Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*)

Rebecca L. Chancellor and Lynne A. Isbell
Department of Anthropology, University of California, Davis, CA 95616, USA

Primate female allogrooming models based on biological markets theory predict that grooming is "time matched" within bouts, that is, the amount of time the first female grooms predicts the amount of time the second one grooms. The models also predict that when female–female contest competition is weak, grooming is traded for grooming, but when female–female contest competition is strong, grooming may be traded for other commodities such as feeding tolerance, and grooming discrepancy between members of dyads is rank related. We tested these predictions using data collected from adult and subadult female gray-cheeked mangabeys (*Lophocebus albigena*) ($N = 26$) in 5 groups in Kibale National Park, Uganda. We found that, overall, females reciprocated in 33% of grooming bouts. Among reciprocated bouts, females in all 5 groups showed time matching. In 2 groups, we also found rank-related grooming discrepancies but showing opposite patterns to each other. Consistent with predictions based on biological markets theory, these groups may have been under greater feeding competition, revealed more by adjustments in ranging behavior than increased agonistic rates. Although these results support current allogrooming models, they also suggest that the models may become more robust if the influence of scramble competition is incorporated. In addition, they emphasize the flexibility and dynamic nature of female competitive relationships within the same population of primates. *Key words:* biological markets, female relationships, gray-cheeked mangabeys, Kibale National Park, *Lophocebus albigena*, reciprocity, time-matched grooming. *[Behav Ecol 20:79–86 (2009)]*

Growing evidence suggests that reciprocal exchange among animals is dynamic and shifts with changing social and environmental circumstances (e.g., Wilkinson 1984; Pusey and Packer 1994; Barrett et al. 2002; Krams and Krama 2002). Allogrooming is one such reciprocal exchange that has been documented in many different species (e.g., mule deer, *Odocoileus hemionus*, Mooring [1989]; bonnet macaques, *Macaca radiata*, Sinha [1998]; herb-field mice, *Apodemus microps*, Stopka and Graciasová [2001]; meerkats, *Suricata suricatta*, Kutsukake and Clutton-Brock [2006]; green wood-hoopoes, *Phoeniculus purpureus*, Radford and Du Plessis [2006]) and has been reported to serve a range of social and utilitarian functions (Sparks 1969; Freeland 1976; Eisenberg 1981; Goosen 1981; Dunbar 1991). In group-living primates, allogrooming is a significant feature of female sociality and variation in grooming reciprocity is influenced by the structure of competitive relationships among individuals (Seyfarth and Cheney 1984; de Waal 1997; Henzi and Barrett 1999; Silk et al. 1999).

Although social interactions among closely related individuals are often interpreted through kin selection theory (Hamilton 1964), various models of reciprocity have been used to predict social exchanges between dyads regardless of relatedness (Hemelrijk 1990; Nowak and Sigmund 1993; Connor 1995; Barrett et al. 1999). Some of the more recent of these reciprocal models have been influenced by biological markets theory, in which exchanges between organisms are compared with commodities trading in human markets (Noë and Hammerstein 1995). Biological markets theory views organisms as traders of commodities and predicts changes in the exchange rates of goods (e.g., food, shelter) and services (e.g., grooming, protection) by shifts in supply and demand ratios (Noë and Hammerstein 1995). The perspective of the biological markets approach is that dyadic relationships are not fixed characteristics of a population or species but change dynamically depending on the current state of the market. Empirical evidence supporting the biological markets approach has been found in the mutualisms between cleaner fish and their clients (Bshary 2001), plants and symbiotic fungi (Hoeksema and Schwartz 2001), and in grooming exchanges in primates (Barrett et al. 1999, 2002; Manson et al. 2004).

Based on biological markets theory, Barrett et al. (1999) and Henzi and Barrett (1999) proposed that in female-bonded primate species (Wrangham 1980), where allogrooming is an important part of female social relationships, grooming is a commodity in its own right rather than just a purely social commodity (e.g., used for coalitionary support or bonding) because an individual is not able to get all the grooming it needs by its own autogrooming efforts. As a result, predictions can be made regarding reciprocity even in the absence of such social tactics. They predicted that females trade grooming for grooming, dividing grooming into short intervals to avoid cheating. In addition, they proposed that rank-related power differences affect grooming balance within dyads so that grooming is also traded for other commodities such as feeding tolerance. Thus, when individuals are close in rank or when female feeding competition is weak, grooming should be "time matched" within bouts, that is, the amount of time the first individual grooms predicts the amount of time the second one grooms. In contrast, when competition for resources is strong and rank affects access to resources, grooming discrepancy between members of dyads should be positively related to the distance between their ranks in that subordinates groom dominants more than the other way around (Barrett et al. 1999). Therefore, the key prediction of the biological markets approach is that grooming durations vary with the supply and demand of particular commodities (Barrett et al. 1999). Barrett et al. (1999, 2002) found empirical evidence to support these predictions in female chacma

baboons (*Papio cynocephalus ursinus*), whereas several other recent studies have also found evidence in support of the predictions (samango monkeys, *Cercopithecus mitis erythrarchus*, Payne et al. [2003]; white-faced capuchins, *Cebus capucinus* and bonnet macaques, *M. radiata*, Manson et al. [2004]; savannah baboons, *Papio cynocephalus cynocephalus*, Silk et al. [2004]).

In this paper, we build on these findings by testing the predictions of Barrett et al. (1999) and Henzi and Barrett (1999) on 5 groups of gray-cheeked mangabeys (*Lophocebus albigena*) living in Kibale National Park, Uganda. Our aim was to test the flexibility of female grooming relationships among different groups within a single population of primates living in tropical forest. Gray-cheeked mangabeys, an Old World monkey species closely related to baboons (Harris and Disotell 1998), live in multimale/multifemale social groups averaging 15 individuals (Waser 1977). Females stay in their natal group throughout their lives and can be characterized as female bonded (Waser 1977; Chancellor RL and Isbell LA, in preparation). Unlike other Old World primate species examined with regard to the biological markets theory, gray-cheeked mangabeys live in evergreen tropical forests. Because habitat type or quality is expected to influence female competitive relationships (Wrangham 1980; van Schaik 1989; Isbell 1991; Isbell and Young 2002), mangabeys represent a good model for testing the generality of the biological markets theory.

Based on previous studies by Barrett and colleagues, we predicted that groups with lower rates of aggression would have more reciprocity. Specifically, we predicted that in groups with lower rates of aggression, females would be more likely to reciprocate, whereas in groups with higher rates of aggression, females would be less likely to reciprocate. We also predicted that within reciprocated bouts, groups with lower rates of aggression would have more time matching between dyads, whereas groups with higher rates of aggression would have stronger rank-related effects on grooming relationships. Agonistic behavior is a good proxy for feeding competition (Wrangham 1980; van Schaik 1989; Isbell 1991). However, agonistic behavior is only one aspect of feeding competition and does not necessarily always reflect the actual intensity of competition, particularly if animals can adjust their behavior in ways that reduce direct confrontation (i.e., scramble competition). Changes in ranging behavior, for example, increased interindividual distances, greater group spreads, and longer travel distances, are quantifiable proxies for more intense scramble competition (Isbell 1991; Isbell and Young 2002). Therefore, we also predicted that groups with lower degrees of indirect feeding competition, as indicated by differences in ranging behavior, would have more reciprocity and time-matched grooming within reciprocated bouts.

METHODS

Study site and subjects

We conducted our project in the Kanyawara study area of Kibale National Park (766 km^2), Uganda (0°34′N, 30°21′W), a semilogged moist evergreen forest located near the foothills of the Rwenzori Mountains (for extended description of the study area, see Waser and Floody 1974; Chapman et al. 1997). It has a mean daily minimum and maximum temperature of 15.5 °C and 23.7 °C, respectively, and a mean annual rainfall of 1778 mm (1990–1998) (Chapman CA and Chapman LJ 2000).

The mangabey population in Kibale has been studied since the 1970s, and multiple groups are habituated. We collected data on 5 study groups (BT2, BT1, MK, CC, and LC; see Olupot 1999) chosen for the locations of their home ranges, number of females, and the relative ease with which females

could be identified and followed. Group sizes of our study groups ranged from 10 to 21 individuals and consisted of 4–7 adult females, 1–9 adult males, and 3–10 immatures (Table 1). Mangabeys live in a variety of habitats within Kibale, from undisturbed to lightly and heavily disturbed forest (Skorupa 1988). All our study groups' home ranges fell primarily within lightly to moderately logged forest except for CC, which ranged primarily in unlogged forest.

Data collection

We collected data from January 2004 to August 2005. All females could be individually identified by natural markings by July 2004. We gathered systematic data on all adult (exhibited visible sexual swellings) and subadult (similar size to adults and exhibited visible sexual swellings within study period) females ($N = 26$) in the 5 groups. Each month, we conducted an average of 3 all-day follows (i.e., ca., 3 rounds) per group. The order of groups sampled within any one round was determined by predetermined random sampling without replacement, or because mangabeys have fairly large home ranges, by knowledge of a group's location on the sampling day. During each round, each female was sampled once for 30 min. The sampling order within groups varied by round, determined by locating the first female not yet sampled during the sampling day. Behavioral data were collected using a combination of focal and all occurrences sampling. Onsets and terminations of grooming bouts were recorded to the second. Relative dominance ranks were determined by the direction of aggressive dyadic interactions including chases, approach avoids, supplants, and physical contact.

Group spread was determined at the end of every 30-min female focal sample by pacing between the 2 farthest points of the group, or if vegetation made pacing impossible, by calculating the distance between the 2 farthest points using a GPS device. Measuring the 2 farthest points of the group is a conventional proxy used for group spread in primates (e.g., Waser 1977; Koenig and Borries 2006; Saj and Sicotte 2007). Three local field assistants were trained to pace the group spread, and a high degree of reliability was found between the assistants' paces and the actual distances (measured with a measuring tape) (Spearman's rho = 0.99, $P < 0.0001$, $N = 25$ per assistant; Martin and Bateson 1993). The average margin of error for the GPS readings was $\bar{x} \pm$ standard deviation $= 7.4 \pm 2.0$ m. One local field assistant was trained to estimate focal female travel distance (recorded in meters), and a high degree of reliability was found between the assistant's estimates and the actual distance (Spearman's rho = 0.99, $P < 0.001$, $N = 330$).

Table 1
Details of study groups

	BT2	BT1	MK	CC	LC
Group size (range over study period)	12–15	10–16	12–16	14–17	17–21
Adult/subadult females	4	5	5	5	7
Adult males	1–3	1–4	1–5	1–3	4–9
Immatures	5–8	3–7	4–7	7–10	5–6
Mean group spread (m)	54	55	60	76	132
Mean group spread/individual (m)	4	4.2	4.3	4.9	7
Mean female travel distance (m)/focal	126	98	136	119	124

Our data set consisted of 532 h of focal follows of 26 females ($\bar{x}$ ± standard error [SE] = 20.3 ± 0.3 h/female). During these focal follows, we observed 482 grooming bouts ($\bar{x}$ ± SE = 96.4 ± 6 bouts/group). Overall, the groups were observed for a total of 2298 h ($\bar{x}$ ± SE = 460 ± 46 h/group).

Statistical analysis

We tested the dominance matrices using MatMan 1.1 (Noldus Information Technology, Wageningen, the Netherlands). Matrices included agonistic interactions from both focal and all occurrences sampling. We used the directional consistency (DC) index, which ranges from 0 to 1 and is calculated by $(H - L)/(H + L)$, where H is the total number of agonistic interactions in the direction of higher frequency and L is the total number of agonistic interactions in the direction of lower frequency (e.g., van Hooff and Wensing 1987; Archie et al. 2006), and we used the percentage of reversals to determine linearity. The DC index and the percentage of reversals are particularly useful when groups are smaller than 6, when tests such as the Landau index (h) or de Vries's corrected index (h') have diminished statistical power (Appleby 1983; Isbell and Young 2002; Archie et al. 2006).

Following Barrett et al. (1999) and Manson et al. (2004), we grouped our grooming data into bouts, where a bout was defined as a continuous period of female–female grooming involving the same 2 individuals. If the identity of one of the individuals changed or if the grooming was suspended for more than 1 min, we considered the bout to have ended. We chose 1 min because a histogram of the time gaps between grooming by the same 2 individuals showed that 1 min was a natural cutoff point. We used only grooming bouts that were initiated during a focal sample. If the focal sample ended before the termination of the bout, we continued data collection until the bout ended. To make our analyses comparable to Barrett et al. (1999) and Manson et al. (2004), we did not discriminate between voluntarily terminated bouts and those that ended due to interference. Grooming trade-offs within grooming bouts were defined as episodes. Therefore, if A groomed B and B reciprocated, the bout consisted of 2 episodes, the episode in which A groomed B and the episode in which B groomed A.

For purposes of comparability, we used a similar method of analysis to Manson et al. (2004). We designated the first groomer as the initiator and the receiver or second groomer as the recipient. Then, we extracted all the grooming bouts for each female in which she was the initiator and organized them into clusters defined by the identity of the recipient. This provided an upper limit of $N(N - 1)$ clusters per group, where N is the number of females in the group. Therefore, there could be 2 clusters per dyad, that is, 1 cluster when A initiated and B was the recipient and 1 when B initiated and A was the recipient. There were a total of 96 clusters (range = 12–30 clusters/group).

We modeled our data using weighted logistic regression and weighted least squares analysis of covariance (ANCOVA). The weights were equal to the reciprocal of the number of bouts in a cluster ($1/n$), where n represents the number of bouts in a cluster. Therefore, although each grooming bout was used as a data point, the weights ensured that clusters with unequal numbers of bouts contributed equally to the models' estimation. The degrees of freedom in each analysis were derived from the number of independent clusters not the number of grooming bouts used in the analysis (see also Manson et al. 2004).

We used weighted logistic regression to test the hypothesis that the duration of the initiator's first grooming episode predicts whether the recipient will reciprocate or not. We log trans-

formed the grooming duration data because of a right-tailed skew. Our model included the duration of the first grooming episode of the initiator, group, and the interaction between the 2 as fixed effects. We used fixed effects because we assumed that there were rates of reciprocation characteristic of each group and that this parameter could be estimated if the groups were observed long enough.

For all reciprocated grooming bouts, we used weighted least squares ANCOVA to test the hypothesis that the total duration of time the initiator grooms predicts the total duration of time the recipient grooms. We log transformed the grooming durations because of a right-tailed skew. Our model included the total grooming duration of the initiator, group, and the interaction between the 2 as fixed effects.

We also used weighted least squares ANCOVA to test the hypothesis that dominance rank predicts grooming balance. We subtracted the log transformed total duration of time the recipient groomed the initiator from the log transformed total duration of time the initiator groomed the recipient and regressed this grooming discrepancy on rank difference. Rank difference was obtained by subtracting the recipient's dominance rank from the initiator's dominance rank, using "1" to represent the alpha female's rank. Our model included rank difference, group, and the interaction between the 2 as fixed effects.

All analyses besides the dominance matrices were conducted using the software program JMP 7 (SAS Institute Inc., Cary, NC). Statistical significance was set at $P = 0.05$, and all tests were 2 tailed.

RESULTS

All groups had linear dominance hierarchies. Agonistic interactions among females were strongly unidirectional and the number of reversals was relatively low indicating that most interactions followed the direction of the hierarchy (LC, DC index: 0.97, reversals: 2%; CC, DC index: 0.82, reversals: 9%; MK, DC index: 0.88, reversals: 6%; BT1, DC index: 0.96, reversals: 2%; BT2, DC index: 0.83, reversals: 9%). Female agonistic rates varied among groups (Figure 1). LC, the group with the lowest rate of female aggression, had an agonistic rate that was
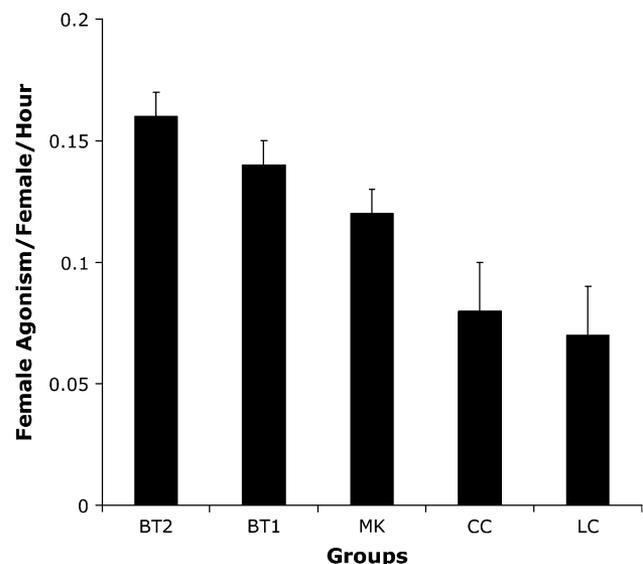

Figure 1
The number of female–female agonistic interactions/female/focal hour for each study group. Bars and whiskers indicate SEs of the means.

less than half that of BT2, the group with the highest rate of female aggression.

Overall, females spent an average of 5% (group ranges, 4–7%) of focal time grooming (Table 2). On average, females reciprocated in 33% (group ranges, 18–40%) of grooming bouts. Of 96 total clusters, 76 (79%) (group ranges, 67–90%) clusters had a bout that was reciprocated at least once. Median rank distance between grooming partners was 2 (group ranges, 1–2). There was no consistent relationship between group size and grooming time as has been found in previous studies (Dunbar 1991; Lehmann et al. 2007).

Reciprocity

There were 482 grooming bouts in 96 clusters in this weighted logistic regression analysis. Neither the main effects of the duration of the first grooming episode of the initiator, group, nor the interaction between the 2 had a significant effect on whether or not the recipient reciprocated in any of the 5 groups. The estimated slope of the initial grooming episode of the initiator was 0.26 (−0.19, 0.72; Figure 2), which suggested that increasing the length of the first grooming episode increased the odds of reciprocation, but it was not statistically significant ($\chi^2_1 = 1.28$, $P = 0.26$).

Time matching within reciprocated grooming bouts

Within reciprocated grooming bouts, there were 156 bouts in 76 clusters. The results of the weighted least squares ANCOVA revealed that the total duration of time spent grooming by the recipient was positively and significantly correlated with the total duration of time spent grooming by the initiator in all 5 groups (Figure 3). We checked the pairwise interactions of the 2 predictors and they were not significant, so we describe only a main effects model. The independent effects of group showed that group intercepts significantly differed from each other (least squares ANCOVA: $F_{4,70} = 4.13$, $P = 0.005$). The independent effects of the total grooming duration of the initiator showed that it significantly predicted total grooming duration of the recipient (least squares ANCOVA: $F_{1,70} = 24.4$, $P < 0.0001$). Therefore, all 5 groups showed time matching. Although group intercepts differed, there was no evidence to suggest that the functional relationship between the total grooming duration of the initiator and the total grooming duration of the recipient differed between groups.

Rank distance and grooming discrepancy

The independent effects of group showed that group intercepts were significantly different (least squares ANCOVA: $F_{4,66} = 2.57$, $P = 0.05$). The independent effects of rank difference showed that it did not significantly predict grooming discrepancy (i.e., the total grooming time of the initiator mi-

nus the total grooming time of the recipient; least squares ANCOVA: $F_{1,66} = 0.33$, $P = 0.57$). However, the interaction between group and rank difference revealed that there were significant differences among groups (least squares ANCOVA: $F_{4,66} = 8.94$, $P < 0.0001$) (Figure 4). Three groups, BT1, BT2,
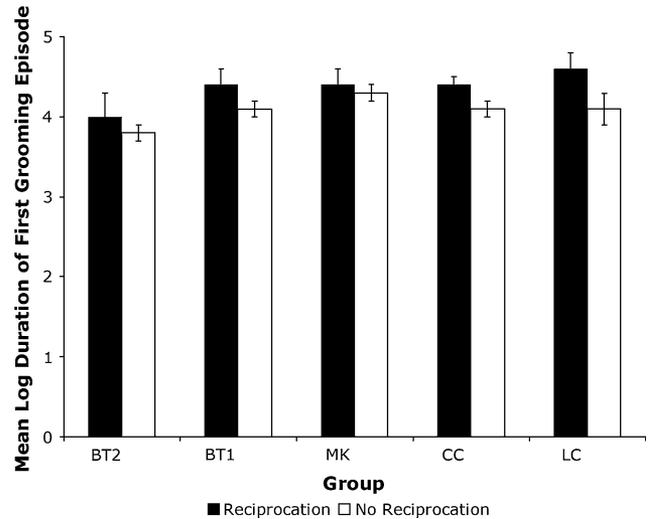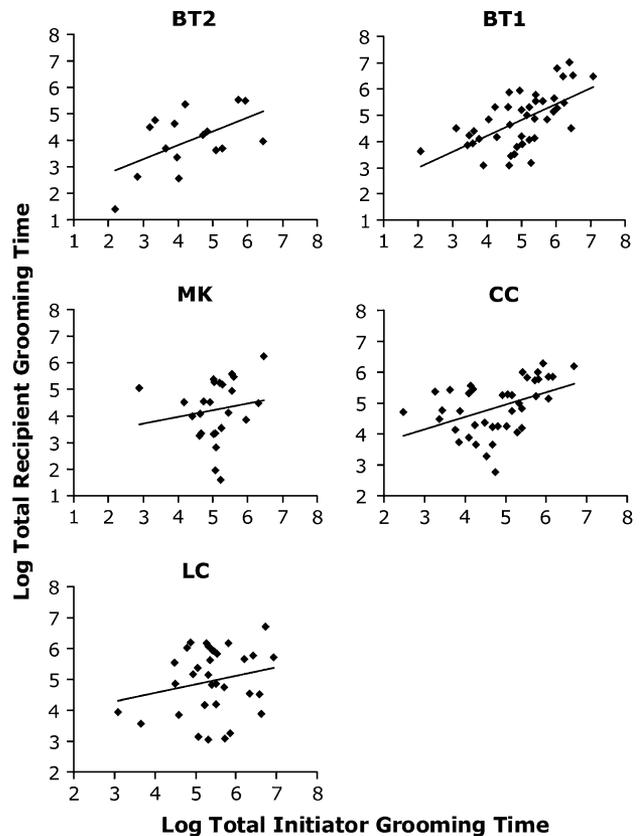

Figure 2
There was a trend that the duration of the initiator's first grooming episode increased the odds of reciprocation in all 5 groups, but it was not statistically significant ($P = 0.26$). Bars and whiskers indicate SEs of the means.

Figure 3
Within reciprocated bouts, there was a significant relationship between the total grooming duration of the initiator and the total grooming duration of the recipient in all 5 groups ($P < 0.0001$).

Table 2
Details of female–female grooming bouts

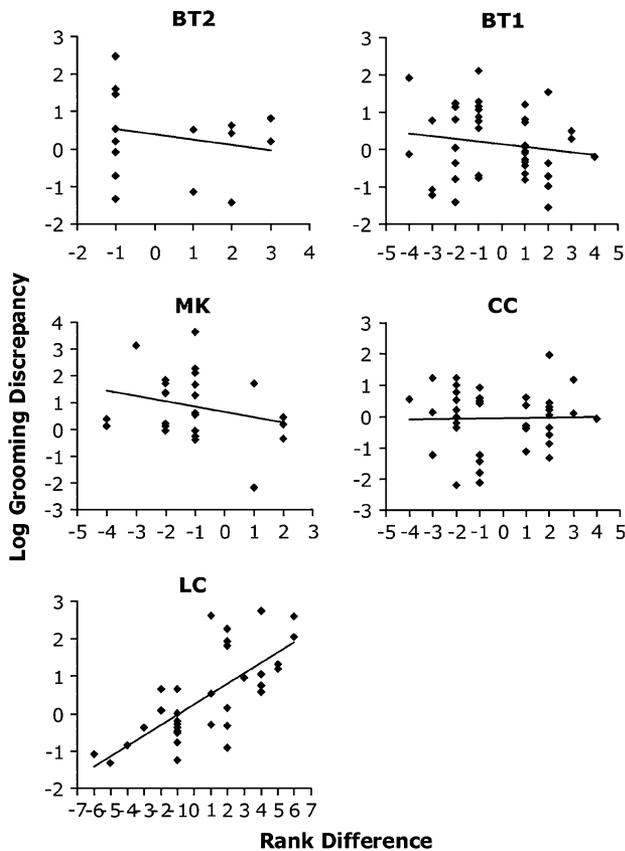|	BT2	BT1	MK	CC	LC
Mean % focal time grooming	4	7	4	6	5
Mean % reciprocated bouts	18	37	29	39	40
Mean % clusters reciprocated at least once	67	90	73	89	73
Median rank distance between partners	1	2	2	2	2

Figure 4
Within reciprocated bouts, there were significant differences between groups in the relationship between the grooming discrepancy (or difference in grooming time between initiator and recipient) and the rank difference of the initiator and recipient ($P < 0.0001$). There was a significant relationship in LC ($N = 33$ bouts; positive slope), and in MK ($N = 25$ bouts; negative slope). However, there was not a significant relationship in BT1 ($N = 42$ bouts), BT2 ($N = 16$ bouts), or CC ($N = 40$ bouts).

and CC, did not show rank-related effects on grooming discrepancy. Grooming discrepancy was positively related to the distance between ranks in 1 of the 5 groups, LC. However, results also showed that grooming discrepancy was negatively related to the distance between their ranks in another of the 5 groups, MK. Thus, in LC, as a higher ranking female was groomed by successively lower ranking females, she tended to reciprocate with smaller and smaller grooming durations. But in MK, the higher ranking female tended to reciprocate with successively longer grooming durations.

Scramble competition and its interaction with contest competition

Agonistic interactions are one expression of competition (contest competition). We also looked at ranging behavior in relation to group size to better understand the variation in grooming discrepancies among groups. Four of the 5 groups (MK, BT1, BT2, and CC) had average group sizes of approximately 15, the average for gray-cheeked mangabeys in Kibale (Waser 1977; Table 1). LC had an average group size of approximately 19 and was the largest of the 5 groups. Females in LC traveled 22% farther per half-hour focal than the females in BT1 (Table 1); the study group that had the greatest overlap with LC in food resources because they shared part of their home ranges. In addition, LC was the only group that

regularly divided into smaller foraging subgroups. LC formed subgroups that were ≥200 m apart in at least 8 of 64 (12.5%) observation days, whereas the other groups never formed any subgroups ≥200 m apart. Their ranging behavior suggests that females in LC were under greater food competition than females in the other 4 groups. These indications of greater feeding competition within LC are consistent with our findings of a significant relationship between grooming discrepancy and rank differences in this group. One way to mitigate feeding competition might be to increase distance between oneself and other group members. In LC, interindividual distances (group spread/number of individuals in the group) were on average approximately 30–43% greater than those of the other groups (Table 1), and they had the lowest rate of agonistic interactions (Figure 1). Indeed, across groups, we found that as the mean interindividual distance increased, the mean rate of agonism decreased (Spearman's rho: $r_s = -1.0$, $P = 0.02$, $N = 5$; Figure 5). This result suggests that behavioral responses to feeding competition are flexible and can include increased agonism or increased interindividual distances.

Although females in MK were intermediate in their rate of agonism, we note that they traveled the farthest and groomed less per hour than several other groups of females. Their pattern of higher ranking females tending to reciprocate with longer and longer grooming durations as they are groomed by successively lower ranking females may reflect time conflicts between foraging and grooming, especially for subordinate females. Subordinate females in MK may not have been able to groom back as long because they were under stronger time–budget constraints. Indeed, within reciprocated bouts, the ratio of higher to lower ranking initiators in MK was 3.3, which means that higher ranking females were much more likely to initiate a grooming bout than lower ranking females. In comparison, the ratio of higher to lower ranking initiators in BT2 was only 1.4; BT1, 1.6; CC, 1.5; and LC, 1.3.

DISCUSSION

Overall, our results were consistent with the predictions of the biological markets model: 1) grooming is a commodity that is traded among females within groups of gray-cheeked mangabeys and 2) local markets within the same population may set different values on commodities such as grooming, depending on the social and ecological environment. These results are consistent with other studies that have also found market flexibility in grooming relationships among females (Barrett et al. 1999, 2002; Henzi et al. 2003).

Thus, variation in the percent of reciprocated grooming bouts in gray-cheeked mangabeys (Table 2) loosely reflected variation in female agonistic rates across the 5 study groups (Figure 1), since BT2, which had the highest rate of aggression, showed the least reciprocity, and CC and LC, which had the 2 lowest rates of aggression, showed the most reciprocity. All groups had a median rank distance between grooming partners of 2, except BT2, which had a median distance of 1 and also had the smallest number of females ($N = 4$). Interestingly, there was no consistent relationship between group size and grooming time. Dunbar (1991) and Lehmann et al. (2007) predict that grooming acts as a way of social networking and increases with group size. Therefore, the females in LC, the largest group, should have spent the greatest amount of time grooming, but this was not the case. One possibility is that the amount of time females spent grooming other females in LC was constrained because females also groom males, and this group had the largest number of males.
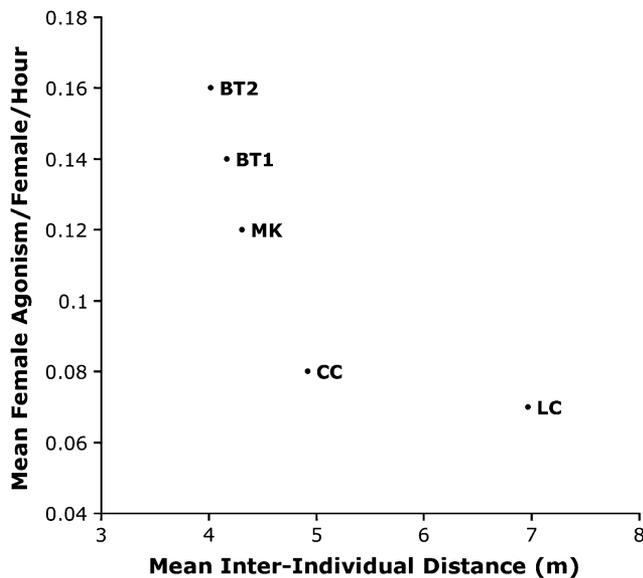
Figure 5
Across groups, as mean interindividual distance increased, mean rate of female agonism decreased ($N = 5$).

Grooming reciprocity ranged from 18% to 40%, which appears to be more similar to baboons than other species (e.g., chacma baboons: 31–51%, Barrett et al. [1999]; bonnet macaques: 5–7% and capuchins: 12–27%, Manson et al. [2004]). Caution is warranted here, however, because even though this variation is likely due to real variation among species, it could also be due to differences in defining grooming bouts (see Manson et al. 2004). Differences in operational definitions of grooming bouts suggest the possibility that there may be meaningful variation in bout lengths among species and may be an important consideration when standardizing methods and comparing across species.

Despite a slight trend, in none of the 5 groups was there a significant relationship between the initial duration of time the initiator groomed and whether or not the recipient reciprocated. Our results differ from a previous study by Manson et al. (2004) that did find a positive relationship between the 2. One possibility is that in all the groups, the unreciprocated grooming bouts were being traded for other services or commodities, such as infant handling or feeding tolerance. Another possibility is that grooming was being exchanged for grooming, but over a longer time scale, such as a day, week, or even longer period of time.

Within reciprocated bouts, we found that in all 5 groups the duration of time spent grooming by the recipient was positively and significantly correlated with the duration of time spent grooming by the initiator. Therefore, grooming in these 5 groups of mangabeys was time matched, and the functional relationship between the initiator's time and the recipient's time was similar between groups. Group intercepts differed, however, revealing that grooming bout lengths varied across groups. MK and BT2 had the 2 shortest mean grooming bout lengths. They also had the 2 longest mean female travel distances, suggesting that time budget constraints may have influenced overall grooming bout lengths. Barrett et al. (1999) also found a difference in overall grooming bout lengths under high- and low-competitive regimes. In particular, MK's shorter bout lengths correlated with the small overall percentage of focal time females in this group devoted to grooming. On the other end, BT1 had one of the longest mean bout lengths, spent the largest overall percent-

age of focal time grooming, and had the shortest mean female travel distance.

Variable consistency with predictions of the biological markets theory

The biological markets theory predicts that low levels of feeding competition result in low rates of agonistic behavior and that grooming is directly traded for grooming without rank-related effects. This was the case for some of our study groups and particularly true for one of our study groups. Excluding LC, the group that may have responded to more severe feeding competition by adjusting individual ranging behavior rather than increasing the rate of agonism, CC had the lowest rate of female agonism, one of the highest percents of grooming reciprocity, and the flattest slope with regard to rank difference and grooming discrepancy. CC was also the only group that ranged primarily in unlogged forest. Previous studies in Kibale have suggested that mangabeys in undisturbed forest have lower levels of feeding competition based on a higher carrying capacity (Chapman et al. 2000) and heavier male body weight (Olupot 2000) in undisturbed forest. CC's relatively low rates of agonism and time-matched grooming were consistent with its location in undisturbed forest and consistent with studies of baboons that also reported time-matched grooming under more relaxed, less-competitive environments (Barrett et al. 1999, 2002).

According to the biological markets theory, when feeding competition is high among females, rank-related grooming discrepancies are likely to be found. Previous studies have used rates of agonism as proxies for the intensity of feeding competition (Barrett et al. 1999, 2002), but our results suggest that this may be too simplistic. Agonistic behavior is but one form of competition (contest competition), and it may not necessarily always reflect the actual intensity of feeding competition, particularly in species that can adjust their ranging behavior in ways that reduce direct confrontation (i.e., scramble competition). Prior to this study, there were several lines of evidence that suggested that mangabeys can indeed adjust their ranging behavior in response to increased competition. First, groups avoid rather than confront each other as they move through the forest (Waser 1976). Second, larger groups (those more than 15 individuals) travel farther per day than smaller groups (Waser 1977). Greater daily travel is thought to be a form of scramble competition whereby larger groups are required to travel farther than smaller groups to obtain the same amount of food per individual (Waser 1977; Isbell 1991). Finally, mangabey groups that range in areas with lower food availability, and are under greater feeding competition as a result, regularly divide into smaller foraging subgroups (Skorupa 1988; Chapman et al. 2000). Our results are consistent with these studies and reveal that the intensity of scramble competition can also be quantified on the level of the individual within groups: Females in LC traveled farther per unit time than females in the group whose home range overlapped the most with LC and they split up into smaller foraging subgroups more often than females in other groups. Our evidence of greater feeding competition in LC is also consistent with predictions of the biological markets theory in that it was the only group in which a higher ranking female tended to reciprocate with smaller and smaller grooming durations when she was groomed by successively lower ranking females.

Interestingly, this group had the lowest rate of female agonism, which is not consistent with traditional expectations that greater intensity of feeding competition is accompanied by higher rates of agonism or the prediction of the biological markets theory that females in LC would have the highest degree of reciprocity and time-matched grooming within reciprocated bouts. Our results suggest that females in LC avoided higher

rates of female aggression despite greater feeding competition by spreading out more. We cannot rule out, however, that their lower rates of aggression were not also influenced by flexible grooming relationships. If the females of LC were trading grooming for feeding tolerance, female agonistic rates need not have increased with increased feeding competition.

The behavior of females in MK group also suggest that the biological markets theory, as it currently stands, may not be sophisticated enough to predict the range of responses that are possible under conditions of increased food competition. However, it may also suggest that females in MK were influenced by factors other than those related to competitive ecological effects. For example, females in MK could have been interchanging grooming for other commodities such as infant handling. Because the number of females per group was relatively small, events such as births could have had an impact on grooming patterns. Henzi and Barrett (2002) found that female chacma baboons interchanged grooming for infant handling. Females in 4 of 5 groups (MK, BT1, BT2, and CC) gave birth during the course of the study period. The only group in which females did not give birth during the study period was LC. If female gray-cheeked mangabeys trade grooming for infant handling, we might expect other groups with infants to have responded as MK did. On the other hand, this may be yet another example of the flexibility of behavior expected from biological markets theory, and in the absence of data on interchange of grooming for infant handling, we cannot rule out the possibility that females in MK uniquely traded grooming for the opportunity to handle infants.

Our results broaden the support for the prediction that female grooming relationships respond to varying levels of feeding competition by testing the prediction on an Old World monkey species living in evergreen tropical forest, the habitat in which the majority of primate species live. However, our results indicate that grooming relationships do not always correspond with predictions based exclusively on rates of agonism because animals can also respond to feeding competition via scramble competition. In the context of the biological markets theory, rates of agonism may not always be the most accurate proxy for feeding competition. We suggest that future tests of the biological markets theory take into consideration this potential by incorporating a scramble component into its predictions.

More generally, our results emphasize the flexibility and dynamic nature of female competitive relationships within the same population of primates. They demonstrate the value of adopting a theoretical framework that specifically deals with variability as information as opposed to random noise. A more categorical approach, as many socioecological models have taken, tends to treat species as fixed entities in which all females respond in a similar way. A more flexible approach would be able to account for the extent of the variability observed within species as well as within populations.

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