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Grooming and Infant Handling Interchange in *Macaca fascicularis*: The Relationship Between Infant Supply and Grooming Payment

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Abstract Female long-tailed macaques are attracted to infants and frequently groom mothers bearing them. Such grooming often involves the groomer contacting the infant and may be a trade of grooming for infant handling. To identify if grooming and infant handling are directly traded, I collected samples on times after female-to-mother grooming and on interactions in which a female groomed a mother and contacted her infant. I determined that grooming tended to promote an exchange with infant handling and that the supply of available infants was related to how long a female groomed a mother. Grooming interactions were longer when infants were scarce in the surrounding social environment than when they were abundant, indicating a possible supply-and-demand effect. This supports that grooming may be payment for infant handling. Grooming-infant handling interchanges tended to be unidirectional as mothers usually did not reciprocate grooming. Instead, infant contact occurred. A larger proportion of grooming-infant handling interchanges involved younger infants, but infant age did not seem to influence grooming durations. The length of female-to-mother grooming had no observable effect on handling time. Lower-ranked females groomed higher-ranked mothers and their infants longer than *vice versa*. Moreover, it was possible to predict up-rank grooming via supply and demand better than down-rank grooming. There was no observable influence of kinship on grooming-infant handling interchange. These results support the conclusion that grooming and infant handling may be traded. Grooming promoted infant handling, while supply and rank predicted the grooming payment a female would offer to access an infant.

Keywords biological markets · grooming · infant handling · interchange · *Macaca fascicularis*

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Mothers with infants are very attractive as social partners. In long-tailed macaques and other monkey and ape species, females tend to group around and to groom mothers bearing newborns more frequently than other females (Lancaster 1971; Maestripieri 1994; Manson 1999; Nicolson 1987; Silk 1999; Wheatley 1999). In such interactions in *Macaca fascicularis*, a female generally approaches a mother that is holding her infant. She then grooms the mother and grooms, touches, grabs, and/or on occasion picks up and holds the mother's infant. The interactions are always associated with an apparent interest in the infant by the groomer expressed through repeated looking, lip-smacking, and vocalization. Often the interactions are rigid and the groomer appears fearful or cautious in contacting the infant.

The increased grooming may result from females attempting to ease interaction with a mother's infant and thus they may be interchanging grooming with infant handling (Henzi and Barrett 2002). It is possible that social animals may exchange valuable acts to gain access to social partners or commodities to which they have limited access and demand to obtain (Noë 2001; Noë and Hammerstein 1994, 1995). The biological market premise predicts that females are seeking out infants and are paying for access to them with grooming (Barrett and Henzi 2001; Henzi and Barrett 2002).

Female macaques are selected to be strongly attracted to infants, which makes better mothers because they will offer more care to their offspring, leading to better offspring survival (Silk 1999). The innate attraction that females have for infants makes them a valuable commodity and can drive their attempts to touch and to interact with them. Having many females attracted to infants creates a demand for infants, resulting in an infant market wherein many females attempt to access infants. Females engage in activities, such as grooming, that increase their probability of accessing and obtaining an infant. Consequently, grooming could be traded with infant handling in a manner that resembles payment for a commodity in a market.

Grooming seems to promote immediate reciprocation of other social acts in long-tailed macaques, e.g., grooming, tolerance, coalition support, and sexual activity (Gumert in press; Gumert 2005; Hemelrijk 1994). Therefore, grooming may also promote an exchange with infant handling. Grooming may promote infant handling by appeasing the mother. Appeasement would make her less likely to move away, more likely to release the infant, and/or more likely to allow access to it without resistance or aggression. If grooming is immediately traded with infant handling, females will increase contact with a mother's infant after grooming her. Another indicator of a grooming-infant handling interchange is that the bouts should mainly consist of unidirectional and not reciprocal grooming. This is because mothers should only offer infant handling in return for the grooming, not infant handling and grooming.

Market theory predicts when social acts are traded, economic forces, such as supply, demand, and advertisement, will influence social exchange by altering the value of the commodities traded (Noë 2001). Because grooming may be a payment to the mother for accessing her infant, the supply of infants available for infant handling at the time of a grooming-infant handling interchange will influence the amount of grooming a female will give to the mother. Scarcity will increase the price of the demanded commodity and overabundance will decrease the price.

I measured grooming payment using the duration of grooming directed toward the mother. Longer grooming duration indicated more time and energy expended, and thus more payment. I measured infant supply for each grooming-infant handling interchange using the number of infants per female within the social context. The measure accounted for both supply and demand because it represents a ratio of potential commodities vs. potential buyers. If grooming is indeed payment for infant access, the ratio of infants per female should be inversely related to the grooming time a female will give to a mother.

Other potential market factors could influence grooming payment. First, newborn infants are generally more attractive (Nicolson 1987) and are marked by a distinct black natal coat that starts to fade after about 2 mo (Wheatley 1999). If newborn infants are more attractive, possibly in that their natal coat attracts females, most exchanges should be directed at accessing younger infants, and female-to-mother grooming may be longer when the infant is younger. A second influence is that the amount of grooming that a female gives to a mother may be proportional to the amount of grooming she gives to the infant while it is handled. If this is true, it might insert a confound for identifying a supply-and-demand market because when supply is low individuals may pay more in grooming the mother, but also obtain more grooming with the infant. When supply is high, they could pay less but also obtain less. If this is the case, it would be difficult to determine if the payment is better explained by supply or by the amount of commodity received.

A social economy does not predict all social exchange because many other factors will influence grooming patterns. Kinship and dominance hierarchy are factors that have large influences on social exchange. Long-tailed macaque societies are matrilineal and hierarchical. The female dominance hierarchy is very stable over time and greatly influenced by kinship (Aldrich-Blake 1980; Farslow 1987; Wheatley 1999). A social economy could function only within the constraints of these 2 parameters. For example, dominance relationships may make social commodities cheaper for higher-ranked individuals and more expensive for lower-ranked individuals. Moreover, kinship may influence social economies by deferring costs for exchanges between kin or by creating barriers for trade between nonkin.

Female rank influences grooming in *Macaca fascicularis* and other cercopithecoid primates. Lower-ranked females direct more grooming toward higher-ranked females than is reciprocated (Seyfarth 1977; Wheatley 1999). This imbalance may occur because lower-ranked females may have more to gain by socially trading with higher-ranked females, such as advancement of social status, tolerance, and agonistic support. In contrast, high-ranked females may not need to groom as much to access commodities from lower-ranked partners, because high-ranked females can exert their social power to obtain access to resources. There may also just be less to gain from low-ranked females. Rank should exert these influences on grooming payment during grooming-infant handling interchanges.

Infants of higher-ranked mothers may have a higher value in an infant market than infants of lower-ranked mothers. If low-ranked infants are cheaper to gain access to, they should be interacted with more because of the greater ease and lower risk to gain access. Therefore, a larger proportion of infant handling interchanges should be directed down rank. Females should groom lower-rank infants for shorter time periods than higher-rank infants because once a female gains access to something of greater value, they should maintain it longer. Overall, grooming of both infants and mothers should be longer in up-rank than down-rank grooming-infant handling interchanges because there is greater cost. Finally, rank may also alter the influence of supply and demand. Up-rank grooming-infant handling interchanges should be better predicted by supply and demand than down-rank bouts because higher-ranked individuals should be less constrained by market effects: they can displace lower-ranked females when competing for commodities and avoid market influences.

Kinship influences social exchange in long-tailed macaques and closely related species (Farslow 1987; Kurland 1977; Wheatley 1999). Females groom individuals they are related to more than nonkin, and this may influence grooming-infant handling interchanges. Kin preferences could make access to infants by kin easier, and thus be associated with shorter grooming payment durations and more frequent interchange with kin. It could also make access to infants of nonkin more difficult, demanding longer grooming payment durations and making nonkin interchanges less frequent. In contrast to the first prediction, grooming-infant handling interchanges between kin could be longer than between nonkin because kin spend more time grooming in general. The influence kinship has could also be associated with the amount of time a female spends interacting with the infant.

I investigated grooming-infant handling interchanges in long-tailed macaques in Kalimantan Tengah, Indonesia. I studied time periods after female-to-mother grooming to determine if infant handling increased during these times. In addition, I investigated the direction of grooming during grooming-infant handling interchanges to assess if they were primarily unidirectional, i.e. female groom mother, mother does not groom female, but female accesses infant. Furthermore, I collected data on grooming bout duration and infant-female ratios to determine if a relationship between infant supply and female-to-mother grooming duration existed. Finally, I divided grooming-infant handling interchanges into up-rank and down-rank directed bouts as well as kin and nonkin bouts. This allowed me to determine if rank and kin affected grooming duration and/or the relationship between grooming duration and infant supply. I examined the results to conclude whether biological market theory could account for the observed results and if grooming was traded for infant handling.

Methods

Subjects

I collected data between June 2003 and July 2004 on female grooming-infant handling interchanges in a group of 48–53 long-tailed macaques at Tanjung Puting National Park (TPNP), Kalimantan Tengah-Indonesia. I recognized all of the group's individuals by facial features. The project was carried out in the 1–1.2 km^2 home range of the macaques along the Sekoyner River and near an ecotourist lodge. The group received provisioning from refuse. Provisioning generally occurred in the mornings when waste was dumped. It also occurred randomly when food items were discarded or given to the macaques throughout the day from lodge staff and guests.

I focused on adult females and infants. The group contained 18 adult females, and I included all of them in the study. I also included 2 adolescent females just becoming sexually active and interested in infants. Seventeen females bore an infant at some point during the study. One female, Helen, was probably sterile because I never observed her with an infant of her own since work at the site first began in 1999, and she did not have elongated nipples from nursing. I constructed the female dominance hierarchy from results of agonistic outcomes. I inferred female matrilineal kin relationships based on patterns of social interaction. No change in female composition or rank occurred during the study.

The number of infants varied between 8 and 13 during the study. I observed 24 infants in total. Fifty percent of them were born to mothers in the top half of the hierarchy; thus, there was an even distribution of infants based on mother's rank. Focal infants were <1 yr.

Data Collection

I used *ad libitum* sampling (Altmann 1974) to collect data on durations of all grooming bouts between 2 females that involved infant handling. I categorized an interaction as a grooming-infant handling interchange if a female groomed a mother and touched her infant. This could occur in any order, and any number of times. The interaction finished when the 2 individuals moved >5 m away from each other. I measured the total duration of grooming that occurred until the 2 females departed from each other. Also, I tallied all females and infants that entered the social context during the grooming interaction. I defined the social context as all individuals that were within sight of the grooming pair.

I collected 10-min focal (Altmann 1974) and post-grooming (PG) samples during this study. I used these data to test if grooming increased the frequency of infant handling. I collected PG samples by focal sampling a subject that had just received grooming. I only used PG samples collected on mothers with their infants. I collected focal samples on mothers with their infants in a social context. I assigned a social context to a sample if the mother engaged in grooming or if any grooming occurred in sight of the focal mother during the sample. During focal and PG samples, I scored all touches, grooming, and pick-ups toward the mothers' infants. To avoid biases, I collected focal samples via a randomized method that accounted for the time of day and potential observer preferences to follow particular individuals. I also collected PG samples on a fixed time schedule and followed only grooming bouts that occurred during scheduled PG collection times.

Infant Handling After Grooming

I analyzed data on touching, grooming, and infant pick-ups collected from focal and PG samples on 16 mothers with infants to determine if receiving grooming promoted infant handling. From focal samples, I determined a baseline rate under social conditions that a mother's infant received contact from other females. From PG samples, I calculated a PG rate at which a mother's infant was contacted by a female that just groomed her. I compared the 2 rates using paired *t*-tests to determine if the rate of touching toward a mother's infant was significantly higher in PG samples than in focal samples.

In addition to the focal-PG comparison, I used a match control (MC) analysis (de Waal and Yoshihara 1983) to account for bias due to proximity. In the focal PG comparison, there was no control over differences in a mother's proximity to other females during focal and PG samples. A bias might exist because in PG samples a mother must be in proximity of the grooming female. In contrast, a mother may or may not be in proximity of females in focal samples. This might inflate female-infant interaction in PG samples, simply as a function of increased proximity. An MC-PG comparison eradicates the potential bias because proximity can be controlled by matching PG samples with comparable focal samples. An MC sample is a focal sample that was matched with a PG sample. I selected an MC sample only if it had a social context and if during it the female that groomed the mother in the matched PG sample came into proximity of the mother. To make selection unbiased, I selected MC samples based on these criteria that were collected closest in time to the PG sample to be matched. I used every PG sample where a suitable MC sample was available. This produced a sample size of 10 females, each with 1 or 2 samples.

Effect of Supply on Grooming Bout Duration

I used the *ad libitum* data collected on grooming-infant handling interchange to determine if there was a negative relationship between the ratio of infants per female in the social context and the female-to-mother grooming duration. I was able to obtain data on 17 of the 20 females investigated for both performing and receiving grooming in a grooming-infant handling interchange. Two of the females for which I obtained no datum were older and less socially active. The other one was a socially active adult that I probably did not observe just by chance to engage in a grooming-infant handling interchange.

I collected 114 grooming bouts with complete data on duration and infant-per-female ratio. For each grooming-infant handling interchange, I measured the duration of female-to-mother grooming in minutes. I also calculated the ratio of infants per female in the social context, which represented the infant supply. I then performed a linear regression analysis to test for a relationship between grooming duration and infant supply.

The regression analysis did not account for the possibility of pseudoreplication because some individuals were represented more than once and therefore some females had more data points than others. Each datum point is unique though because it represents a unique combination of a pair in a particular infant-per-female ratio context. Consequently, one might consider each dyad equivalent to a single subject. No single dyad is represented more than 4 times in the data set. Therefore the data set could not have been largely biased by any one particular dyad. Moreover, I performed an ANOVA to check if there was significant variation among individuals and if there were any interaction effects with supply. This provided a test of whether any individuals had the potential to bias the data by performing differently from others.

Effect of Infant Age and Handling Time on Grooming Duration

I analyzed grooming-infant handling interchanges that contained data on infant age and female-to-infant grooming duration to see their effects on female-to-mother grooming duration. Sixty-two samples had data on infant age. First, I used a binomial test to determine if significantly more grooming-infant handling interchanges involved newborns ($\leq$2 mo) than not. Second, I used a regression analysis to test for a relationship between infant age and female-to-mother grooming duration. One hundred fourteen samples had data on female-to-infant grooming duration. For this data, I used a regression analysis to test whether female-to-infant grooming duration was related to female-to-mother grooming duration.

Reciprocal vs. Unidirectional Grooming

One hundred thirty-eight samples contained sufficient data on the direction of grooming between females and mothers in grooming-infant handling interchanges. I calculated the number and proportion of interchanges that contained unidirectional and reciprocal grooming. I then used a binomial test to determine if unidirectional female-to-mother grooming bouts occurred significantly more frequently than the expected proportion of reciprocated grooming. I determined the expected proportion for reciprocated bouts from a randomized set of 275 PG samples.

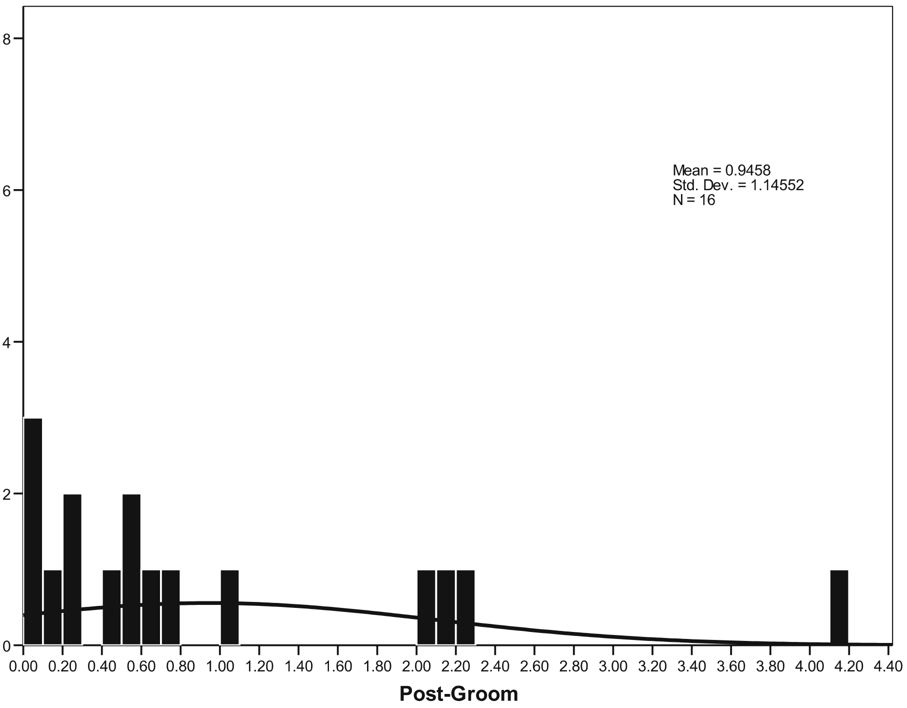
Effect of Rank and Kin

I used the *ad libitum* data on grooming-infant handling interchanges to determine if the rank of the mother was related to grooming duration. I divided all interchanges into 2 groups: ones directed up-rank and ones directed down-rank. In up-rank interchanges, the female groomed a mother of higher rank. In down-rank interchanges, she groomed a mother of lower rank. I used a binomial test to assess if there was more up-rank or down-rank grooming. I also used an independent t-test to determine if the up-rank mean grooming duration was larger than the down-rank mean. I used a second t-test to determine if female-to-infant grooming duration was different between up-rank or down-rank interchanges. Finally, I ran a regression analysis on both up-rank and down-rank interchanges to determine the relationship between female-to-mother grooming duration and infant supply in both rank conditions.

I separated grooming-infant handling interchanges between kin and nonkin to determine if kin relationship influenced grooming duration and the relationship between female-to-mother grooming duration and infant supply. I used only dyads for which kinship was obvious from behavioral patterns. I used independent t-tests to test for significant differences in female-to-mother grooming duration and female-to-infant grooming duration between groups. I used a regression analysis to examine the relationship between grooming duration and infant supply in both kin conditions.

Results

I analyzed data on 16 mothers to determine the mean rate of contact toward their infants in PG and baseline social conditions. In baseline social conditions, the mean rate of touches from all females toward infants with their mothers is 0.11 touches per 10-min sample. After female-to-mother grooming, the mean rate of touches toward infants from the grooming female is 0.95 touches per 10-min sample. The PG rate of infant contact is significantly higher than the baseline rate of contact (paired t-test: df=15, t=2.938, p=0.010; Fig. 1).



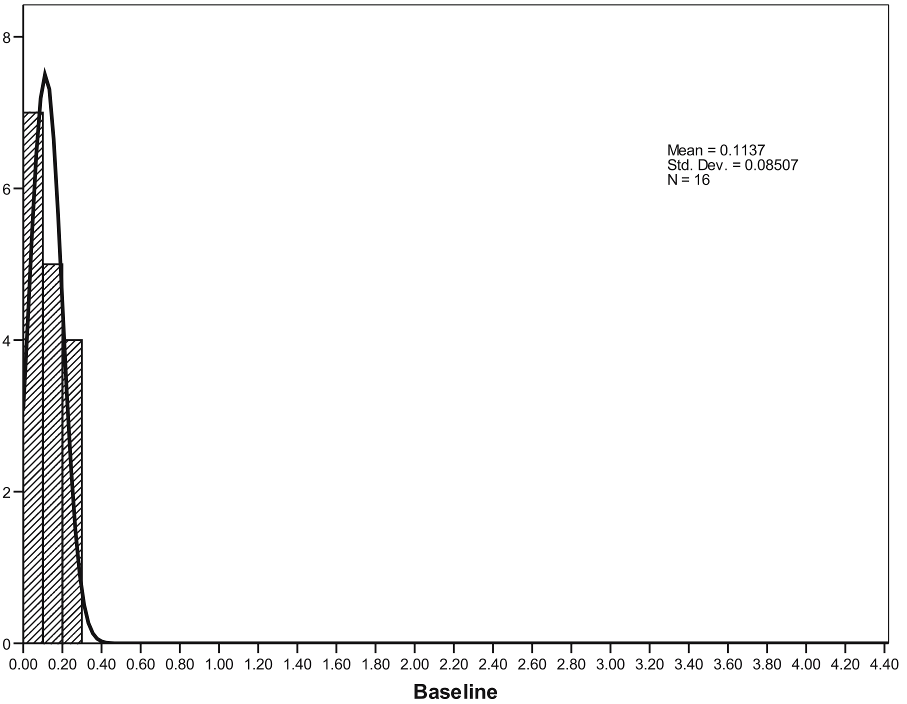


Fig. 1 Distribution of the data for a sample of 16 females, showing that a mother's infant is contacted more frequently after she had been groomed than in baseline social conditions.

The MC-PG analysis indicates that contact with infants was higher after a female groomed a mother than in times in which she and the mother were just in proximity. On average, the mother's infant was touched by the grooming female 1.9 times per 10-min sample following the initial grooming. The average number of touches when the same female from the PG samples was in proximity to the mother is 0.3 touches per 10-min sample. The PG sample rate of infant touching is significantly higher than the MC sample (Paired *t*-test: df=9, $t=4.824$, $p=0.001$).

I scored grooming-infant handling interchanges to determine if they were reciprocal or unidirectional. Of 138 interchanges with sufficient data, 89% ($n=123$) were unidirectional and 11% ($n=15$) were reciprocal. In most interchanges, females groomed the mother and the mother did not groom back. I compared the proportion to an expected proportion of reciprocation determined from 235 randomized PG samples collected during the study. The expected proportion is P=0.39. Unidirectional grooming represented a significantly higher proportion of grooming-infant handling interchanges than the proportion observed in the randomized sample (binomial test: $N=138$, $P=0.39$, $p < 0.001$).

I also scored grooming-infant handling interchanges for the total duration of female-to-mother grooming that occurred during the interaction and for the number of infants per female in sight of the grooming pair. One hundred and fourteen interchanges had sufficient data. There is a significant negative relationship between female-to-mother grooming duration and supply of infants (linear regression: $r=0.385$, $F=19.53$, $p < 0.001$, $r^2=0.148$, df=112). The relationship demonstrates that when infants were abundant, grooming durations were shorter; when infants were scarce, grooming durations were longer (Fig. 2).

To account for bias potentially caused by pseudoreplication, I used a factorial ANOVA to test for variation across individuals and levels of infant supply on female-to-mother grooming duration. There is a significant main effect for infant supply on grooming duration, but no significant main effect for individuals or an interaction effect. Although nonsignificant results are inconclusive, I am unable to provide evidence that individual variation existed and therefore do not have support that any individual's idiosyncrasies could have solely accounted for the results. If this is true, pseudoreplication could not have seriously affected the results.

A sample of 62 grooming-infant handling interchanges with data on the exact age of infants revealed that 43 of the grooming bouts involved infants <2 mo and 19 involved older infants. The oldest infant in the sample was 7 mo. The proportion is significantly different from chance, showing a significantly greater proportion of the interchanges involved newborn infants (binomial test: $N=62$, $P=0.50$, $p=0.003$). There is not significant relationship between infant age and the duration a female groomed the mother or the infant.

I ran a regression analysis on the duration of female-to-mother and female-to-infant grooming to account for any relationship between them. I aimed to find out if a female's payment was influenced by how much contact she was able to obtain with the infant, as this could confound any evidence for a relationship between female-to-mother grooming duration and infant supply. There is not significant relationship between the length of time a female groomed a mother and the length of

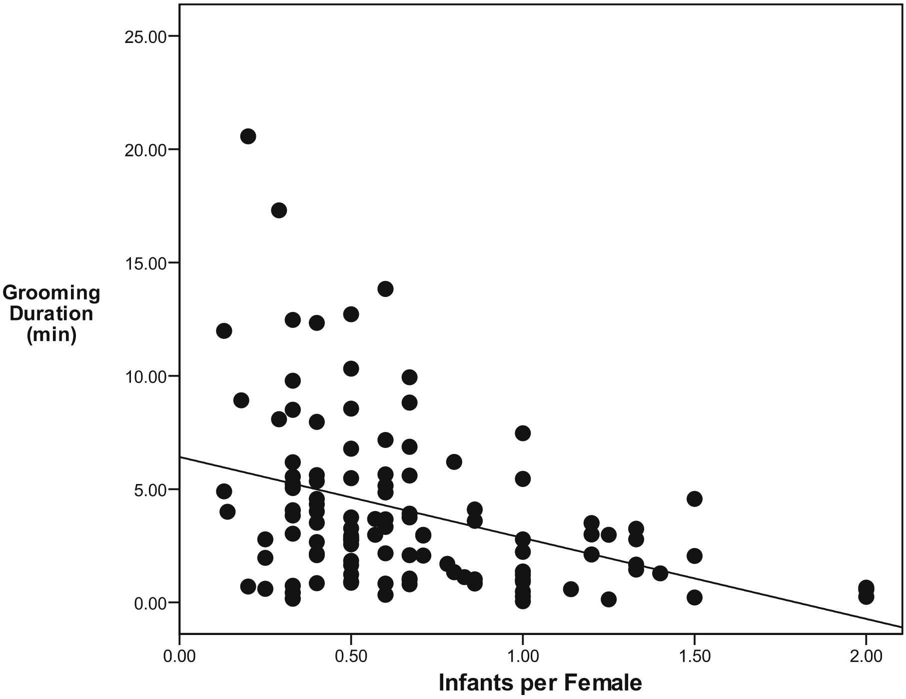


Fig. 2 A regression analysis indicates a negative relationship between the ratio of infants per female and the length of female-to-mother grooming bouts in a sample of 114 grooming-infant handling interchanges. If infants were scarce in the immediate social context of the interchange, grooming durations were shorter than if infants were abundant.

time she groomed the infant. Consequently, I cannot provide evidence that it could confound the relationship I found between infant supply and female-to-mother grooming duration.

I also analyzed whether grooming up or down rank influenced grooming-infant handling interchange. I categorized 138 samples as either up-rank or down-rank grooming bouts. In 83 cases, a female groomed down rank, and in 55 cases she groomed up rank. There are significantly more down-rank interchanges than up rank (binomial test: $N=138$, $P=0.50$, $p=0.021$). The mean up-rank grooming duration is 4 min 55 s and the mean down-rank grooming duration is 3 min 24 s. A Levene's test for equal variances showed the variances of the 2 groups are significantly different. Because independent *t*-tests assume variances are equal, I conducted a *t*-test accounting for the difference between each group's variance. After this adjustment, the means of the 2 groups are significantly different (*t*-test: df= 85.510, $t=-2.204$, $p=0.030$). Females also groomed higher-ranked infants significantly longer than lower-ranked infants (*t*-test: df=64.671, $t=-2.059$, $p=0.044$), and this test was also adjusted for unequal variances. Finally, there appeared to be an influence of rank on the relationship between grooming duration and infant supply. More variance is accounted for in up-rank grooming, than in down-rank grooming (down-rank, linear regression: r=0.277, F=5.91, p=0.018, r^2=0.077, df=71; up-rank, linear regression: r=0.496, F=12.73, p=0.001, r^2=0.246, df=39; Fig. 3).

There is no observable significant difference in grooming duration between kin and nonkin for female-to-mother grooming or female-to-infant grooming. There was no observable preference for engaging in grooming-infant handling interchange with kin. In addition, I separated the regression analysis of grooming duration and infant per female ratio between kin and nonkin. The regression lines in each analysis are very similar in variance accounted for and slope (kin: r=0.435, F=9.11, p=0.004, r^2=0.189, df=39; nonkin: r=0.368, F=9.70, p=0.003, r^2=0.135, df=62).

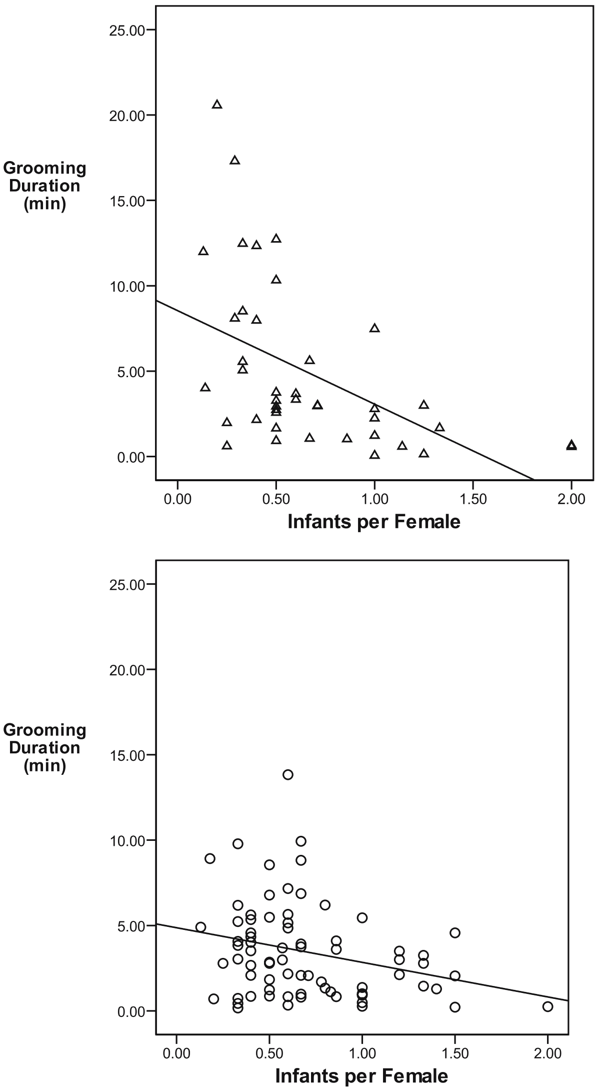


Fig. 3 An analysis divided the sample of 114 grooming-infant handling interchanges into up-rank and down rank-grooming. In both samples, there is a negative relationship between ratio of infants per female and length of female-to-mother grooming bouts. In up-rank grooming bouts more variation is accounted for, making the slope of the linear relationship steeper for up-rank grooming bouts than in down-rank bouts.

Discussion

Long-tailed macaque females trade grooming and infant handling. The first result that supports this conclusion is that grooming promoted exchange with infant handling. After a female groomed a mother, the rate at which her infant was contacted by the grooming female was almost 10 times higher than the rate at which her infant was contacted by all females during baseline social conditions.

The comparison between PG and baseline rates may have been biased because in baseline samples mothers potentially had fewer proximate social partners than in PG samples. This would have lowered the opportunity for females to contact the infant, thus lowering the rate of contact and biasing the test. The MC-PG analysis accounted for the bias and controlled for proximity by making sure the grooming partner was proximate to the mother under both conditions. The MC-PG analysis also demonstrated a greater rate of touching after grooming than in a sample of matched controls. The use of the 2 methods together provides evidence that grooming promoted subsequent infant handling.

Another potential bias is that subjects could simply have reciprocated grooming for more grooming and that infant handling occurred as a byproduct during the grooming exchange. To account for this problem, I recorded the direction of grooming in each grooming-infant handling interchange. If the grooming in the interchanges indeed promotes infant handling, then I did not expect to see grooming reciprocated, but instead that infant handling was interchanged. Since most grooming-infant handling interchanges were unidirectional my prediction is supported, indicating that the infant handling is not a byproduct of reciprocal grooming exchange. Instead, it is a direct interchange of grooming and infant handling.

The ratio of infants per female present in the immediate social context of any grooming-infant handling interchange was related to the duration of grooming a female directed toward a mother. The result supports the biological market prediction that scarcity of available partners increases their value, while abundance of partners decreases it. Grooming indicates the amount of investment a female puts into any single interchange, and the ratio indicates supply. Grooming therefore appears to be an indicator of the infant's value in an infant market. Because grooming promotes infant handling and there is an economic influence on the exchange, it is reasonable to conclude the 2 acts were traded.

Again, the interpretation of the analysis is limited because I used individuals repeatedly within the sample of 114 bouts, which could create a pseudoreplication bias. I ran an ANOVA using individuals and infant supply as independent variables and female-to-mother grooming duration as the dependent variable. There is no significant difference among individuals, though the infant per female ratio accounted for a significant part of the grooming duration variance. Therefore, no individual appeared to have significantly altered the data providing no support that pseudoreplication could have seriously altered the results.

To establish the relationship between female-to-mother grooming duration and supply, I also needed to account for the possibility that any increase in grooming payment could also be accompanied by a greater length of time a female handled the infant. Such a finding would confound any evidence for the effect of supply on grooming duration because if females groom more when supply is low they may also receive more, i.e., they are not actually investing more relative to the handling opportunity they obtain. I found no evidence that female grooming time was directly proportional to the amount of time they could groom an infant. As a result, the biological market relationship with supply and demand seems to be genuine and not confounded by the possibility that variation in the amount of infant access received might have better accounted for grooming payment.

Grooming-infant handling interchanges more often involve newborn infants <2 mo. There is no significant relationship between infant age and the amount of grooming payment invested by a female to a mother. Because younger infants are more attractive than older ones (Nicolson 1987), females might be expected to pay more to access them. According to my study, it appears the frequency of interactions with younger infants changes, but the duration of grooming during infant handling interactions are unaltered. Females attempt to access newborns more, but when they attempt to access an older infant, they still perform the same amount of grooming on the mother.

Females also did not groom newborn infants longer than older infants during handling, suggesting that females may typically handle all infants for the same duration. The reason may be that mothers are restrictive in earlier months than later, as in *Macaca mulatta* (Breuggeman 1973) and *M. fuscata* (Hiraiwa 1981). Consequently, females may be restricted from grooming newborns for longer periods. It may also just be that handling time of infants is not related to infant age.

Rank appeared to influence grooming-infant handling interchanges. Lower-ranked females groomed higher-ranked mothers for longer durations than *vice versa*. The difference could indicate that the infants of higher-ranked mothers have more value in an infant market and that lower-ranked individuals will pay more for interacting with a higher-ranked partner. The results indicate how rank might corrupt a social market and skew social exchanges to benefit higher-ranked individuals. They may be able to take more from and give less to lower-ranked individuals in social trades than *vice versa*. The results might also indicate that higher-ranked females are more valuable partners for grooming-infant handling interchange.

Females also groomed the higher-ranked infants they handled longer than they groomed lower-ranked infants, providing evidence that higher-ranked infants are of greater value on the infant market than lower-ranked infants. When a female obtains access to a higher-ranked infant, she maintains interest and interacts with it longer than if it were a lower-ranked infant. Moreover, I found a significantly higher proportion of down-rank grooming-infant handling interchanges than up-rank. Females may access lower-ranked infants more often because they are easier to obtain and therefore these interactions may be a low cost way to satiate a female's attraction to infants. Higher-ranked females can easily access lower-ranked infants but lower-ranked females are more constrained in up-rank interactions. Low-ranked infants may be groomed for a shorter time because they are accessed more frequently, whereas higher-ranked infants may be groomed for longer because they are less commonly obtained. High-ranked infants may also just be more valuable because of their association to a high-ranked female and thus groomed longer.

Cercopithecines generally groom higher-ranked individuals more (Seyfarth 1977). Behavior of *Macaca fascicularis* is congruent with this pattern (Wheatley 1999). The up-rank grooming pattern may occur because lower-ranked individuals can obtain social commodities from higher-ranked partners, such as agonistic support, tolerance, or even infant handling. Despite the tendency to groom up-rank, I observed more down-ranked infant-related grooming, though when up-rank grooming-infant handling interchange occured was observed, the duration of grooming time invested followed the general pattern of investing more in higher than lower-ranked partners. Based on amount of grooming investment per bout, high-ranked infants may be more valuable to handle than low-ranked infants and this may be owing to their association with higher-ranked females and greater difficulty to handle. Consequently, infant handling interchanges may be partly explained by Seyfarth's (1977) theory stating higher-ranked partners are more valuable in a social market.

The relationship between grooming duration and infant supply appeared different between up-rank and down-rank grooming. Up-rank grooming had more variance accounted for by infant per female ratio than down-rank grooming did, further supporting that down-rank grooming was less influenced by economic factors than up-rank grooming was. The reason for the difference may be that higher-ranked partners can displace and take away resources from lower-ranked partners (Bernstein 1981). Overall, up-rank groomers seem more constrained than down-rank groomers in terms of their ability to facilitate social exchange.

My findings support the results of past research on chacma baboons (*Papio ursinus*) and vervets (*Cercopithecus aethiops*) that have also demonstrated that the supply of infants can influence the duration of grooming bouts related to infant handling (Henzi and Barrett 2002; Scheid and Noë 2005). Henzi and Barrett (2002) measured infant supply based on how many total infants were in a group and found that grooming durations were related to that number. They did not measure infant supply for each specific interaction. I took into account the current supply of infants for each grooming bout to show the immediate relationship between partner availability and social decision-making. Although group-level characteristics such as the total number of infants certainly affect social exchange, one would expect social markets to be influenced on a moment-to-moment basis by the current environment of surrounding available social partners. Biological market theory predicts that individuals should obtain and utilize information on the immediate social condition and act accordingly.

In chacma baboons, a test of all infants in the troop may be adequate to test how decision-making is influenced by the current social market in situations where they live in an open environment and all infants in the troop are visible and available for each grooming-infant handling interchange. In the TPNP long-tailed macaques, only I studied, only rarely were all infants in sight because their forested habitat obstructed visibility and individuals formed into isolated subgroups. Consequently, each grooming interaction was characterized by a unique combination of available infants and competing females, providing the opportunity to test how variation in the immediate social market influenced grooming-infant handling interchanges. The variation under differing infant per female ratios indicates that market forces can influence decision-making based on the unique conditions of an individual's immediate social environment.

Henzi and Barrett (2002) also demonstrated that grooming-infant handling interchanges were generally unidirectional, which O'Brien (1993) further supported in work on wedge-capped capuchins (*Cebus olivaceus*). In addition, Henzi and Barrett

(2002) provided evidence that rank influenced grooming-infant handling interchange. As in my study, they found their research found that rank predicted the length of grooming durations. They demonstrated a relationship between rank distance and grooming duration, and found that the greater the rank distance between a lower-ranked female and a mother, the greater the duration of time she groomed the mother, and *vice versa*.

My results and those of other researchers indicate that grooming-infant handling interchanges are an example of how 2 social commodities can be traded and how supply and demand can drive the cost of a commodity within a biological market. Grooming is one way a female primate can pay to access a social commodity. Dominance rank seems to skew an infant market by changing the grooming payment for infants. Kinship, however, did not have an observable effect on the infant market at TPNP. Overall my results suggest that biological markets, such as infant monkey markets, may indeed be useful in making predictions about social decision-making and patterns of exchange in primates.

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