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Mate choice or polyandry: reconciling genetic compatibility and good genes sexual selection

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ABSTRACT

Sexual selection for good genes is based on the assumption that 'good genes' are equally good for all females. In contrast, selection for genetic compatibility is based on the assumption that offspring viability will depend on the interaction between male and female genotypes, and hence one male may not be good for all females. Here we present a simple model to examine the relationship between the genetic compatibility hypothesis and good genes sexual selection. We examine the circumstances under which selection arising from genetic compatibility will favour an increase in the number of males a female mates with. Our model shows that if there is some cost of mating, then some form of sperm selection based on compatibility is essential for the evolution of polyandry for compatibility. Furthermore, we found that when both good genes and compatibility selection are in operation, selection for compatibility can reduce directional sexual selection by causing females to mate with males of lower genetic quality.

Keywords: female choice, female control, incompatibility, indicator mechanism.

INTRODUCTION

Evidence suggests that both post-copulatory genetic compatibility selection and directional sexual selection for good genes can operate within the same species (Simmons, 1986, 1987; Reynolds and Gross, 1992; Tregenza and Wedell, 1998; Evans and Magurran, 2000). The occurrence of these two phenomena within a species appears paradoxical, however, because good genes models intrinsically assume that males with good genes are good for all females (Pomiankowski, 1988; Grafen, 1990; Iwasa *et al.*, 1991; Johnstone and Grafen 1992; Andersson, 1994; Johnstone, 1995; Rowe and Houle, 1996), while genetic compatibility selection arises because the genes that are good for one female may not be good for another (Zeh and Zeh, 1996, 1997, 2001; Brown, 1997; Birkhead, 1998; Tregenza and Wedell, 2000).

Under good genes models of sexual selection, males vary in their genetic quality, a quality that is of interest to females, but which females cannot observe directly

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(Pomiankowski, 1988; Grafen, 1990; Iwasa *et al.*, 1991; Johnstone and Grafen, 1992; Andersson, 1994; Johnstone, 1995). Therefore, females must base their choice on indicators of quality – that is, male secondary sexual traits (Andersson, 1986; Grafen, 1990). Most important is that good genes models intrinsically maintain that the males with the most elaborate secondary sexual traits have genes that are good for all females. This assumption leads to directional selection because all females prefer males with the most elaborate traits.

In contrast to good genes models of sexual selection, the genetic incompatibility hypothesis does not require that the genetic quality of some males be intrinsically superior, rather it proposes that male genetic quality depends upon the interaction between male and female genotypes and, as such, is non-additive (Zeh and Zeh, 1996, 1997, 2001; Brown, 1997; Tregenza and Wedell, 2000). The basis of this hypothesis is that females possess cellular and cytological mechanisms by which the compatibility of male genotypes can be assessed directly. Thus, selection for genetic compatibility does not use indicators, but relies on direct assessment (Zeh and Zeh, 1997; Tregenza and Wedell, 2000). Given that the compatibility of a male depends on the female genotype and that female genotypes will differ, this process is unlikely to result in directional selection (Birkhead, 1998). Post-copulatory selection for genetic compatibility is largely dependent on the occurrence of polyandry; only if females are able to discriminate between sperm from a single ejaculate can selection for compatibility operate without polyandry. As a benefit of polyandrous mating, the genetic compatibility hypothesis predicts an increase in the number rather than the quality of offspring (Zeh and Zeh, 1996). However, we note that if viability is measured from the time that the nuclear material of the sperm and egg fuse, any reduction in the number of offspring through death during embryogenesis can be seen as poor viability and thus surviving offspring as higher-quality offspring. This concept makes selecting compatible combinations of genes very much akin to selecting good genes.

THE MODEL

We have formulated a model in which we assume that a female is faced with two males: alpha and beta. She must decide whether to mate only with the alpha male (a choosy female) or to mate with both (a polyandrous female). The male (or males) that a female mates with can affect the fitness of her offspring in two ways. Males may differ in genetic quality and genetic compatibility. Genetic quality is in the traditional 'good genes' sense, such that a high-quality male has genes that are good for all females, and this quality can be observed by females through indicator traits. We assume that the female has already observed these indicator traits and is left with the two males with the highest values of the indicator traits. Differences in quality mean that the beta male will produce offspring with a fitness of $(1 - Q)$ relative to the alpha male (defined as producing offspring of fitness 1). Thus Q represents a cost of having a low-quality father and can take values between 0 (when the alpha and beta males are the same quality) and 1 (where the offspring of beta males all die before reproducing).

In contrast to genetic quality, genetic compatibility is due to an interaction between the male and female genotypes; therefore, a male that is compatible with one female may be incompatible with another. Unlike genetic quality, in our model the compatibility of a male cannot be determined by a female before she mates. However, if a female mates with two males, only one of which is compatible, she can exert some post-copulatory control so that a proportion, p, of her eggs are fertilized by the compatible male. Any male has a probability, C, of being compatible with any female, and this is entirely unrelated to either the genetic

quality of the male or the strategy of the female. Offspring of incompatible matings have a fitness of $(1 - I)$ relative to those of compatible matings (defined as producing offspring of fitness 1).

Finally, the fitness of a female is affected directly by the number of times that she mates. Multiple mating is likely to be costly, and polyandrous females pay this cost by only being able to produce a proportion $(1 - K)$ of the number of offspring of a similar choosy female. We ignore the possibility that females might obtain some non-genetic benefit of mating (i.e. through nuptial feeding) because, in species where this occurs, understanding the evolution of polyandry is straightforward.

If we assume that all these fitness effects act independently (and so can be combined multiplicatively), we can determine the fitness of the two types of females. The fitness of choosy females (W_c) is straightforward to determine. Because the alpha male always has a genetic quality of 1, it is simply the fitness of offspring from compatible and incompatible matings, each weighted by the probability of such a mating, which, after rearrangement, leads to the expression

$$W_c = 1 - I(1 - C) \tag{1}$$

The situation for the polyandrous female (W_p) is more complex, as there are four possible combinations of male compatibility types (both males compatible, alpha compatible and beta incompatible, and so on), each producing different expected offspring fitness (Table 1). The fitness of a polyandrous female is the sum of each fitness weighted by the frequency of that male combination and then scaled to the relative number of offspring that multiple mating females produce $(1 - K)$:

$$W_p = (1 - I(1 - C)(1 - C(2p - 1)))(1 - K)(1 - Q/2) \tag{2}$$

Females will be selected to be choosy if $W_c > W_p$, otherwise females will be selected to be polyandrous. To understand how the different variables affect the mating behaviour of a female, we now explore the behaviour of this inequality under several different scenarios.

Scenario 1: no post-copulatory control

If females are unable to exert any post-copulatory choice based on incompatability ($p = 0.5$), the fitness of promiscuous females simplifies to

$$W_p = 1 - I(1 - C)(1 - Q/2)(1 - K) \tag{3}$$

The first part of this expression is exactly the same as the fitness of a choosy female (equation 1). Thus, choosy and polyandrous females have the same basic fitness for each

Table 1. The possible combinations of males for a polyandrous female

Male combination	Probability	Offspring fitness
Both males compatible	C^2	$(2 - Q)/2$
Only alpha compatible	$C - C^2$	$p + (1 - p)(1 - Q)(1 - I)$
Only beta compatible	$C - C^2$	$(1 - p)(1 - I) + p(1 - Q)$
Neither male compatible	$(1 - C)(1 - C)$	$((1 - I) + (1 - Q)(1 - I))/2$

egg. However, polyandrous females pay two additional costs associated with reduced offspring quality ($1 - Q/2$) and reduced fecundity ($1 - K$). Since both of these terms will be less than 1, the fitness of polyandrous females will always be lower than that of choosy females. Without some form of post-copulatory female choice, polyandry cannot evolve in this model.

Why doesn't polyandry increase the basic fitness of an egg? Multiple mating increases the probability that some of a female's eggs will be fertilized by a compatible male but, unless the female has some post-copulatory control, the probability that any particular egg is fertilized by a compatible male is not changed by polyandry and so there is no benefit to the average egg of multiple mating.

Scenario 2: complete post-copulatory control and mating is cost-free

If we now assume that post-copulatory control is absolute ($p = 1$) and mating is cost-free ($K = 0$), polyandry becomes a possibility. If there is no difference between the quality of the alpha and beta males ($Q = 0$), the fitness of the polyandrous females simplifies to

$$W_p = 1 - I(1 - C)^2 \tag{4}$$

Again, this is similar to the basic fitness of the choosy female, except that the $(1 - C)$ has been replaced by $(1 - C)^2$. This makes intuitive sense because the monogamous female will produce incompatible offspring if the alpha male is incompatible, while a polyandrous female will only produce incompatible offspring if both the alpha and beta males are incompatible. $(1 - C)$ will always be less than 1, and so the fitness of the polyandrous females will always be higher than the choosy females under this scenario. Thus, with no quality differences between males, polyandry will always evolve in this model. However, even if there is a difference between the alpha and beta males ($Q > 0$), polyandry is still able to evolve under some conditions. Under this scenario, the fitness of the polyandrous females becomes

$$W_p = (1 - I(1 - C)^2)(1 - Q/2) \tag{5}$$

This is the same as the previous expression, except that fitness is reduced by a factor $(1 - Q/2)$ due to the polyandrous females sometimes producing offspring fathered by the beta male. Now whether monogamy or polyandry evolves will depend on whether the costs of having lower-quality offspring outweigh the benefits of having compatible offspring. As the cost of incompatibility increases, this favours polyandry; as the difference between males increases, this will favour monogamy (Fig. 1). The greater the cost of incompatibility, the lower the quality the beta male can be and still select for polyandry. Thus, incompatibility can select for multiple mating even if this requires that a female mates with males of lower genetic quality.

Scenario 3: complete post-copulatory control and mating is costly

The effect of adding a cost of multiple mating is to reduce the fitness of the polyandrous females still further. Even if there is no difference in quality between the alpha and beta males, the fitness of a polyandrous female becomes

$$W_p = (1 - K)(1 - I(1 - C)^2) \tag{6}$$

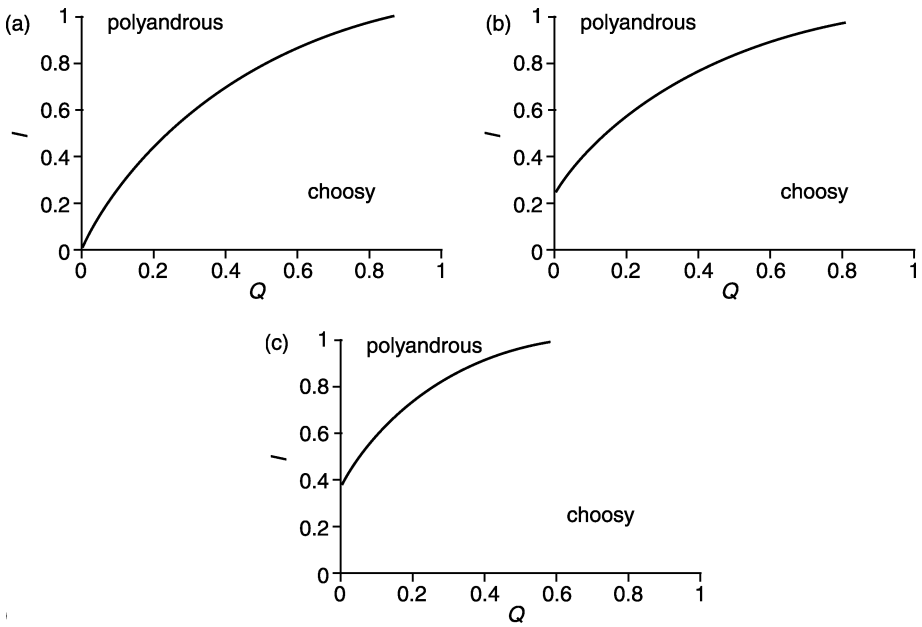

Fig. 1. Model results under three different scenarios. The line represents the values of I and Q for which the fitness of choosy and polyandrous females is equal. Below the line choosy females have highest fitness, whereas above it polyandrous females have highest fitness. Parameter values are: (a) $K = 0$, $p = 1$; (b) $K = 0.05$, $p = 1$; and (c) $K = 0.05$, $p = 0.8$. In each case, $c = 0.2$.

The addition of this cost means that the fitness of polyandrous females may now be lower than that of monogamous females, even when there is no difference between the quality of the males. However, unless the costs are extremely high or the difference in quality between the two males is very great, polyandry can still evolve if incompatability is costly enough (Fig. 1).

Scenario 4: incomplete post-copulatory control

Although some degree of post-copulatory control is necessary for polyandry to evolve in this model, it is not necessary that this control is perfect. This can be seen by considering the case where there is no difference in male quality ($Q = 0$) and no cost of multiple mating ($K = 0$). In these circumstances, the fitness of the polyandrous female becomes

$$W_{\mathrm{p}} = (1 - I(1 - C)(1 - C(2p - 1))) \tag{7}$$

If we compare this to the fitness of females with complete post-copulatory control (equation 4), it is clear that the lack of perfect control reduces the fitness of polyandrous females, because in cases where only one of the males is compatible, some of the paternity still goes to the incompatible male (and so the females still pay some of the cost of incompatibility). However, as long as there is some post-copulatory control ($P > 0.5$), the fitness of polyandrous females will still be higher than that of monogamous females. If we also include costs of multiple mating and differences between the males, the amount of

post-copulatory choice can play an important role in determining whether polyandry or monogamy is favoured. Imperfect female control will reduce the benefits of polyandry and may do so to such an extent that polyandry can no longer evolve under conditions in which it could with perfect control (Fig. 1c).

DISCUSSION

If both good genes and incompatible combinations of genes are present in a population, a female may be faced with a dilemma: to mate only with the highest quality male or to mate with several males to ensure compatibility. We have shown that selection for compatibility can evolve even when there are differences in male genetic quality, but only if the cost of incompatibility is high and there is some degree of post-copulatory selection for compatible offspring.

An essential requirement for polyandry to evolve in our model is the existence of some form of post-copulatory female choice. This provides no support for polyandry simply as a bet-hedging strategy (Stockley *et al.*, 1993) and confirms previous verbal arguments (Zeh and Zeh, 1997). The function of sperm selection is to ensure that the offspring are biased towards males with compatible genotypes. Although active or passive sperm selection is most plausible (Zeh and Zeh, 1997; Birkhead, 1998; Tregenza and Wedell, 2000), there may be other mechanisms that can lead to such a bias. For example, if females fertilize more eggs than they will ultimately try to raise and are then able to selectively abort incompatible offspring, this would provide another potential mechanism. Such 'reproductive compensation' has been suggested to occur in mice (Charlesworth, 1994).

Our model predicts that when the cost of incompatibility is high enough, the good genes choice may be relaxed, reducing the average genetic quality of a female's mates. Consequently, at the population level, this will tend to decrease directional selection acting on traits indicating genetic quality, by reducing the variation in mating success among males with different levels of trait expression. Of course, if there are many males of equally high genetic quality available to the female, she will be able to get the best of both worlds by mating multiple times among those males to ensure compatibility. In this case, multiple mating will not reduce selection for good genes.

We have assumed that the indicator trait of a male is a perfect indicator of his genetic quality. Thus, in essence, a female can observe directly the male's quality genes. In reality, such traits will be affected by many other factors, which will remove the perfect correlation between the perceived value of a male's trait and his genetic quality (Johnstone and Grafen, 1992). Other models that look explicitly at the effects of perception error in indicator traits have found that error makes little difference (Johnstone and Grafen, 1992), and we expect that the same will be true of our model.

In conclusion, when both good genes and incompatible combinations of genes are present, females can be selected to mate multiple times even if this requires them to decrease the average quality of males that they mate with. This will reduce the directional sexual selection acting on the male indicator traits. In the extreme, if mating is cost-free, and the offspring of incompatible matings are completely inviable, females should essentially ignore the trait indicating genetic quality and mate with all but the very poorest quality males. Under these circumstances, directional sexual selection would be almost entirely removed.

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