The logic of Ménage à Trois

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Recent studies of socially monogamous species have shown that in many cases females do not copulate exclusively with their pair mates, but are also receptive to other males. The explanation usually given for unfaithful female behaviour is that most females are unable to bond with a male they would prefer as genetic father to their offspring. To secure male assistance the female therefore pairs with an available male but also copulates with males of supposedly higher genetic quality. Here we offer an alternative evolutionary explanation for female infidelity, which does not rely upon this 'Good Genes' hypothesis of female choice. We show with a simple model that in an evolutionary game between three players, a male, a female and a male lover, solutions exist in which the female can secure more assistance from her mate by being receptive to other males. We conclude that female sexuality can have a decisive role in regulating social behaviour, in which the fertile female is the driving force.

Keywords: monogamy; sexual behaviour; extra-pair copulation

1. INTRODUCTION

Traditionally, monogamy has been looked upon as a male and a female living faithfully together, copulating only with one another. However, molecular methods for analysing paternity together with careful behavioural studies of a number of monogamous species have changed this view. Both females and males seek extra-pair copulations and, as a consequence, offspring may have different social and genetic fathers (Smith 1988; Gowaty & Bridges 1991; Wagner 1992; Birkhead & Møller 1992). The frequency of extra-pair paternity can be surprisingly high with figures above 20% not unusual (Birkhead & Møller 1992). Consequently many cases of monogamy are today looked upon as a reproductive coalition (social monogamy) in which males and females tend their common offspring rather than as sexual monogamy (see Gowaty 1996).

Proposed hypotheses explaining female infidelity include the idea that copulating with several males safeguards against males being sterile (Birkhead & Møller 1992), and that sexual relationships may give direct benefits in return to the female (Davies 1992; Gray 1997). However, the only idea that appears to have widespread support is the 'Good Genes' hypothesis (Trivers 1972; Birkhead & Møller 1992) in which monogamous females are trying to get the best of two worlds: attain good genes for their offspring as well as male assistance. The Good Genes hypothesis assumes that females can assess the genetic quality of males, and that there is heritable genetic variation in quality among males. The latter assumption has mixed theoretical support and is much debated (Williams 1992; Andersson 1994).

An alternative explanation for female infidelity may be found in the games played between the sexes (Lumpkin 1983). As has been shown in birds, mammals and insects, male presence during the fertile period can benefit the female in several ways, such as protection and defence of resources (Clutton-Brock 1991). However, males may pay less attention to their mates if instead they can use that time to reproduce with other females (i.e. pursuing extra-pair copulations or bonding with a second female).

In this paper we suggest that female strategies can counteract male infidelity and propose that females accomplish this by producing cues which elicit more attention from their mates. If a female is sexually interested in (i.e. receptive to) other males and thereby attracts them, her pair mate may decide not to stray (see figure 1). This could lead to an increase in male assistance to the female during the fertile period. For instance, a male may contribute to the female's food intake, provide protection against predators and prevent harassment from other males (Ashcroft 1976; Lumpkin 1983). In addition, males who remain with their pair mate will find it more difficult to bond with a second female (Maynard Smith 1982). Consequently, males should evolve sensitivity to cues indicating their risk of being cuckolded, and females should try to produce these cues. To investigate the logic of these arguments we formulate a simple evolutionary game involving three players: the female, her pair mate, and her lover.

2. MODEL

Assume that a male and a female live together. The female is in reproductive condition with probability p and the cost to the female of being receptive is c. When the pair is reproducing the male's assistance increases the success of their joint breeding. The reproductive output is $V + u$ if the male provides full assistance and only V if the assistance is partial. We assume that a potential lover exists with a probability of q. If the lover stays, the male can expect to lose d paternity to the lover if he shows the female full attention and e if the attention is only partial ($e > d$). A lover that decides to leave the pair receives pay-off y. A lover that decides to continue courting the female we refer to as being present.
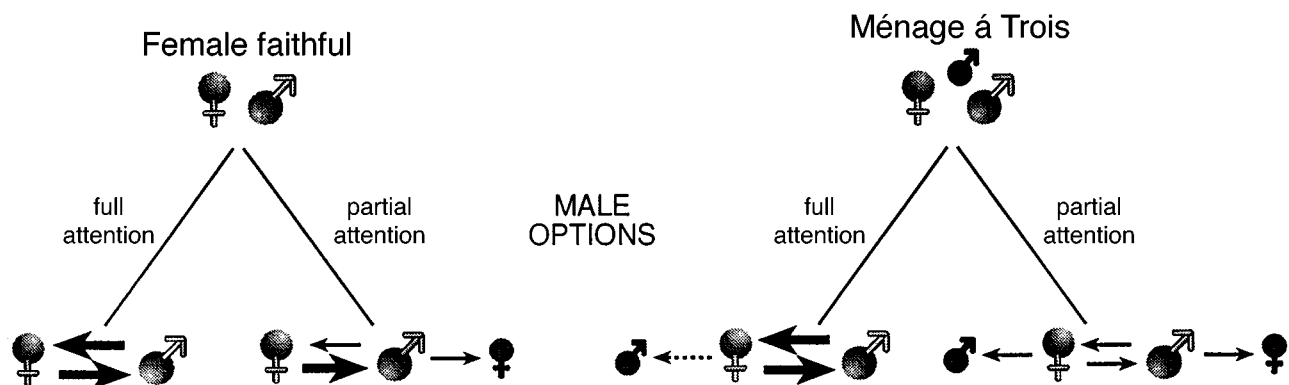
Figure 1. The logic of Ménage à Trois. The figure compares two possible female strategies in social monogamy. In the first case (left), the female is faithful whereas in the second case (right), representing Ménage à Trois, females are also receptive to other males. The male has two options. He can either remain faithful to his pair mate by giving her full attention, or he can spend time away from her courting other females (partial attention). In the first case the cost to the male of only giving partial attention is small, whereas in the Ménage à Trois case the cost may be considerable (by loss of paternity) if he does not give the female full attention. By being receptive to another male (the Ménage à Trois solution), the female may be able to manipulate her pair mate into giving her his full attention. Thus in the Ménage à Trois case there is more of a power balance between the male and the female.

A female strategy defines when to be receptive and towards whom depending upon her reproductive condition. A male strategy defines whether to stray or not, and is potentially influenced by the presence or absence of a lover. A lover strategy defines whether to continue courting the female or leave, and this is potentially influenced by the female's behaviour. Our game theory analysis considers all these possibilities as alternative strategies.

The Ménage à Trois solution we consider is a strategy triplet consisting of a 'Sexy Female', a 'Cautious Male' and an 'Opportunistic Lover'. The Sexy Female is receptive towards both the male and the lover during her fertile period and ignores them otherwise. The Cautious Male guards and assists the female if a lover is present; otherwise he spends time away from his mate who thereby receives little or partial assistance. The Opportunistic Lover courts a receptive female but quits if the female ignores him. Thus, the presence of a lover is to a certain extent under female control since the lover will only remain if the female is receptive.

To evaluate whether the triplet making up the Ménage à Trois solution can be evolutionarily stable we consider all alternative strategies. The strategy sets are discrete and we use Maynard Smith's original definition of evolutionary stability (Maynard Smith 1982). Thus, the triplet is evolutionarily stable if each strategy is a unique best reply towards the other strategies in the triplet (unique best replies may not be necessary for stability but these limiting cases are not important here). Figure 2 gives the pay-offs for the alternative strategies available to the different players (see above) when playing against the other two strategies of the Ménage à Trois triplet. For instance, pay-offs to the various female strategies are the pay-offs against the Cautious Male and Opportunistic Lover. The pay-off to the Sexy Female is affected by the male assistance and a cost of receptivity. The male's pay-off is affected by his assistance to the female, the potential loss of paternity and the fitness obtained by spending time away from the female. The lover's pay-offs depend on the female and on some alternative activity.

By focusing exclusively on evaluating the stability of the Ménage à Trois solution we could limit the game to the three players. In reality though, the game is not played just within a trio since the pay-off to certain options depends on what other players in the whole population are doing. For instance, the pay-off to males for leaving the female will depend upon the strategies used by other females in the population. We interpret the values of parameters affected in this way as those that would occur if the Ménage à Trois strategy were played by most members of the population.

The conditions for the triplet to be evolutionarily stable are as follows. For the female the sexy strategy is a unique best reply to Cautious Male and Opportunistic Lover if there are benefits of male assistance ($u > 0$), there is some cost to the female of being sexually active ($c > 0$) and $0 < p < 1$. Cautious Male is a unique best reply to Sexy Female and Opportunistic Lover if the following is true. First, that a potential lover sometimes but not always exists ($0 < q < 1$). It is also required that the increased loss of paternity is greater than the net benefit from spending time away from the female when a lover is present ($(w - u) < (e - d)$). In addition, it is required that $w > u$ for there to be an incentive for males to stray. From these conditions it follows that $e > d$ and $e > 0$, that is a philandering male loses paternity. Otherwise the flirtatious behaviour of the female would, in game theory language, be an empty threat and the triplet would not be stable. Opportunistic Lover is a unique best reply to Sexy Female and Cautious Male if the gain from courting a female receptive to a lover is greater than the gain from quitting ($d > y$). Thus it is also required that $d > 0$, i.e. a faithful male who guards his mate must also lose some paternity. In conclusion, this game has under rather broad conditions the Ménage à Trois as an evolutionarily stable solution.

It is important to recognize that a Ménage à Trois solution depends on conditional strategies. In a game theory model certain complexity is needed for conditional behaviour to occur because non-strategic variation has to be introduced. In reality, of course, non-strategic variability is common. In the model described here the risk of cuckoldry varies and the lovers experience different reproductive success with different females. This variation was
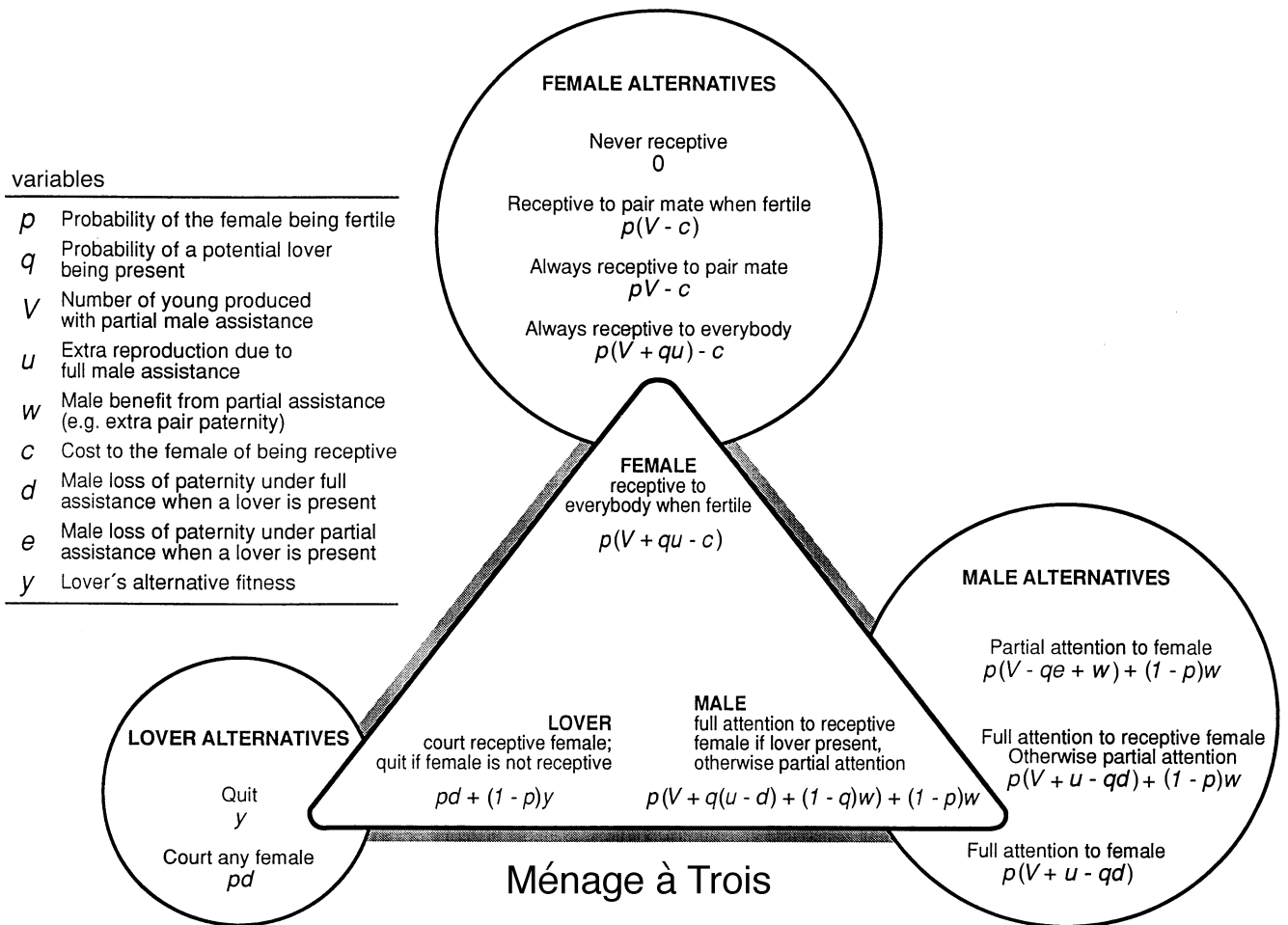
FEMALE ALTERNATIVES

Never receptive
0

Receptive to pair mate when fertile
$p(V - c)$

Always receptive to pair mate
$pV - c$

Always receptive to everybody
$p(V + qu) - c$

variables

p Probability of the female being fertile

q Probability of a potential lover being present

V Number of young produced with partial male assistance

u Extra reproduction due to full male assistance

w Male benefit from partial assistance (e.g. extra pair paternity)

c Cost to the female of being receptive

d Male loss of paternity under full assistance when a lover is present

e Male loss of paternity under partial assistance when a lover is present

y Lover's alternative fitness

FEMALE
receptive to everybody when fertile

$p(V + qu - c)$

MALE ALTERNATIVES

Partial attention to female
$p(V - qe + w) + (1 - p)w$

Full attention to receptive female
Otherwise partial attention
$p(V + u - qd) + (1 - p)w$

Full attention to female
$p(V + u - qd)$

LOVER ALTERNATIVES

Quit
y

Court any female
pd

LOVER
court receptive female;
quit if female is not receptive

$pd + (1 - p)y$

MALE
full attention to receptive female if lover present, otherwise partial attention

$p(V + q(u - d) + (1 - q)w) + (1 - p)w$

Ménage à Trois

Figure 2. Pay-offs to strategies played against the Ménage à Trois triplet. Within the triangle are the pay-offs of the Ménage à Trois triplet. The three circles list alternative pay-offs for the different players. The pay-offs to obviously unproductive strategies are not included but can easily be calculated.

coarsely generated by including a probability of there being a potential lover (i.e. $0 < q < 1$) and a probability of the female being in reproductive condition (i.e. $0 < p < 1$). To see that this variability is important, consider for instance the case in which a potential lover always exists ($q = 1$). In such a situation it is best for the male to always stay with a fertile female (or to always stray) and there is no 'need' for conditional behaviour in this respect. If males always fully assist their mates, then the advantage to the female of being flirtatious vanishes and might even become a disadvantage if there are associated costs. This in turn has consequences for the lover. The classic 'battle between the sexes' (Dawkins 1976), which studies the same problem as the Ménage à Trois game, does not consider the possibility of conditional strategies. Consequently, the female strategy able to counteract philandering (called Coy) in 'battle between the sexes' is not evolutionarily stable (Dawkins 1976; Schuster & Sigmund 1981). By allowing for more biological realism, such as conditional strategies and non-strategic variability, stable and biologically more plausible solutions are possible (e.g. Enquist & Leimar 1993).

The strategies in the model can be elaborated by taking into account additional information that is likely to be available to individuals in reality. Female sexual behaviour may be more flexible in responding to the risk of losing male assistance. Alternatively, if the female is fully attended by her mate it may be more beneficial for her to resist courtship attempts by other males. Infidelity also has potential costs in terms of reactions from the mate. Males may adjust the degree to which they assist the female according to their opportunities for obtaining extra-pair copulations.

3. DISCUSSION

The Ménage à Trois solution described above generates a number of predictions that are consistent with empirical observations. Females do direct their sexual interest to more than just their pair mate, by either approaching and displaying to other males or responding to their courtship (Richardson 1987; Bartlett 1988; Birkhead & Møller 1992; Cubicciotti & Mason 1978; Palombit 1994). The female may even solicit copulations from other males in the presence of the pair mate (Gubernick & Nordby 1993; Birkhead & Hoi 1994). If one cue to the pair male is the interest other males show towards his mate, then our model could also explain why females of monogamous species sometimes are highly ornamented, because this could help them attract more attention from other males. It is also predicted from the Ménage à Trois solution that males should be sensitive to varying risks of cuckoldry.

There is plenty of evidence that males guard females against other males and may spend days in close proximity to their mate when she is fertile compared with when she is not (Ashcroft 1976; Birkhead & Møller 1992). However, whether the presence of other males influences male behaviour has seldom been studied. In dunnocks, *Prunella modularis*, dominant males guard females more carefully when their female mates solicit copulations from subordinate males (Davies 1992).

It is crucial for the Ménage à Trois solution that lovers, at least on average, are rewarded. Empirical data from different groups of animals show that females are fertilized by males other than their pair mate (Bartlett 1988; Müller & Eggert 1989; Birkhead & Møller 1992). In the model there is only one lover, but in reality several males may be involved.

The Ménage à Trois hypothesis and the Good Genes hypothesis generate similar predictions and may be difficult to separate based on the empirical data available. They both predict that a female should be receptive to other males and that extra-pair paternity should exist. The two hypotheses differ, however, in how females are predicted to behave and about the consequences to males of straying. A female playing a Ménage à Trois game is not expected to express any strong preferences towards particular extra-pair males, unlike females searching for good genes, who would be expected to prefer particular males and to have evolved accurate paternity control. Empirical data on paternity do not reveal the existence of accurate mechanisms for paternity control in monogamous species. For instance, most offspring are fathered by the pair-male even when he is of supposedly low genetic quality (Birkhead & Møller 1992). In addition, the extreme variation in the frequency of extra-pair copulations and extra-pair paternity among species is difficult to explain from a good genes perspective. There are also empirical observations that favour the Good Genes hypothesis and which are difficult to explain by a Ménage à Trois game. Most obvious, preferences for particular extra-pair males do exist. For instance, there are field studies showing that males of a specific phenotype have more extra-pair paternity than other males, because females prefer to mate with these males and not due to male−male competition (Kempenaers *et al.* 1992; Hasselquist *et al.* 1996). Other field studies are, however, less conclusive (Westneat 1993; Dunn *et al.* 1994; Rätti *et al.* 1995).

The Ménage à Trois hypothesis also predicts that any male neglecting his mate should suffer loss of paternity. In contrast, the 'Good Genes' hypothesis suggests that males that are successful in obtaining extra-pair paternity should be of high genetic quality and should thus not suffer from cuckoldry themselves as their female mates should have nothing to gain by copulating with other males. In pied flycatchers, *Ficedula hypoleuca*, Brün *et al.* (1996) have shown that polygynous males do suffer significantly more from extra-pair paternity than monogamous males. In starlings, *Sturnus vulgaris*, females become sexually more active when their mates court another female (Eens & Pinxten 1996). In addition, Hoi (1997) found that in the bearded tit, *Panurus biarmicus*, females paired to high-ranking males had a higher extra-pair solicitation frequency than those paired to low-ranking males. In socially monogamous burying beetles (Silphidae), a system exists that in practice punishes male negligence. Usually the female has been inseminated before establishing a pair bond with a male. However, Müller & Eggert (1989) have shown that the pair male is able to fertilize most eggs if he remains faithfully with his mate. If the male leaves the female will use the stored sperm for fertilization from another male or males. Not all data, however, point in the direction predicted by the Ménage à Trois game. At least two studies show that males that are successful in obtaining extra pair copulations (due to female choice) suffer less from extra-pair paternity themselves (Kempenaers *et al.* 1992; Hasselquist *et al.* 1996), thus supporting the Good Genes hypothesis. Studies of yellow warblers, *Dendroica petechia*, and house sparrows, *Passer domesticus*, show inconclusive results. Males who were successful in achieving extra-pair copulations were just as likely to lose paternity with their social mate as other males in the population as a whole (Yezerinac *et al.* 1995; Wetton *et al.* 1995).

In conclusion, empirical data provide a somewhat unclear picture regarding the support for the two hypotheses. We regard, however, the Ménage à Trois hypothesis as a serious alternative to the Good Genes hypothesis. Alexander & Noonan (1979) and Lumpkin (1983) have discussed sexual behaviour as being a means for females to maintain social control. Our model shows that female sexuality can play a decisive role in regulating social behaviour, with the fertile female being the driving force. A question that is of considerable interest in the light of this conclusion, but not studied here, is whether truly faithful monogamy is ever evolutionarily stable.

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