ANIMAL BEHAVIOUR, 2007, 74, 1655–1667
doi:10.1016/j.anbehav.2007.03.009

Payment for sex in a macaque mating market

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(Received 18 September 2006; initial acceptance 26 October 2006; final acceptance 13 March 2007; published online 5 November 2007; MS. number: A10560R)

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.

Keywords: biological markets; grooming; interchange; *Macaca fascicularis*; macaque; mating; sex; social exchange

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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0003–3472/07/$30.00/0

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.