 0.157$, $p = 0.88$, $N = 12$ females). Rank distance also did not affect whether the non-mother groomed the mother or handled the infant first ($z = -1.01$, $p = 0.31$, $N = 13$ females) or whether the female was rough or gentle in her handling of the infant ($z = 0.45$, $p = 0.65$, $N = 13$ females).

Females groom mothers longer when they groom first and then handle the infant

For each female we compared the average duration of grooming she gave to mothers in bouts in which she also handled the infant to bouts in which she did not handle the infant. When females handled a mother's infant they spent more time grooming the mother than when they did not handle a mother's infant (no handling $\mu = 87.1 \pm 24.5$ s; handling $\mu = 231.4 \pm 41.4$ s; $z = -3.059$, $p = 0.002$, $N = 12$). Females also provided significantly more grooming to their partners with infants when they groomed the mother before handling the infant ($\mu = 297.4 \pm 47.6$) than when they handled prior to grooming the mother ($\mu = 166.1 \pm 25.7$, $z = -2.551$, $p = 0.01$, $N = 13$).

Table 2. Bout type and the act of handling an infant in bouts with mothers affects non-mothers grooming contributions.

	Sum of squares	df	<i>F</i>	<i>p</i>
Type bout	555 922.53	1	15.64	0.0001
Infant handling	602 451.59	1	16.95	0.0001
Type bout × Infant handling	207 634.34	1	5.84	0.017
Model	795 732.83	3	22.38	0.0001
Residual	35 550.18	174		
Total	48 434.64	177		

Type bout indicates whether the bout was unilateral (0) or bilateral (1). Infant handling indicates whether the non-mother handled the mother's infant (1) or not (0) during their grooming bout. The dependent variable was the duration of grooming provided by the non-mother during a bout with a mother. Both the type bout and the act of handling an infant significantly affect the amount of grooming given by the non-mother.

Females groom mothers longer in bilateral bouts that involve infant handling

On average bilateral bouts are longer than unilateral bouts of grooming and bouts that involve infant handling are longer than bouts when the non-mother does not handle the infant. A multivariate analysis indicates that both the type of bout (bilateral/unilateral), the act of handling or not handling the partner's infant, and the interaction of the two significantly increase the duration of grooming provided by the non-mother (Table 2).

Discussion

The data presented here show that adult females preferentially groom mothers of young infants, and spend more time grooming mothers whose infants they handle, but market forces seem to have little effect on the 'price' non-mothers pay for access to infants in this population. Non-mothers groomed mothers more often than expected based on their availability, and played a more active role in grooming interactions with mothers than with non-mothers. However, unlike female chacma baboons (Henzi & Barrett, 2002), females in this group did not offer more grooming to mothers when there were fewer infants in the troop, and they did not give more grooming to mothers or handle their infants differently as the rank distance between them

increased. Thus, mothers did not seem to take advantage of their biological market power to demand higher prices from some consumers than from others.

It may be worthwhile to consider alternative explanations for the patterns that Henzi & Barrett (2002) observed. In contrast to the assumptions underlying biological market models (Noë & Hammerstein, 1994), Henzi & Barrett acknowledge that high-ranking females might take commodities by force; some high-ranking animals handled infants without grooming their mothers first (Henzi & Barrett, 2002). In some populations, high-ranking females handle infants more roughly than lower ranking females do (Altmann, 1980; Nicholson, 1987), although this was not true in this study. This suggests that lower ranking mothers may be particularly wary of higher-ranking handlers, and may be increasingly tense as the overall demand for their infant increases (Henzi & Barrett, 2002). Henzi & Barrett found that females groom mothers in shorter bouts than non-mothers, suggesting that females “groom only as long as is necessary to obtain maternal tolerance” (Henzi & Barrett, 2002, p. 920), which is also not true of females in this study. It is possible that in a troop with a steep dominance hierarchy, such as reported for the chacma baboons (Henzi & Barrett, 1999, 2002; Henzi et al., 2003), higher-ranking females use grooming to reduce maternal tension (Boccia, 1987; Schino et al., 1988). If mothers are more tense when there are fewer infants in the group, and they are the targets of more attention, then more grooming may be necessary when the supply of infants is low.

Across species, females spend more time grooming up the hierarchy as rank differences become more extreme and tend to engage in less balanced grooming exchanges within bouts (Schino & Aureli, 2008). In this troop, rank does not affect the balance of grooming within bouts (Frank, 2007) or the amount of grooming non-mothers give to mothers. Rank distance also did not vary between cases of rough and gentle infant handling. Thus, females in this troop may not need to spend more time grooming lower-ranking mothers as the supply of infants declines.

The results presented here suggest that females alter their grooming exchanges when commodities other than grooming are available for trade. When neither partner in a dyad has an infant, grooming was more evenly balanced within dyads. However, when one of the two females has an infant, grooming is very poorly balanced within dyads. This suggests that non-mothers frequently trade grooming in kind, but when there is an infant to

handle, non-mothers sometimes swap grooming for access to infants. Non-mothers frequently handle infants during grooming bouts with mothers and spend more time grooming a mother when they also handle her infant. But it is not clear that they compete for access to infants by raising their grooming offers to mothers. Both unilateral and bilateral bouts with mothers were just as long as bouts with non-mothers. Within dyads, females did not consistently groom their partner longer when she had an infant than when she did not have an infant. These results suggest that access to infants is not a more valuable commodity than grooming, and that females do not differ in their ability to provide sufficient grooming to satisfy mothers' demands. Potential handlers do not compete for access to infants by escalating their bids.

Our data suggest that the unbalanced grooming between mothers and non-mothers is more a result of changes in mothers' behavior. While females contribute a larger proportion of the total bout when their partner is a mother than when she is not, they do not consistently increase the amount of time that they devote to grooming their partners. Instead, when a female has a young infant she grooms her partners for shorter amounts of time. Mothers may shift the currency of reciprocation, repaying grooming with access to their newborn infant. Alternatively, mothers may simply have less energy to reciprocate grooming relationships while caring for an infant, and spend more time foraging or resting in order to have enough energy available for lactation (Altmann, 1980; Barrett et al., 2006) and non-mothers may prolong a mother's willingness to rest and let her infant be handled by grooming her for longer and interspersing that grooming with short bouts of handling. The end result looks much the same.

In the Chololo baboons, grooming is less balanced within bouts than across bouts over time, suggesting that females keep track of their interactions and reciprocate over extended periods (Frank, 2007). These findings, and the data presented here, suggest that a market model of grooming may not be sufficient to account for the dynamics of grooming among females. Although females do adjust the commodities that they exchange with their partners, there is little evidence of bidding competition and the pricing of services does not reflect the supply of valuable commodities or partner value. This suggests that variation across dyads may reflect forces that are outside the purview of market models, such as kinship and contingent reciprocity (Silk et al., 2006a,b). To fully understand the patterning of cooperation among individuals, we may need to integrate models that emphasize

the effects of short-term market forces and models that focus on the benefits derived from long-term social bonds with kin and reciprocating partners.

Acknowledgements

The authors thank the Leakey Foundation and the UCLA Department of Anthropology for providing funding for this study. Permission to work in Kenya was provided by the Office of the President, in connection with Shirley Strum and the Uaso Ngiro Baboon Project and research protocols were approved by the UCLA Animal Research Committee. We thank Shirley Strum, Joseph Manson, Gabriele Schino and an anonymous reviewer 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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