

Increased fitness from multiple matings, and genetic heterogeneity: a model of a possible mechanism

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We present a model demonstrating that female multiple matings, and thus increased genetic heterogeneity within a brood, can result in increased female fitness. The model is applicable to species where male contribution to the female is restricted to his transfer of genes and where the female controls her receptivity, and in which populations occasionally are small and isolated.

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Introduction

Females from various taxa may mate with several males before the conception of a brood. Examples include insects (Cobbs 1977), snakes (Stille et al. 1986), birds (Gladstone 1979, Gowaty and Karlin 1984), and mammals (Bertram 1975, Hanken and Sherman 1981). Several explanations have been suggested to account for the evolutionary background for this behaviour in particular groups of animals (e.g. langurs, Hrdy 1974; lions, Bertram 1975; blue birds, Gowaty and Karlin 1984). However, most of the proposed explanations are based on female-male social interactions after mating (eg. male paternal care, male infanticide). Here we present a model that is applicable to species where male contribution to the female is restricted to his transfer of genes and where the female controls her receptivity, and in which populations occasionally are small and isolated.

Gladstone (1979) suggested that an advantage of heterogeneous offspring could explain the occurrence of multiple matings and multiple paternity of a brood. A verbal model in support of this suggestion is given by Knowlton and Greenwell (1984). Their model is based on soft selection (Wallace 1975) within broods yielding a maximum mean fitness of the offspring. Our model

assumes that there exists a variation in male genetic suitability with respect to a particular female, resulting in a variation in offspring viability. Thus our model differs from Knowlton and Greenwell's (1984) in that a critical variable is the number of viable offspring (hard selection, *sensu* Wallace (1975)).

It may seem that a strategy where a female mates with one "good" or one "bad" male in successive years should have the same fitness as a strategy where a female annually mates with, on average, one "good" and one "bad" male (and have half the brood fathered by each male). However, the presented model suggests that a females' fitness really may be increased by dividing brood paternity of each brood.

Consider the following case: Compare a female that each year has five viable offspring in a brood of 10 (a female that has mated with one "good" and one "bad" male), with a female that has 10 offspring with a 50% chance of survival for the whole brood (a female that mates with one "good" or one "bad" male). (a) If there are no other young in the population (e.g. after a colonizing event or catastrophic mortality has killed most of the individuals in the population) the multiple mating female will have a 100% chance of founding a population while the single mating female will only have a 50% chance. (b) If there are 10 other young in the

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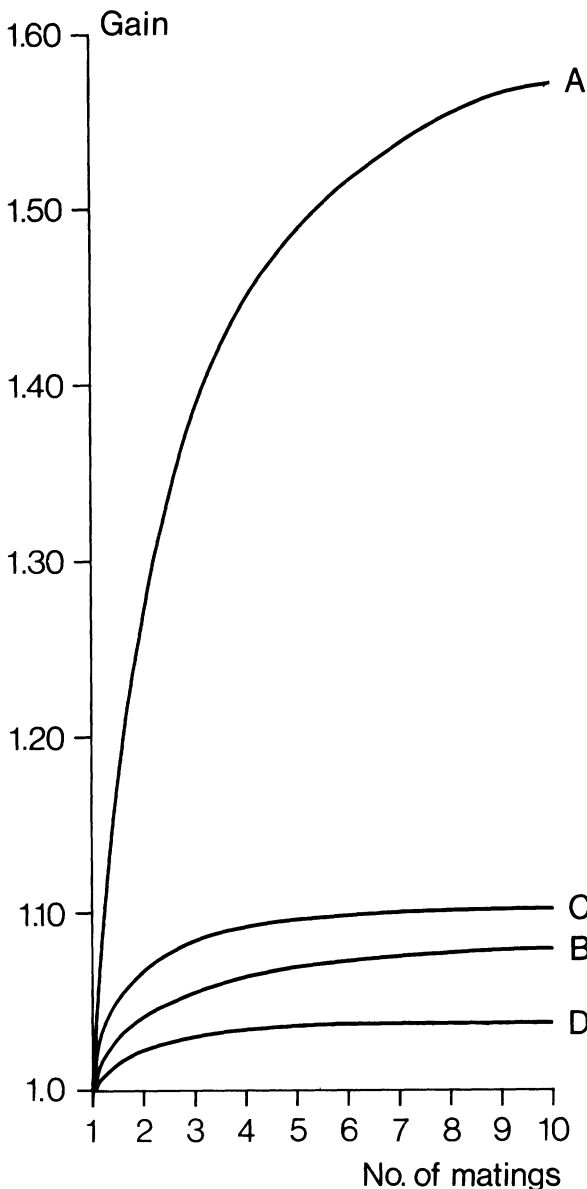


Fig. 1. The influence of number of matings on female fitness. Four cases are considered (A, B, C and D). These represent different combinations of proportion of "good" and of distinctness between "good" and "bad" males.

	"Good" males proportion of all males (%)	Proportion of viable offspring to these (%)	"Bad" males proportion of all males (%)	Proportion of viable offspring to these (%)
A:	20	100	80	0
B:	20	80	80	20
C:	80	100	20	0
D:	80	80	20	20

All graphs represent the case where maximum brood size is equal to the number of competing offspring (to other females). The x-axis gives the number of matings and the y-axis the females' gain from multiple matings. The latter is expressed as the mean proportion of offspring in future equilibrium populations after m matings divided by that after one mating. An elaboration of this index is given in the last paragraph of the introduction.

population (with a fitness equal to that of viable young of the considered female), the offspring of a female using a "double mating strategy" will on average represent 33% (5 out of 15) of future equilibrium populations while the offspring of female only mating with one male will on average represent 25% (0 out of 10 or 10 out of 20) of future equilibrium populations. The "gain index" for a double mating female is $33/25 = 1.32$ (Figs 1 and 2). Thus selection would favour a female using a multiple mating strategy.

The model

Assume that:

- 1) There is a large variation in male suitability when mating with a particular female.
- 2) Multiple matings result in broods with multiple paternity.
- 3) A female can not tell the difference in quality (to her) between males.
- 4) The populations are isolated and,
 - a) gravid females colonize new habitat patches or,
 - b) the populations are small or,
 - c) catastrophic mortality occasionally kills all but a few individuals in large populations.

After colonization or catastrophic mortality, the population size increases. The representation of a female's genes in such a population is assumed to be proportional to the fraction of the population made up by her viable offspring during low population density. For the purpose of this model all viable offspring are equally fit. We assume that what matters in terms of female fitness is the number of offspring in future populations.

A female with a multiple mating strategy will mate 0,1,2... or M times with good males (where M is the total number of matings). The number of offspring to a female which mates with i "good" males and has brood size B is:

$$\frac{i}{M} \cdot B \quad (1)$$

If there are C viable offspring to other females in the population, the considered female's fraction of representation in the future population is:

$$\frac{i}{M} \cdot B / \left(\frac{i}{M} \cdot B + C \right) \quad (2)$$

The average representation of a multiple mating female is computed from the average of all her possible brood sizes, weighed by the probability for each brood size. The probability of each case depends on the binominal distribution and the proportion of "good" males in the population (x), (the female has the same probability to mate with all males in the population):

$$\sum_{i=0}^M \binom{M}{i} x^i \cdot (1-x)^{M-i} \cdot \frac{\frac{i}{M} \cdot B}{\frac{i}{M} \cdot B + C} \quad (3a)$$

The average representation of a single mating female is:

$$x \cdot B / (x \cdot B + C) \quad (3b)$$

The assumption that all offspring of “bad” males are inviable is restrictive. A more general case is obtained if only a certain proportion of the offspring from “good” males, and a lower proportion from “bad” males are viable. If viability of offspring from “good” and “bad” males is p and q respectively (where $p > q$), the fitness is obtained by rewriting the latter part of Eq. 3a as:

$$\frac{\frac{i}{M} \cdot p \cdot B + \frac{i}{M} \cdot q \cdot (B - i)}{\frac{i}{M} \cdot p \cdot B + \frac{i}{M} \cdot q \cdot (B - i) + C} \quad (4)$$

Analysis of the model gives the following results:

- 1) Most of the advantage from multiple matings is reached after five matings (with different males) (Fig. 1).
- 2) The advantage is most pronounced if “good” males are scarce and if the difference in expected viability between offspring of “good” and “bad” males is great (Fig. 1).
- 3) The advantage of multiple mating compared with mating with only one male is most pronounced if there are few potential competitors from other females (Fig. 2).

Discussion

Williams' (1975) “elm-oyster model” invokes a mechanism, “the lottery ticket”, corresponding to that in our model. However, the purpose of his model is quite different from ours; to explain the evolution of sex. Williams' model has been criticized by Maynard Smith (1978), as sibs compete in environments which differ from those of their parents, and by Shields (1982) as it is not applicable to low and medium fecundity organisms. None of these objections is valid for our model as the setting assumed is quite different.

Do the assumptions required to make our model feasible and profitable exist in the real world? There are at least two situations where one can expect drastic genetical inferiority of certain males towards a particular female. One is inbreeding; mates of close kin often produce inferior offspring (Ralls and Ballou 1982). The deleterious effects arise from the expression of lethal

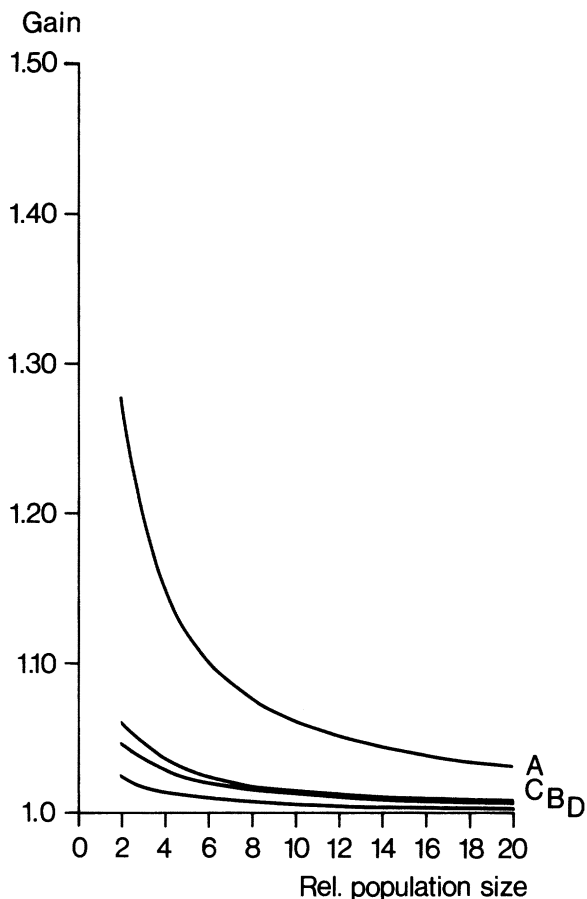


Fig. 2. The effect of relative population size on the advantage of multiple matings. Parameter values for the four graphs are those given in Fig. 1. The x-axis gives the relative population size, measured as brood size divided by the number of competing offspring (from other females). The y-axis gives the fitness gain if the female mates five times. Gain is measured as in Fig. 1 and exemplified in the text.

and sublethal recessive alleles. Another possibility is genetic incompatibility between certain males and females. Examples of such systems in humans are the Rh+/Rh- syndrome (Münzing 1967: 409) and sickle cell anemia. It is unknown how common corresponding syndromes are in the animal world.

Whether genetic incompatibility is associated with characters that females could perceive and thus form a potential basis for female choice of mates is, to our knowledge, not known for any species.

Local extinction of isolated populations has repeatedly been documented in modern man-made landscapes (Merriam 1984). Whether this has been equally common in the evolutionary history of modern species can be discussed but seems very likely.

If the assumptions discussed above are fulfilled we think that the present model may give an explanation for female multiple matings in species where male contribution to the offspring is restricted to his genes.

Parker (1984) points out that genetic heterogeneity may be advantageous if sib competition is present in insects. Parker (1984) "cannot envisage that even this selective force will be as powerful as that acting on males to assure paternity." We interpret this to mean that female multiple matings have not evolved by female choice but rather by male competition over females. However, we believe that the interest of the female is at least as important as male paternity assurance in the evolution of mating behaviour. Thus, there is no reason to assume that multiple matings in females is necessarily a result of forced copulations. The presented model gives one possible female rationale for multiple matings in many species.

An application

Female adders (*Vipera berus*) frequently mate with more than one male (Madsen 1987) despite the risks involved; mating is conspicuous and could thus attract predators. As in all other species of snakes (Porter 1972), male contribution to a female's offspring is restricted to his genes. Multiple matings result in broods with multiple paternity (Stille et al. 1986). Adder populations in southern Sweden are isolated and small (Madsen, unpubl.) and they are occasionally subjected to dramatic fluctuations in numbers (Andrén and Nilson 1983, Madsen, unpubl.). When studying offspring condition in three adder populations in southern Sweden, we found that 9% (N = 69), 4% (N = 84), and 31% (N = 159) were crippled and/or stillborn (unpubl. data). This could be a result of genetic incompatibility. With this population structure the fitness of multiple mating females will be higher than for females mating only once. The model thus gives one reasonable explanation for multiple matings in female adders and possibly in other snakes.

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