



Payment for sex in a macaque mating market

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In primate sexual relationships, males and females can cooperate through social trade. Market-like trading of sexual activity has been theorized, but no data have yet been presented that clearly show its existence. I collected data to test whether biological market theory could account for exchanges of male-to-female grooming and sexual activity in longtailed macaques. I explored male-to-female grooming, rates of sexual activity, and grooming–mating interchanges, which were male-to-female grooming bouts that directly involved mating. Male-to-female grooming mainly occurred when females were sexually active, and males groomed females longer per bout when mating, inspection, or presentation of female hindquarters was involved. Moreover, male-to-female grooming was associated with an increase in female rates for all forms of sexual activity, where in contrast, female-to-male grooming was associated with decreased rates of mating in the groomed males. Males did not preferentially mate with swollen females or invest more grooming in them during grooming–mating interchanges, as swellings did not seem to be a reliable indicator of female fertility. Rank status was correlated with grooming payment during grooming–mating interchanges in favour of higher-ranked males and females. In support of a biological market interpretation, the amount of grooming a male performed on a female during grooming–mating interchanges was related to the current supply of females around the interaction. The results provided evidence of a grooming–mating trade that was influenced by a mating market.

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Cooperation can be a large component for success in sexual relationships, and trade may be one mechanism for how two sexual partners with conflicting interest can cooperate. Biological market theory is an explanatory framework for social exchange focusing on how proximate economic conditions can influence trading (Noë et al. 1991; Noë & Hammerstein 1994, 1995; Noë 2001, 2006) and thus may be useful in explaining trades of social acts relating to sex (Barrett & Henzi 2001). This economic paradigm may be a useful model for understanding social exchange, but to date only a small amount of work has been done to support its premises in specific relation to social behaviour (Noë et al. 2001; Barrett & Henzi 2006). Although there is a larger body of work showing the importance of biological market modelling to predict cooperation and mutualism in systems such as mycorrhizal mineral-exchange systems and cleaner fish markets

(Bshary 2001; Wilkinson 2001), supporting research is lacking and needed for social behaviour exchange. Particularly in relation to sexual relationships, data are needed to assess whether biological markets can be used to predict male–female interactions.

When applied to the social realm, biological market theory models social trade as if payment for social acts or partners occurs (Noë 2001). The model states that individuals trade social behaviour in a social market, and in this market there are differing classes of social partners that are distinguished by what they can offer to others (i.e. social commodities: Noë 2001). One class holds access to a social commodity (i.e. holding class) and another class seeks access to that commodity (i.e. demanding class). The dynamic between the two classes is the basis for a system of exchange where the demanding class offers something to the holding class to gain access to a social commodity. This system of trade will follow basic principles of economics. Factors such as supply, demand, advertisement and partner value will influence exchange in situations where the trade partner is not forced to

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cooperate (Noë & Hammerstein 1995; Noë 2001). For example, the relative abundance of potential partners in the holding class should alter how much individuals in the demanding class will offer them for access to the commodity they hold, if the demanding class is trading and not just taking the social commodity based on their social power. When the holding class is scarce, the demanding class should offer more, and when abundant, should offer less.

Recent work in primates has yielded conflicting results in how well biological market theory can truly predict social behaviour exchange (de Waal 2000b; Leinfelder et al. 2001; Colmenares et al. 2002; Watts 2002; Payne et al. 2003; Schino et al. 2003; Manson et al. 2004; Scheid & Noë 2005; Stevens et al. 2005; Barrett & Henzi 2006; Gumert 2006; Judge and de Waal 2006). Since the results of these works have been mixed, it has been difficult to draw clear conclusions about the role that economic forces play in social exchange. Work has mainly focused on exchanges between several elements of social behaviour that include grooming, food sharing, tolerance, infant handling, aggression, dominance gradient (i.e. steepness) and coalition support. None of these studies have determined whether there are direct exchanges for sex or the attainment of sexual information.

Barrett & Henzi (2001) argued that it seems probable that sexual activity or mating opportunity would be a commodity traded between males and females. They argue that males will use grooming to gain tolerance from a female, which will increase the probability that the male can engage in sexual activity with the female. More importantly, biological market theory predicts that if a trade of grooming and mating occurs, then a relationship between grooming payment and female supply should be observable. Additionally, partner value may also influence the grooming payment and this could include rank in the hierarchy and the ovulatory state or reproductive value of the female, possibly advertised by swelling of the perineal skin. Determining a variation in price of a social commodity based on the influence of partner supply in the current social environment is the critical test of the theory of biological markets. To date, researchers have not reported a relationship between grooming and female supply in grooming–mating interchange.

Past research has produced indirect evidence and conflicting results on whether a grooming–mating interchange exists. An overview of male-to-female grooming interactions in anthropoid primates suggests an exchange because there is a trend across the data showing that males groom females more frequently when females are swollen or receptive to mating (Mitchell & Tokunaga 1976; Goosen 1987). Specific investigation on the subject revealed that chimpanzee, *Pan troglodytes*, and hamadryas baboon, *Papio hamadryas hamadryas*, males do groom swollen females more frequently than nonswollen females (Hemelrijk et al. 1992; Colmenares et al. 2002). Moreover, a significant relationship showing that males groom the same females they mount has been reported for chimpanzees, longtailed macaques, *Macaca fascicularis*, and bonnet macaques, *Macaca radiata* (Kurup 1988; Hemelrijk et al. 1992; Gumert 2000). Contrastingly, work on Assamese

macaques, *Macaca assamensis*, showed no clear link between male-to-female grooming and mating activity (Cooper & Bernstein 2000). In this work, the researchers did not take into account the grooming context and therefore the study was not specific enough to detect direct relationships between grooming and sexual activity. Additionally, these data were collected during the breeding season, and as would be expected if male Assamese macaque grooming was related to sexual activity, they found that males groomed females more frequently than females groomed males during this time period.

The Mating Market

In primate species that follow the classic prediction of sexual selection theory, males are more apt to exchange grooming with sexual activity than are females. Ever since Darwin (1871), it has been speculated that natural selection led males to evolve traits and skills that increase their ability to attract and obtain females as mates. This suggests that the male must invest some level of effort to gain sexual access to a female whose level of cooperation in mating is largely based on the male's ability to perform or show something that will attract her. Work on understanding grouping patterns and sexual selection in primates suggests that sexual access is the limiting resource for male primates. Over evolutionary time, natural selection favoured males that were better at securing immediate mating access, but favoured females with adaptations that helped them secure relationships that would assist in their offspring's survival and fecundity (Wrangham 1980; Kappeler & van Schaik 2004).

Longtailed macaques fit this model well because males seem to be the sex more actively pursuing sexual opportunities. Generally, males maintain consortships with females (van Noordwijk 1985) and more frequently initiate sexual activity (unpublished data). Given this sort of mating system, females do not need to exert much effort to obtain opportunities to mate because they will be presented with many more mating opportunities than they can and need to engage in. Rather, females will play the selective role of allowing males to mate that are the most successful at attracting them, which may be directly related to how much the particular male invests in a female. Females are also less frequently receptive to sexual activity than males because of their monthly cycles and long periods of time spent pregnant or with young offspring. Unlike females, males do not have long periods where they seem unable or disinterested to pursue sex. In addition, females show receptivity through behavioural readiness to mate as their swellings are not reliable predictors of ovulation (van Noordwijk 1985; Engelhardt et al. 2005, 2007). The demand therefore seems to be on males to use strategies that help satiate their sexual drive by increasing a female's receptivity or by at least maximizing their potential to secure access to a female when she is receptive. Consequently, evolution would have better adapted male macaques rather than females with strategies to gain sexual access. Grooming is one possible social act that could be exchanged with a female for readiness to engage in sexual activity.

Grooming Payment in a Social Market

Grooming has been observed to be linked to reciprocity and interchange in ways consistent with a trade of social acts. There is evidence suggesting that grooming may be a form of payment that can lead an individual to obtain another social commodity from a partner. For example, grooming appears to be time-matched and thus traded reciprocally for itself in chacma baboons, *Papio hamadryas ursinus* (Barrett et al. 1999), white-faced capuchins, *Cebus capucinus*, and bonnet macaques (Barrett et al. 1999; Manson et al. 2004). Matrix correlation approaches that provide a measure of the balance of exchange between partners have shown grooming reciprocity in chimpanzees (Hemelrijk & Ek 1991; Watts 2002), bonobos, *Pan paniscus* (Stevens et al. 2005), longtailed macaques (Gumert 2000), Japanese macaques, *Macaca fuscata* (Ventura et al. 2006) and hamadryas baboons (Leinfelder et al. 2001). Ventura et al. (2006) also found that grooming might be exchanged with tolerance at feeding sites. More detailed experimental tests have shown that grooming promotes coalition support in longtailed macaques (Hemelrijk 1994) and vervet monkeys, *Chlorocebus aethiops* (Seyfarth & Cheney 1984), and food sharing in chimpanzees (de Waal 1989). A study on wood mice indicated that grooming was directly exchanged with access to sexual information (Stopka & Macdonald 1999).

Other studies have been able to relate their findings on social exchange to biological market theory by detecting an influence of supply and demand on exchanges involving grooming. It has been particularly noted that grooming duration is related to infant supply in grooming–infant handling interchanges in longtailed macaques (Gumert, in press), chacma baboons (Henzi & Barrett 2002) and vervet monkeys (Scheid & Noë 2005). Gumert (in press) showed that the ratio of infants per female in the social context surrounding a grooming–infant handling interchange was related to female-to-mother grooming duration. Other studies (Henzi & Barrett 2002; Scheid & Noë 2005) indicated that the total number of infants in the group was negatively related to the grooming duration that females directed towards mothers in these interchanges. Effects on grooming exchange are also apparent in relation to demand for tolerance (i.e. the reduction of aggression). Dominance steepness can influence grooming–tolerance interchange by decreasing grooming reciprocity when the dominance gradient between two partners is steep and tolerance is needed more by the subordinate partner (Barrett et al. 2002; Stevens et al. 2005).

Not all of the work that has tested the predictions of biological markets in primates has been able to clearly illuminate market effects governing exchange. Colmenares et al. (2002) were not able to find any clear market effects of male-to-female ratios on grooming exchange in hamadryas baboons nor could they find effects related to grooming–tolerance exchange expected by dominance gradient. Studies by Schino et al. (2003) on Japanese macaques and Leinfelder et al. (2001) on hamadryas baboons were also unable to find relationships between grooming and dominance steepness, and therefore,

a grooming–tolerance interchange. These studies showing a lack of evidence for biological markets make the influence of market factors on social exchange unclear. Are market forces nonexistent, or do these studies fail to clearly isolate the context in which these social acts are exchanged? Another possibility is that these studies were all carried out on captive groups. Consequently, their results may be due to subtle social alterations of captivity that affect market exchange systems that are not present in free-ranging and wild populations.

Colmenares et al. (2002) pointed out that biological market effects may be difficult to observe unless the grooming context, and the trading and demanding classes are clearly identified. Schino et al. (2003) concurred that indeed when classes are clear, as in the infant market studies, biological market effects seem more evident. Their position emphasizes the need to focus on drawing clear contextual definitions for specific types of social grooming or other forms of exchange to assess parameters influencing social exchange. In this present study, I identified how much of male-to-female grooming was directly related to sexual activity. More importantly, I categorized the acts of male-to-female grooming that were studied for market effects into a sexual context. This made it clear that the grooming analysed was indeed sex-related and therefore should be influenced by market forces if there truly was a trade of grooming and sex.

In this study, I observed how males interacted with females in a group of longtailed macaques, and I looked at how they exchanged grooming with mating and other sexual activity. If male-to-female grooming was exchanged for sex in a social market, I predicted the following. First, males should mainly groom females that can offer sex. Therefore, male-to-female grooming should occur most when females are sexually active and males should groom females longer when sexual activity is associated with the grooming bout. Second, male-to-female grooming would need to promote the occurrence of sexual activity with the groomed female for exchange to be possible. Therefore, grooming of a female should increase the rate that she engages in sexual activity with her grooming partner and decrease the rate of her sexual activity with others. Furthermore, since females are not paying for sex, when females groom males the sexual activity of males should not increase and males should not restrict their sexual activity to their grooming partner only. Third, the amount of grooming investment offered in such interchanges should be based on each individual's value as a partner relative to others in the group. From this assumption I made the following two predictions. (1) Females with swellings would not be of higher value to the male because swellings in this species fail to reliably signal fertile state. (2) High-ranked individuals should have an advantage in a grooming–sex market, where high-ranked males groom for shorter durations and high-ranked females receive longer durations of grooming during grooming–mating interchanges. Finally, if any grooming–mating exchanges are observed between males and females, then it would be necessary to show that such exchanges are in fact influenced by a market of potential partners for exchange. Therefore, I predicted

that the duration of grooming during grooming–mating interchanges should be related to the supply of females per male.

METHODS

Two researchers collected data on male-to-female grooming and sexual activity for this study between July 2003 and February 2005 from a longtailed macaque group in the northwestern portion of Tanjung Puting National Park (TPNP). TPNP is a 304 000-ha reserve located in Kalimantan Tengah, Indonesia (112°E latitude, 3°S longitude). The group varied in size throughout the study between 48 and 53 individuals, fluctuating with births, deaths, adolescent male emigration, and adult male immigration. The group was composed of five adult males, 18 females, and the rest juveniles or infants. Two of the five males immigrated into the group during the study. One male arrived in the first month of observation, July 2003, and the second arrived in November 2003. Researchers recognized individuals by facial characteristics. The macaques resided in a 1–1.2 km² home range located along the Sekoyner River near an ecotourist facility on the border of the park. The macaques were inconsistently provisioned from lodge refuse, mainly in the mornings when left over rice from the day before was discarded behind the lodge.

Focal Data Collection

The researchers followed the group 5–7 days a week with some breaks over the 20-month observation period. The researchers collected 10-min focal subject samples (Altmann 1974) according to a predetermined randomized time schedule. All sexual activity involving the focal subject was recorded, which included mounting, genital inspection, and female presentation of the hindquarters. The researchers also collected postgrooming (PG) samples based on a predetermined time schedule. PG samples were 10-min focal samples taken on a female or male that had just received grooming from an opposite-sexed partner. The samples began immediately following the cessation of the initial grooming act. A grooming act was considered over if 30 s expired with no grooming activity, if there was a change in direction (i.e. B starts grooming A), if the grooming became directed to a third party, or another social act occurred. During PG samples, the researchers scored all sexual activity that involved the focal subject that had just received grooming. If a subject went out of the researchers' view during an observation, the sample was cut short.

Determining the Effect of Grooming on Sexual Activity

The researchers collected data on all male-to-female grooming interactions observed during the study. This set of grooming data was used to assess under what conditions males groomed females. I determined whether more male-to-female grooming bouts occurred when females

were receptive to mating versus times periods where they were not. A female was defined as sexually receptive if she had been observed engaging in mating within 3 days of a male-to-female grooming bout. Grooming bouts were further broken down into sex-related bouts and nonsex bouts. Sex-related grooming bouts were directly associated with mating, investigation, or female presentation of her hindquarters, while nonsex grooming bouts did not occur in conjunction with any sexual activity. I compared these two sets to see whether there were differences in grooming duration between sexual and nonsexual conditions.

In addition, I calculated each subject's rate of sexual activity in focal samples and in PG samples to determine whether male-to-female grooming increased the frequency that sexual activity occurred. Focal sample rates were determined from samples where opposite-sexed partners were in sight and available, and indicated the subject's overall rate of activity with all partners. In PG samples, I obtained two rates for each activity. I determined each subject's rate of sexual activity with their partner (i.e. partner rate) and each subject's rate of sexual activity with third parties (i.e. third-party rate). Rates were measured as the number of acts per hour. Average focal observation time over the study was 5 h 32 min/female and 7 h 21 min/male, and average PG observation time was 1 h 13 min/female and 3 h 9 min/male.

I used the rates generated from focal samples as the expected baseline rates of mating, inspection, and female presentation. Rates obtained from PG samples were the test sample used for comparison. Each male and female's PG rate of sexual activity was compared with their baseline rate to test my hypotheses about the effect of grooming on rates of sexual activity. Additionally, each individual's third-party PG rate was compared with their baseline rate and also with their PG partner rate. These comparisons were used to determine whether grooming promoted partner-specific sexual activity. Tests on males were with an $N = 5$ and tests on females were with an $N = 15$ because there were not sufficient PG data in three of the 18 females. All tests consisted of small sample sizes owing to limits on subjects available in a study on a single social group. Since data of this nature may not be normally distributed, I tested each sample distribution for the normalcy of its curve using Kolmogorov–Smirnov tests before deciding on the proper statistical comparison. I used paired t tests for comparisons where both sample distributions were not significantly different from normal, and used Wilcoxon matched-pairs signed-ranks test for comparisons where at least one sample set was found to be significantly different from a normal distribution. All statistical tests in this study were $\alpha = 0.05$ and two tailed.

Assessing Female Swellings

Female swellings were monitored during the study and the researchers collected data recording which females were swollen and on what dates. Females were recorded as swollen or not swollen each day they were observed. I used swelling data to ascertain basic female swelling

patterns. Furthermore, I used the swelling data to assess the influence of female swellings on mating and grooming to see whether males targeted swollen females for mating and whether they offered more grooming payment to swollen females per grooming bout. It was also necessary for me to determine whether males mated more with swollen females and whether females mated more when they were swollen than when they were not. I used focal sample data to assess this question. For males, I determined two rates of mating: one with swollen and another with nonswollen females. I compared these two rates to assess whether males mated more frequently with swollen than with nonswollen females. For females, I divided focal samples into two categories: one where they were swollen and one where they were not swollen. I compared the two rates to assess whether females mated more frequently when they were swollen than when they were not swollen.

Testing the Influence of Rank on Grooming and Mating

Rank may also be a factor that could influence a grooming–mating interchange market because it may be an indicator of the value of a male to a female and vice versa. Therefore, steps were taken to evaluate the role of rank on grooming and mating using data from my focal sample and ad libitum data sets. Dominance ranks were assigned to each individual using the outcomes of agonistic interactions and submission gestures. I used Spearman rank correlations to test for three relationships with dominance rank. First, whether there was a relationship between male rank and rate of mating in focal samples. Second, whether there was a relationship between male rank and the grooming bout duration in grooming–mating interchanges. Third, whether there was a relationship between grooming received in grooming–mating interchanges and female rank.

Testing Female Supply and Swelling Effects on Grooming Duration

Ad libitum sampling (Altmann 1974) was used to collect data for grooming–mating interchanges. Grooming–mating interchanges were defined as grooming bouts where a male both groomed and mounted the female in the same interaction. Such an interaction was considered completed when the pair separated, but in some cases they did not separate and so a cap was set for when 30 min had expired and no grooming or mating had occurred between the pair. The sequence of grooming and mating could occur in any order and any number of times. Any time an interaction like this was observed, the total duration of time the male spent grooming the female during the grooming–mating interchange was scored. Additionally, all males and females within potential sight of the grooming pair were scored as the social context. I used this social context data set to calculate a ratio of females per male surrounding the grooming–mating interchange. This ratio was used as an immediate measure of

the supply of females per male for the context of the interaction. Finally, I recorded whether the groomed female was swollen or not.

I needed a data set that had precise grooming durations to be able to test for a relationship between grooming length and female supply and so all potentially interrupted or disturbed samples were removed. Grooming bouts that were obviously externally interrupted by other macaques or human activity were cut from the test sample. Furthermore, bouts that were less than 1 min in duration were excluded from analysis, since they may have been cut short for reasons unknown to the observer. After this, the data were assessed using a univariate general linear model (GLM) in SPSS 14.0 (SPSS Inc., Chicago, IL, U.S.A.) where the dependent variable was grooming duration from grooming–mating interchanges. The swelling condition of the female and the ratio of females per male were entered as fixed variables in the model. For swelling, two levels were defined. The female was swollen or not swollen. For ratio, three levels were defined. The first level was one or fewer females per male. The second level was between 1.01 and three females per male. The third level was more than three females per male. Male identity was input as a random variable. Female identity was not entered into the model because there were not enough data to test each female in all the conditions of the model.

The model was customized and all main effects were tested (i.e. male identity, female per male ratio and swelling condition). Additionally, all possible interaction effects with the ratio factor were tested. Since the ratio factor was the critical test of biological market theory, it was necessary to test for any possible interactions that might have affected its influence on grooming duration. The lowest-ranked male's data, Fagan (FG), were removed from the GLM because he did not have enough data to be tested in each of the ratio conditions. Finally, the data were also put into a linear regression to test whether a relationship still existed when the data from Fagan were included.

RESULTS

Grooming and Sexual Activity

I compiled and assessed all male-to-female grooming bouts to see how many of these bouts were associated with sexual activity or female receptivity. After compiling this data set, there was a sample of 243 male-to-female grooming bouts. I found that the majority of grooming bouts were directed at females that were recently receptive to mating. Of all male-to-female grooming bouts, 89% of them were directed towards this receptive class of females while only 11% were directed to nonreceptive females. Fifty-seven per cent of all male-to-female grooming bouts were sex-related, defined as being directly associated with sexual activity (i.e. mating, inspection, or presentation of the female's genital region). Thirty-seven per cent, or 91 bouts, were directly associated with mating and defined as grooming–mating interchange to be further studied for

influences by market forces. Furthermore, the average grooming duration of sex-related grooming and nonsex-related grooming was determined for each male. Averaging the means of each male, sex-related grooming had a mean of 9 min 18 s and nonsex-related grooming had a mean of 5 min 43 s. Males groomed females significantly longer during sex-related than nonsex-related grooming bouts (paired t test: $t_4 = 3.325$, $P = 0.029$), indicating that males invested more grooming per bout to females when sexual activity was involved.

Male grooming of females seemed to be associated with an increase in sexual activity. In samples collected in time periods after males groomed females, groomed females engaged in a greater rate of sexual activity with their male partner than their baseline rate of mating would predict. After being groomed, the female rate of sexual activity with her partner was 3.53 acts/h. This was significantly more frequent than the female baseline rate of sexual activity of 1.56 acts/h, which was calculated only from focal samples where males were present in their subgroup (paired t test: $t_{14} = -2.570$, $P = 0.022$; Fig. 1). Moreover, females engaged in sexual acts with males other than their partner only 1.02 acts/h after being groomed. The third-party data set was significantly different from normal (Kolmogorov–Smirnov test: $D = 0.378$, $P = 0.028$), therefore a Wilcoxon matched-pairs signed-ranks test was used in place of a t test. The female third-party rate was significantly less than their baseline rate of sexual activity ($T = 0$, $N = 15$, $P = 0.002$; Fig. 1). These two results indicate that male-to-female grooming facilitated sexual activity to occur specifically between the male–female pair, because females increased their rate of sexual activity with their male partners while lowering their rate with other males. Grooming had the effect of increasing the

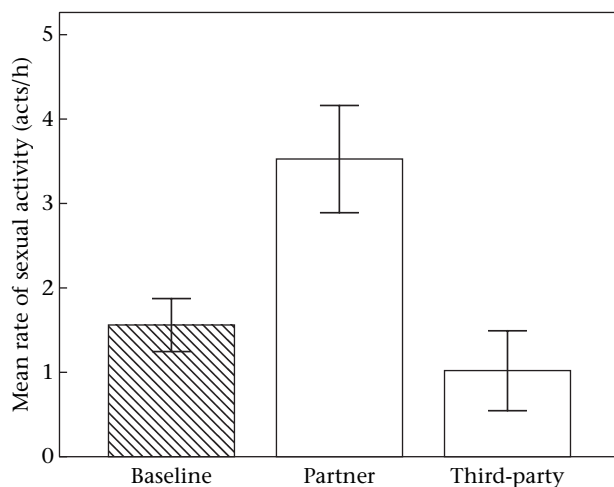


Figure 1. Mean rate of sexual activity \pm SE for females. The hatched bar represents the mean from focal sample data where males were present. The white bars represent means from postgrooming (PG) time periods. The bars show that after being groomed by a male, females engaged in significantly more sexual activity with their male partner and they showed partner specificity because they mated significantly more with their partner than with other males.

likelihood that a female would mate with her male groomer over other males.

After female-to-male grooming, a different effect on sexual activity was observed in the receiver of grooming than was seen after male-to-female grooming. In samples taken after a male had been groomed by a female, the male rate of sexual activity was 2.26 acts/h. This was less frequent than the male baseline rate of 4.12 acts/h, but the difference was not significant (paired t test: $t_4 = 1.949$, $P = 0.123$). Only one male, the lowest-ranked male, Fagan, engaged in more sexual activity after being groomed by a female than baseline. When he was removed from the analysis, the difference between baseline and PG situations was significant for the remaining four males. For these four males, baseline sexual activity occurred at a rate of 4.80 acts/h when females were available and PG sexual activity occurred at a rate of 2.08 acts/h ($t_3 = 5.013$, $P = 0.015$). If only mating was compared between the two samples for all males, I found that males mated with their female grooming partners at a rate of 0.64 mounts/h following female-to-male grooming, but during baseline conditions where females were available, they mated at a rate of 2.13 acts/h. The PG rate was nearly four times less frequent than the male baseline rate of mating and this difference was significant ($t_4 = 8.826$, $P = 0.001$; Fig. 2). Furthermore, female-to-male grooming did not appear to promote partner specificity because males were not found to engage in mating significantly more or less with their partner ($\bar{X} = 0.64$) than with third-party females ($\bar{X} = 1.02$, $t_4 = -0.691$, $P = 0.527$; Fig. 2). Overall, these results show that male-to-female grooming was different from female-to-male grooming in its effect on the grooming receiver during this study.

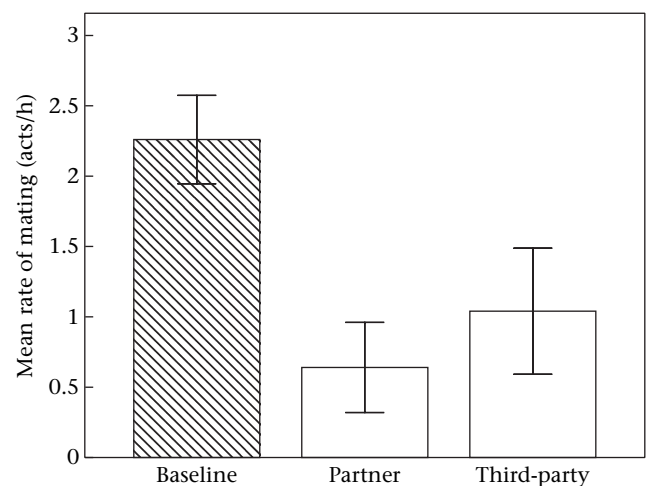


Figure 2. Mean rate of mating \pm SE for males. The hatched bar represents the mean from focal sample data where females were present. The white bars represent means from PG time periods. The bars show that after being groomed by a female, males engaged in significantly less mating with their female partner and no specificity of partner was observable because they did not mate more with their grooming partner compared to other females.

Female Swellings

In this group of longtailed macaques, female swellings appeared unpredictable and seemed to vary from female to female and in the context expressed. It, therefore, seemed that swellings may not be an advertisement to males of female ovulation. Only 10 of the 18 adult females ever expressed obvious swellings and these swellings occurred under the base (or root) of the tail, were skin-coloured most of the time (i.e. only a few females' swellings showed a red colour), and did not incorporate the vulva or anus as many primate sexual swellings do. During the study, three younger females expressed very large sac-like swellings at the base of their tail for several months that did not change obviously during the monthly cycles of these females. Additionally, eight of the 10 females that obviously swelled showed swellings 1 month or more after being pregnant, further suggesting that swellings are not a true signal of ovulation. Five of the seven females in the group that conceived during the study expressed swellings during their likely time of conception, although their swellings were not limited to a short period that could have been ovulation.

Female swellings did not predict whether males mated. The rates at which males mated with swollen females and nonswollen females were compared to see whether males restricted their mating to swollen females. The comparison showed that males actually mated more frequently with nonswollen females than with swollen females (paired t test: $t_4 = -3.363$, $P = 0.028$). This result probably occurred because there were fewer swollen females in the group at any particular time and males mated both classes of females, rather than males preferring nonswollen females. In either case, the result shows that males did not restrict their mating to swollen females and sought out mating with nonswollen females also.

After assessing males, I compared female mating rates between swollen and nonswollen conditions for eight females that were known to swell and had enough mating data in their focal samples. Swellings were not found to reliably predict female mating, although there was individual variation. Overall, the rate of mating when females were swollen was not significantly different from their rate of mating when nonswollen (paired t test: $t_7 = 0.557$, $P = 0.595$). There was a negative correlation between the swollen and nonswollen female mating data sets and this was because four females only mated when swollen, while three only mated when nonswollen in focal samples ($r = -0.768$, $N = 8$, $P = 0.026$). The last of these eight females mated in both conditions during their focal samples. Given that female swellings did not seem to be a reliable advertisement of female reproductive state, my results did not support the notion that swellings would be of any more or less value to a male when seeking sexual opportunity.

Rank, Mating and Grooming Payment

I found a perfect positive relationship showing that higher-ranked males mated more frequently than lower-ranked

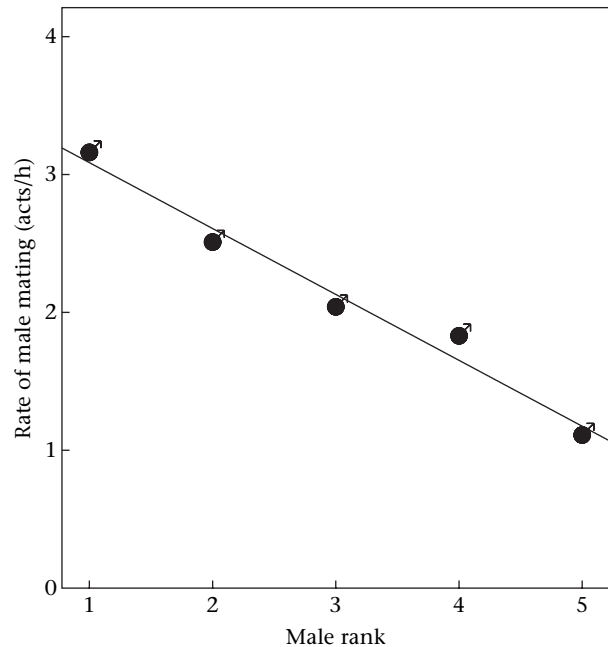


Figure 3. The relationship between male rank and the mean rate that males mated during focal samples.

males (Spearman rank correlation: $r_s = 1.00$, $N = 5$, $P < 0.0001$; Fig. 3), indicating that it was easier for them to attain mating opportunities. Dominance rank was also related to grooming payment in grooming–mating interchanges and it appeared to be in favour of high-ranked males and females. There was a significant negative correlation between male dominance rank and mean grooming duration for grooming–mating interchange ($r_s = -0.900$, $N = 5$, $P < 0.037$;

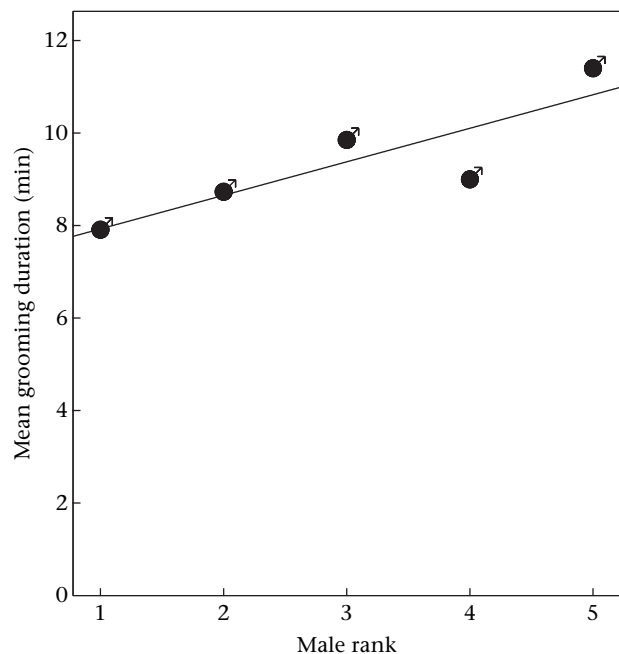


Figure 4. The relationship between the mean grooming duration that each male gave to a female during grooming–mating interchanges and his rank.

Fig. 4). As rank decreased, a male's mean grooming duration increased, further supporting the greater ease that high-ranking males had at obtaining mating opportunities. A similar result was found in females. There was a significant positive correlation between the mean duration of grooming received during grooming–mating interchanges and the rank of the female ($r_s = 0.500$, $N = 16$, $P = 0.049$; Fig. 5). As female rank decreased, the mean duration of grooming they received also decreased. These results show that the dominance hierarchy was related to the market exchange between grooming and mating. Dominance rank seemed to skew the amount of grooming investment in the benefit of higher-ranked individuals.

Grooming Duration, Female Supply and Swelling

The researchers observed 91 grooming–mating interchanges during the study and these samples were used to assess whether the supply of available females influenced grooming investment by males. Only data on 67 of these 91 grooming–mating interchanges were used. This was because only bouts that were undisturbed, observed to completion, and occurred for longer than 1 min were used in this analysis. One male's data, Fagan, which contained five data points, were discarded for not having data in each level of the ratio factor. The 62 remaining data points were put into the GLM to determine the effects of female per male ratio, swelling condition of the female, and male identity on grooming duration. After the GLM was run, I found that there was significant heterogeneity of variation in the error variance. I therefore adjusted α from less than 0.05 to less than 0.01, as recommended by Keppel (1991),

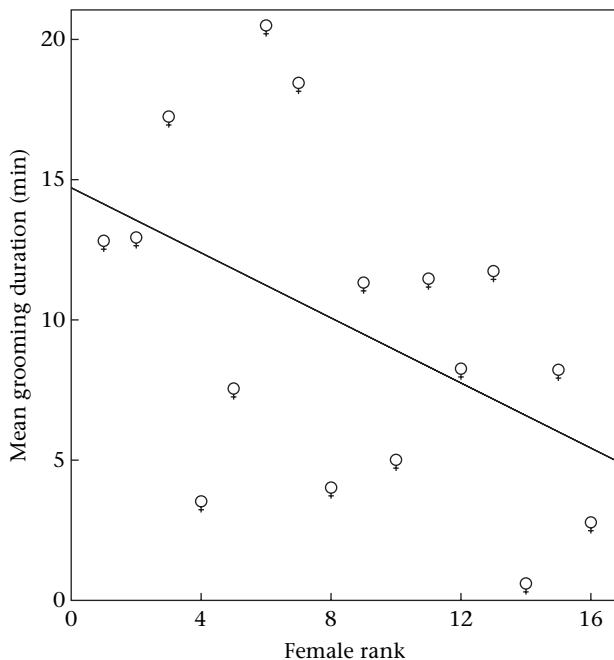


Figure 5. The relationship between the mean duration of grooming that each female received from males during grooming–mating interchanges and her rank.

Table 1. The list of variables used in the general linear model

| Parameter | Numerator Denominator | | F | P |
|---------------------|-----------------------|--------|-------|-------|
| | df | df | | |
| Ratio | 2 | 9.889 | 8.488 | 0.007 |
| Swelling | 1 | 5.963 | 0.136 | 0.725 |
| Male | 3 | 6.666 | 0.785 | 0.541 |
| Ratio*male | 6 | 5.921 | 0.381 | 0.867 |
| Ratio*swelling | 2 | 5.705 | 0.270 | 0.773 |
| Ratio*male*swelling | 6 | 41.000 | 1.128 | 0.363 |

Ratio and swelling condition were entered in the model as fixed factors and male identity was entered as a random variable. All main effects and possible interactions with the ratio factor were tested in this model.

for accounting for this violation of GLM assumptions. By adjusting α to less than 0.01, I was able to correct for the possibility that α might be artificially inflated by the heterogeneity of error variation by guaranteeing that α could not be greater than 0.05.

The results from the GLM analysis showed that there were no significant findings except for differences between the three conditions of the ratio factor. Male identity and female swelling did not appear to have any significant effect on grooming duration (Table 1). Tukey's post hoc tests showed that condition 1 (i.e. <1.01 female/male level) had a mean grooming duration difference that was 7.57 min longer than in condition 3 (i.e. >3.00 level). This difference was significant ($P = 0.004$). There were no significant differences between conditions 1 and 2 or between conditions 2 and 3 ($P = 0.141$ and $P = 0.191$). Assessment of the estimated marginal means of the four

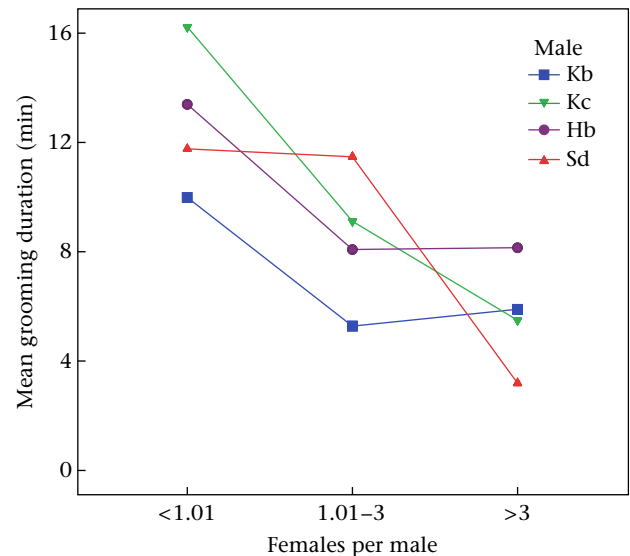


Figure 6. A plot of the estimated marginal means of grooming durations in grooming–mating interchanges under three conditions of females per male ratio for four males. Each male showed the same general linear relationship between these two variables, indicating that grooming duration decreased as the females per male ratio increased. Males are ranked from highest rank to lowest, Kb, Kc, Hb and Sd.

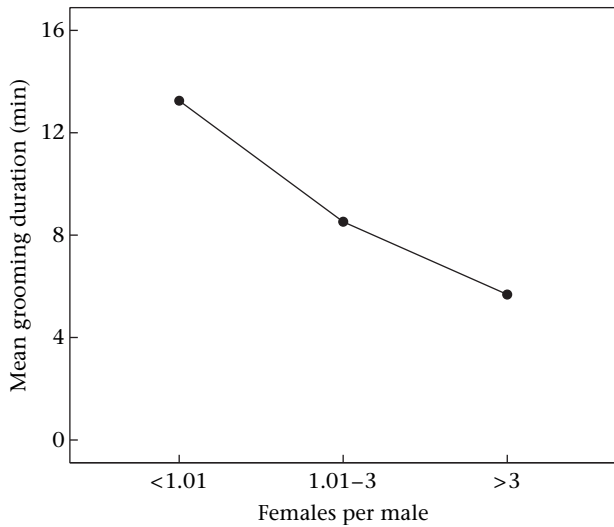


Figure 7. A plot of the total estimated marginal means showing the linear relationship between male-to-female grooming duration in grooming–mating interchanges across three conditions of females per male ratio.

males showed a negative linear relationship for each male between grooming duration and ratio of females per male (Fig. 6). Across all males, a clear negative linear relationship was also observable between grooming duration and the ratio of females per male surrounding the grooming–mating interchange (Fig. 7). Finally, a regression analysis showed the line of best fit for all 67 undisturbed grooming–mating interchanges for all five males (linear

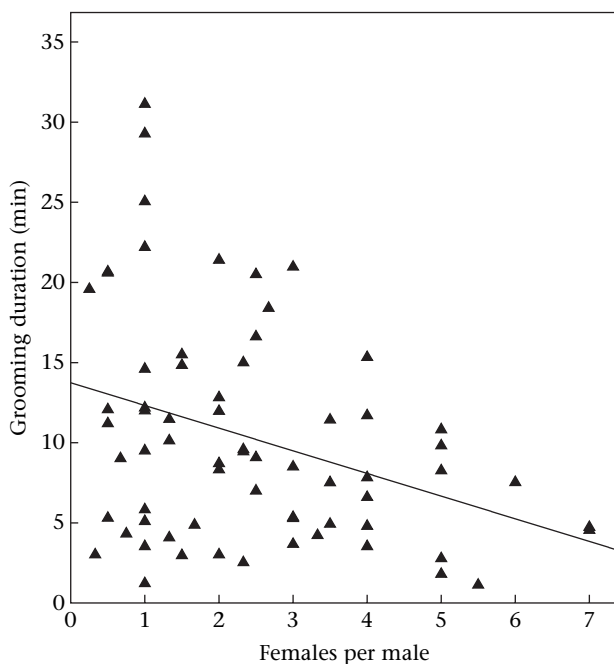


Figure 8. A scatter plot and regression line showing 67 grooming–mating interchanges from five males and the negative linear relationship that was found between male-to-female grooming duration and ratio of females per male.

regression: $r = 0.342$, $r^2 = 0.117$, $F_{1,65} = 8.620$, $P = 0.005$; Fig. 8).

DISCUSSION

My report here is the first to link a clear trade between grooming and the obtainment of sexual opportunity in a primate species, where grooming payment for mating was influenced by a mating market. Male-to-female grooming seemed to occur mainly when females were receptive and males groomed females longer when sexual activity was involved. Furthermore, male-to-female grooming promoted sexual activity during or after the grooming bout (Fig. 9), whereas female-to-male grooming did not. This study also showed that swelling did not seem to be an important factor in male-to-female grooming–sex trades but that dominance rank was related to grooming payment. High-ranked males paid less in grooming and high-ranked females received more in grooming during grooming–mating interchanges. In terms of biological market theory, the critical result of this study was that the



Figure 9. Photographs showing an example of a grooming–mating interchange where a male groomed and mated a female. During mating, the female looked back at the male. Grooming bouts such as this example are context specific to mating because males mate with females during these interactions. The amount of grooming that a male gives in these interactions is related to the ratio of females per male in the surrounding area of the grooming–mating interchange.

grooming duration in grooming–mating interchanges was related to the supply of females around the grooming bout, clearly showing how a social market can influence interchange trading. All together, these findings support a biological market interpretation of grooming–mating interchanges.

Sexual selection theory has postulated that males should be concerned with the immediate task of obtaining mating and females should be more concerned with strategies that involve the long-term reproductive costs of having offspring (Darwin 1871; Kappeler & van Schaik 2004). My report shows that grooming is one strategy that males use to obtain immediate access to sexual resources. In contrast, females did not seem to be doing the same and thus may be more concerned with resources other than sex from their social partners when performing grooming. Female grooming of males may be more linked to maintaining social relationships because this could later protect their offspring by forming bonds with the males of their group. Bonded males may more likely remain in the group and protect infants, reducing the risks of infanticide and infant mortality (Palombit 2000). Female grooming may also act more immediately to appease males and allow females to avoid or stop further sexual interaction, because sexual activity can lead to aggressive outbreaks and can be disruptive to a female's activities.

This study does not show that grooming is a necessary instigator of sexual activity and mating, but rather shows that grooming is one of several strategies that males can use to obtain sexual opportunity. One option males have may be to use grooming to obtain mating opportunity or gain sexual information through inspection. This may occur in a manner similar to the pattern of wood mice, *Apodemus sylvaticus*, a species that grooms for sexual information, where a male grooms a female and slowly works down to the genital region of the female and inspects her (Stopka & Macdonald 1999). The use of grooming to obtain sexual opportunity is a trading-based strategy and it is possible that other social acts could be traded as well for this opportunity, for example, coalition support or tolerance at feeding sites. Grooming is a more direct manipulation of the female though, making it a more likely act to be used to directly facilitate a sexual opportunity.

Many male–female sexual interactions occur without grooming. These interactions may occur for other reasons than the grooming that occurs between a male–female pair, although it is possible that a single act of grooming payment might secure more than one sexual opportunity. Trading is based on relationships, and once a settlement on trade is negotiated or established it may not be necessary to barter on every single interaction. The relationship will probably need to be reaffirmed and renegotiated from time-to-time and therefore male-to-female grooming will occur periodically between the pair. Whenever these grooming bouts occur the grooming payment will be based on whatever the social market is composed of at that particular time. What is of most importance here in sexual interaction is that in most circumstances it is necessary to have a certain degree of cooperation to successfully mate and engage in other sexual activity. This characteristic of sexual activity promotes

cooperation-based strategies such as trading grooming for sexual opportunity.

Other strategies exist for males to sexually access females and a common method of securing a mate in longtailed macaques and other primates is consortship, where the male monopolizes the female and attempts to mate-guard her from other males (Manson 1997). Consortship is different from a trade because it is based on displacement of other males and coercion of the female. Consorting males are excluding other males from the female and limiting her options of mate choice, possibly at times where ovulation is most likely to occur. When consortships are broken up by another male, the consorting male can seriously aggress and bite the female that has mated outside the consortship. Such interaction shows that consortship is based, to some degree, on force and coercion, acting to keep the female away from other males. Market forces do not have as much impact on social exchanges where force, displacement, or coercion is the major influence (Noë & Hammerstein 1994). Rather, market forces exert more influence in situations where the social commodity being sought can be obtained through cooperative trading of acts, and competition is dealt with by out-bidding others, not displacing them agonistically. Biological market theory is a model for cooperation-based exchanges, such as grooming–mating interchanges. If consortship is to be analysed using biological market theory, some sort of trade of acts needs to be isolated first.

Although grooming occurs in consortship, it is difficult to assess whether the grooming that occurs in this context is directed at obtaining sexual opportunity or simply to keep the female away from other males (i.e. grooming for proximity). Because of this contextual confound, consortship grooming alone was not analysed in this study as a class of grooming related to sexual activity. The only grooming analysed from consortship contexts were those bouts that occurred during an interaction that directly involved sexual activity. In this study, I isolated grooming that was directly related to sexual activity and mating, whether it occurred in consortship or not. This allowed for a better test of biological market theory because this method targeted the specific exchanges of grooming and mating. It may be important to begin researching how social markets might influence male–female interactions in consortship as well. Specifically, this would need to explore male-to-female grooming as payment for increased proximity and behavioural synchrony, and would need to clearly isolate specific contexts where the two acts are directly exchanged.

The dominance effect found on grooming–mating interchanges shows the effects that social power and coercion might have on a social market. High-ranked individuals may not need to offer as much, possibly because their social power allows them to have easier access to resources they are seeking. Moreover, higher-ranked individuals may also be able to receive more payment for the social resources they can offer. This effect skews any market in favour of high rankers and has a corruptive effect on trade because it makes payments unbalanced and variable between individuals depending on their social status. Another explanation for this

relationship between grooming duration and rank is that higher-ranked individuals are indeed more valuable partners and, therefore, are just worth more in a social market. This could be the case in grooming–mating interchange, because high-ranked males may be better protectors of females and their future offspring and so engaging in trade relationships with high-status males may have other benefits that waive the need for more grooming payment in the immediate interaction.

High-ranked females too may be of greater value to a male on the mating market. For example, high-ranked female longtailed macaques have been reported to produce more offspring with better survivorship than lower-ranked females at Ketambe in Sumatra (van Noordwijk & van Schaik 1999). If this is also true of macaques at Tanjung Puting in Kalimantan, then males may value higher-ranked females over lower-ranked females because they will be more likely to sire successful offspring if born to high-ranked females. It is difficult to assess if macaques could invest in such a long-term benefit in their trading, and the more parsimonious explanation is that the immediate influence of social power alters the immediate grooming investment. My findings are congruent with Seyfarth's (1977) model for female-to-female grooming, where individuals groom higher-rank partners more because it may have the long-term effect of gaining returned benefits to them in future, such as support in altercations. The influence of dominance on social trade has also been shown in grooming–infant handling markets, where higher-ranked mothers received more grooming during grooming–infant handling interchanges (Henzi & Barrett 2002; Gumert, in press).

Another possible indicator of female value is their swellings. It has been suggested that female sexual swellings can signal the reproductive status and the timing of ovulation (Hrdy & Whitten 1987). It has also been argued that in wild olive baboons, *Papio hamadryas anubis*, sexual swellings are an indicator of lifetime reproductive success, because females with larger swellings reach sexual maturity earlier, produce more offspring, and have more surviving offspring per year. Males also tended to fight more over females with larger swellings, indicating that males were willing to exert greater effort and take more risk for securing access to females with such swellings (Domb & Pagel 2001). If swelling is a true indicator of these qualities, then swelling would be an important advertisement to males in a mating exchange market.

In this study, female swellings did not appear to influence a market of grooming and mating interchange. It did not appear that males were any more interested in swollen females than nonswollen females, nor did swellings predict female mating behaviour reliably. Others have also reported that longtailed macaque swellings seem to be unreliable cues of the female fertile phase (van Noordwijk 1985; Engelhardt et al. 2005, 2007), indicating that these swellings are not always honest signals of reproductive value. The meaning of primate swellings probably varies from species to species, and therefore so would its significance as an advertisement to males. Longtailed macaque swellings are structurally different from other

primate swellings, expressing at the base of the tail, not around the vulva and anus, and only occasionally showing a red coloration. The only common trend observed in longtailed macaque swellings seems to be that their size decreases with age (van Noordwijk 1985; Engelhardt et al. 2005).

The swellings expressed by female longtailed macaques may have a different function or cause and may not be a reliable indicator of reproductive status or future reproductive success, as in baboons and some other macaque species. Because of this, male longtailed macaques may not exert extra effort to gain access to swollen females. Engelhardt et al. (2007) have shown that maximum female swelling sizes do not differ between pre- and postconception time periods, and they argue that these swellings may invite males to engage in postconception mating to confuse paternity and ward off infanticide. Such a deceptive signal has decreased the value of swellings in this species as an honest signal of reproductive value. Since males do not appear ubiquitously attracted to swollen females, it may be an indication of the evolutionary arms race between the sexes based on this signal. Given this, there may be other more subtle cues, not explored in my study, that may more reliably signal ovulation, such as the female reaching back and touching their sex partner (Fig. 9) during the act of mating (Engelhardt et al. 2005, 2007). Future work should look at whether males invest more grooming in females currently expressing such behaviour.

Biological market theory explains the dynamics of cooperative relationships based on a market of potential partners and competitors (Noë 2001). Sexual relationships too may be explained in this way because cooperative trade is one way to achieve sex. Animals faced with the dilemma of how to interact with a cooperative sexual partner should assess information in their immediate social environment by evaluating the current mating market. Individuals should invest only as much as is needed to secure a cooperative relationship and should base their partner choice on what their partner can offer to them. The amount of investment needed will be influenced by parameters such as supply, demand and relative value (i.e. dominance rank, reproductive status, etc.) compared to other potential partners in a social market.

Although a biological market framework may predict a grooming–sex trade, it does not account for the mechanism driving such exchange. Grooming–mating interchanges may result from a process like attitudinal reciprocity (de Waal 2000a; Brosnan & de Waal 2002), rather than a calculated system of exchange. Since grooming is known to be followed by tolerance, tension reduction (Schino et al. 1988), and the lowering of heart rate (Boccia et al. 1989; Aureli et al. 1999), it could also promote a cooperative attitude between the pair. Grooming may also be associated with lower levels of stress, in both receivers (Gust et al. 1993) and actors (Shutt et al. 2007), and monkeys also show increased beta-endorphins in their cerebrospinal fluid after receiving grooming (Keverne et al. 1989). Physiological mechanisms such as these may have evolved to motivate individuals to cooperate through reward and stress reduction. Consequently,

grooming may alleviate the stress and fear involved in social interaction and thus may facilitate social trade. Overall, the physiological changes associated with grooming might make the male more at ease to attempt a sexual act and the female more tolerant of his sexual advances. The effect of supply probably has a similar proximate basis, where the parameters of the social market may trigger physiological states that modulate how motivated males and females are to cooperate depending on the abundance of potential partners and competitors.

Future studies that aim to better isolate trading contexts may bring our attention to other types of social markets in primates and other organisms. Future studies will also need to assess the physiology behind partner choice and social exchange. This will help us understand the mechanisms of social trade that presumably have evolved to motivate individuals to behave optimally in their social world. Natural selection is the result of competition over a limited supply of resources important to survival and reproductive success. Resource-based competition expresses itself in the social world as well, and therefore social selection may result from competition over limited access to cooperative partners that can improve an individual's effectiveness and reproductive success in a society. Given this, it is not surprising that systems of social exchange show evidence of organisms responding to the relative abundance and value of social resources in a social market.

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