



## FORUM

## 'Friendship' for fitness or 'friendship' for friendship's sake?

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**H**emelrijk et al. (1999), using data from a captive chimpanzee, *Pan troglodytes*, colony, state that there is no evidence to suggest that individuals trade 'social services' for fitness benefits. While fitness benefits are indicative of the evolutionary success of a given strategy, we suggest that Hemelrijk et al. (1999) do not pitch their investigation at the correct level of analysis, nor do they control for the fact that individuals will differ in the amount they have to 'pay' to gain a benefit. In this particular study, and for this species, we argue that copulations are the tradable commodity rather than fitness per se.

The concept of trade as a mechanism in so-called biological markets was formally defined by Noë et al. (1991; see also Noë & Hammerstein 1994) as the situation in which two collaborating individuals that differ in terms of the commodities that they possess behave in such a way that the symmetry of an exchange depends on the level of supply and demand (as in real-world economic markets). Such commodities can be, for example, resource-holding potential (RHP) or grooming provided to other individuals. Asymmetries in the possession of different commodities have resulted in trade documented in, for example, groups of baboons (Barrett et al. 1999) where grooming was traded for grooming and possibly for other social services such as tolerance around food sources. The latter was suggested to occur when the 'demand' for food was much higher than the 'supply' in their natural habitat.

Hemelrijk et al. (1999) assume that if trading between males and females is to be evolutionarily stable, it must have positive fitness consequences. Therefore, according to Hemelrijk et al. (1999), if there is no correlation between realized paternity score per male and his invest-

ment in the female in terms of services, then there is no evidence for trade. Our opinion is that Hemelrijk et al. (1999) oversimplify the nature of the trading relationship and that their assumption of what is traded is incorrect. Aside from the fact that there were only four males and 10 females in their captive colony, we suggest their approach does not provide adequate tests of this hypothesis for the following reasons.

(1) Before any correlation between fitness and frequency of allogrooming (or any 'service') is performed, one must control for variation in the quality of males and allogrooming rates provided. Not doing so may bias results for two reasons.

(a) Low-quality males may overcompensate for their quality by providing more allogrooming bouts to oestrous females (and, therefore, changing the correlation coefficient). This could account for the fact that 'males that showed more affiliative behaviour towards females in general did not sire more progeny'. Previous work cited by Hemelrijk et al. (1999) themselves is also indicative of the greater effort that relatively unsuccessful males are willing to invest in providing social services: in Tutin's (1980) study, these males were observed to form cooperative relationships with females in order to consort with them and 'compared with other males, such males groom oestrous females more often and share food more frequently with females in general'.

(b) More importantly, a male of high quality should be preferred by the females and, therefore, may have a lower 'price to pay' to gain mating access. Data from wild chimpanzees in the Mahale Mountains indicate that adult males are more successful at courtship overall than adolescent males. In addition the courtships of adolescent males failed more often than those of adult males whenever there were higher-ranking males present. This was a result not just of male–male competition but also of females' acceptance or refusal of a courting male (Matsumoto-Oda 1999). At the beginning of oestrus,

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females at Mahale mated promiscuously with many males, but, as they reached peak fertility, they tended to copulate repeatedly with only higher-ranking males and their rate of grooming of these males increased substantially. Females may, therefore, use grooming to ensure that the male of their choice remains their partner during the period of highest fertility so that they obtain a good-quality father (Matsumoto-Oda 1999).

The fact that females increase their rate of grooming and appear willing to 'pay' for increased mating with their preferred partners suggests that high-ranking, good-quality males need pay, if anything, only a very small price to obtain matings. Given that females are not passive vessels but active traders in the mating market place, we should not necessarily expect to find a simple relationship between male grooming of females and male reproductive success (i.e. 'high fitness benefits' in Hemelrijk et al.'s 1999 terminology). Consequently, Hemelrijk et al. should have controlled for these kinds of effects by statistically removing correlates of male phenotypic quality before any inference about trade was made. However, because of Hemelrijk et al.'s (1999) statement '... during all periods examined here the position of the alpha male was unclear...' statistical removal of this bias appears to have been impossible.

(2) Given that the females experience oestrus or pregnancy at different times, one can assume that the percentage of suitable females available for mating changes over time. This means that the 'price' of any commodity such as grooming provided to females may change alongside the opportunities for reproduction (i.e. the sex ratio prediction in the paper by Noë et al. 1991). This has a direct relation to biological markets, where price slides with increasing availability as its relative value diminishes (analogous to inflation after overproduction of banknotes). It may also alter the ranking of mate quality (critical to the points raised in 1 above).

(3) Because males do not know the outcome of any one copulation, females could 'deceive' them into trading services for copulations regardless of actual paternity. Thus, while an overall relationship between copulation frequency and paternity can be expected, competition in the market place (as detailed above) means that the 'price' that males 'pay' for mating is likely to be independent of the success (in terms of fertilization) of that copulation. More importantly, since fertilization is 'invisible' to both males and females, it cannot be traded as a commodity in return for short-term grooming benefits. Within a promiscuous society like that of the chimpanzee, females cannot guarantee paternity for any particular male, no matter how many services the male provides, and males can never be certain that a copulation will be successful, no matter how high the price they pay. Consequently, Hemelrijk et al. (1999) do not deal with the correct level of analysis in their paper since they focus on an attribute that is not a tangible commodity within the chimpanzee's mating market place. This in turn means that we should not expect to find a simple relationship between realized paternity and the provision of social services.

It is more likely that males have been selected to trade for a more proximate cue of paternity, copulation

frequency, since each act of copulation increases the probability of paternity. Copulations are the only direct cue male chimpanzees have available to them to assess possible paternity (while males may also be able to use the stage of the female's fertile period as a further guide to paternity, this will be useful only if they achieve matings and is therefore of secondary importance). Thus, it is this behaviour that natural selection should act upon. We find this point crucial because an earlier study by Hemelrijk et al. (1992) showed that when using copulations as the tradable commodity, 'captive chimpanzees groomed more often those oestrous females with whom they copulated more frequently'. This is precisely what one would predict if trade is occurring (see e.g. Noë & Hammerstein 1994).

In addition, if one were to follow Hemelrijk et al.'s (1999) argument to its logical conclusion, then fitness of the offspring (regardless of the father) should be correlated with social services, rather than fitness benefits accruing to the male. This is because Hemelrijk et al. (1999) do not use the term 'fitness benefits' correctly, nor do they take account of all the possible mechanisms by which social services could have such benefits. Hemelrijk et al. (1999) use the term 'fitness' when really they are measuring male reproductive success; fitness is a long-term measure and they do not have the data to demonstrate fitness benefits, strictly speaking. In addition, they consider only one route to fitness benefits: namely that grooming increases male reproductive success and realized paternity. However, social services themselves may have fitness benefits if females who receive more grooming have higher reproductive success and higher long-term fitness. Males who father offspring with females who receive more social services (whether from the male himself and/or other animals) may therefore gain long-term fitness benefits via this more indirect route. So if one talks about 'fitness benefits' rather than reproductive success as Hemelrijk et al. (1999) did, then one has to look at the long-term fitness of offspring regardless of the father, and take both these possible routes into account.

We raise these issues concerning Hemelrijk et al.'s (1999) paper to highlight the fact that if we are to conduct useful tests of the theory of biological markets, we must be very careful to select the right variables to measure and to make sure that they are measured as accurately as possible. Hemelrijk et al.'s (1999) paper showed that there was no simple exchange of grooming for fitness. However, this was only to be expected since partner choice and levels of supply and demand (which they did not take into account) are an integral and essential part of trading within a biological market. Nevertheless, we believe Hemelrijk et al.'s (1999) paper serves as a valuable contribution towards a debate on defining what goods are at stake and how one might test their importance.

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