

SHORT COMMUNICATION

Adaptiveness of a Rare Male Mating Advantage Under Heterosis

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*It is shown that minority mating advantages, so commonly observed in *Drosophila*, would be selectively advantageous in a heterotic system. When an allele is below the equilibrium frequency maintained by heterosis, females mating with that homozygote produce offspring of highest mean fitness.*

KEY WORDS: rare male mating advantages; sexual selection; heterosis; *Drosophila*.

Petit (1958) first reported that male *Drosophila* of the mutants bar and white had increased mating success when rare. Subsequently, minority mating advantages have been reported for a wide variety of phenotypes and genotypes in seven species of *Drosophila*, the flour beetle *Tribolium*, and a wasp (see reviews by Petit and Ehrman, 1969, and Ehrman and Propper, 1978). The phenomenon has potential as an evolutionary force in the maintenance of polymorphisms without incurring a genetic load (Dobzhansky, 1970); in spite of this potential, the possible selective advantages accruing to females that mate with rare phenotypes have thus far received little attention in the literature. In fact, O'Donald (1978) has stated that "On evolutionary grounds . . . a general tendency to mate with the more unusual phenotypes would be maladaptive." I present here a demonstration that minority mating advantages can serve to maximize the fitness of a female's offspring in heterotic systems and thus may be preserved by natural selection acting on female mating behavior.

First, I assume that a female cannot directly assess her own genotype. The distribution of genotypes in a population therefore reflects the

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probability that a female is of any given genotype. I further assume that the number of fertile eggs laid by a female is independent of the paternal genotype. For a single-gene, two-allele system, frequencies and fitnesses are denoted as follows:

Genotype	A_1A_1	A_1A_2	A_2A_2
Frequency	$(1 - q)^2$	$2q(1 - q)$	q^2
Fitness	$1 - s_1$	1	$1 - s_2$

The mean fitness of the offspring of females that mate at random would be

$$\begin{aligned}\bar{w}_{\text{random}} &= (1 - q)^2(1 - s_1) + 2q(1 - q)(1) + q^2(1 - s_2) \\ &= 1 - s_1(1 - q)^2 - s_2q^2\end{aligned}$$

The mean fitness of the offspring of females that mate with A_2A_2 males would be

$$\begin{aligned}\bar{w}_2 &= (1 - q)^2(1) + 2q(1 - q)^{1/2}[1 + (1 - s_2)] + q^2(1 - s_2) \\ &= 1 - s_2q\end{aligned}$$

By setting $\bar{w}_2 > \bar{w}_{\text{random}}$, it is found that females that mate with A_2A_2 males will have offspring of greater mean fitness than those showing either the reverse mating propensity or none at all if and only if $q < s_1/(s_1 + s_2)$, given that s_1 and s_2 are positive. When $q > s_1/(s_1 + s_2)$, females mating with the A_1A_1 genotype will have the most fit offspring. Mating equilibrium is reached when $q = s_1/(s_1 + s_2)$, at which any genotype would father equally fit offspring.

If the heterozygote is of lower fitness than the homozygotes, i.e., $s_1 \leq 0$ and $s_2 \leq 0$, then females mating with A_2A_2 males will produce the most fit offspring only when $q > s_1/(s_1 + s_2)$. If the heterozygote fitness is intermediate ($s_1 > 0 > s_2$ or $s_2 > 0 > s_1$), then the most advantageous mate at all frequencies is simply the selectively superior homozygous genotype. Table I lists these general conclusions and the predicted mate selections for some sample values of s_1 and s_2 .

The above calculations lead to several predictions. Rare male mating advantages can be accounted for by this model only if there is heterozygote superiority. (Homozygote superiority would lead to a common male mating advantage.) Sexual selection should favor a genotype only if it is below that frequency at which a heterotic balanced polymorphism is at equilibrium [$q = s_1/(s_1 + s_2)$]. Thus sexual selection would not alter the final equilibrium maintained by heterosis, although it could greatly accelerate the rate with which equilibrium is reached. (This is true because the increase in the frequency of the A_2 allele per generation, Δq , has two positive components when q is smaller than the equilibrium value of q (\bar{q}): a constant component

Table I. Gene Frequencies at Which Females Mating with A_2A_2 Males Would Produce Offspring of Highest Mean Fitness

s_1	s_2	Frequencies
0.1	0.1	$q < 0.50$
0.1	0.2	$q < 0.33$
0.2	0.3	$q < 0.40$
0.2	0.1	$q < 0.67$
-0.1	-0.1	$q > 0.50$
-0.1	-0.2	$q > 0.33$
0.1	0	all q
0	0.1	no q
in general:		
>0	>0	$q < s_1/(s_1 + s_2)$
>0	≤ 0	all q
≤ 0	>0	no q
≤ 0	≤ 0	$q > s_1/(s_1 + s_2)$

due to the selective advantage of the heterozygote over the A_1A_1 homozygote and a frequency-dependent component. The frequency-dependent component is positive when $q < \hat{q}$ and negative when $q > \hat{q}$, because the male type below its equilibrium frequency has a mating advantage.) Furthermore, if all genotypes are distinguishable, it is never to a female's advantage to mate with a heterozygous male. If the population is not at equilibrium, one allele will be favored by selection, and females mating with males homozygous for that allele will produce the most fit offspring.

This model certainly cannot be the only evolutionary cause of frequency-dependent mating success. The advantage of males that are rare only with respect to the environment in which they were raised could not be the result of heterosis; nor could the finding that white-eyed *Drosophila* are the preferred mates when rare or abundant (but not at intermediate frequencies) be explained so simply. Yet the most important aspect of this model is the ease with which it can be tested for any phenotype by measuring both the fitness values of the genotypes and the extent to which a minority mating advantage exists.

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