

Frequency-dependent selection: Minority male mating advantage in *Drosophila*

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In frequency-dependent selection the fitness of a given genotype depends on its frequency. Frequency dependence may be positive or negative. In the positive case any rare variant is at a disadvantage, whereas rare forms are favoured in the negative case. One of the best-studied examples of frequency-dependent selection is the rare male mating advantage or minority male mating advantage (negative frequency-dependent selection). This could be of considerable evolutionary significance as it can maintain high levels of genetic polymorphism without any genetic load at equilibrium. Rare male mating advantage has been extensively studied in the genus *Drosophila* where its existence has been proved in twelve species. It has also been demonstrated in other insects and vertebrates. It has been shown to occur in morphological mutants, inversion karyotypes, isozyme variants, geographic strains, strains reared at different temperatures and those having behavioural differences. Rare male mating advantage has been shown to occur in inversion karyotypes of natural populations of certain species of *Drosophila*. In certain cases, the rare male mating advantage was tested for, but its existence could not be proved. The expression of rare male mating advantage may be affected by age of the females, temperature or experimental protocol, exposure to other flies, previous mating experience and sex ratio. The generality of this phenomenon where rare males are favoured in mating has been accepted, but there is still much discussion and controversy concerning its causes. A number of explanations have been proposed to account for the rare male effect.

THE force of natural selection is seldom constant and changes with the physical and biological factors in the environment. Since the discovery of the high level of genetic variability existing in natural populations, the study of the possible mechanisms responsible for the maintenance of this variability has become one of the main topics in population genetics. The classical mechanisms for maintaining genetic variability such as over-dominance, are based on the supposition that the selective values (fitness) of genotypes are constant.

However, experimental data indicate that selective values are not always constant, but may vary with factors such as population density or genotypic frequency within a given population. Frequency-dependent selection is a mechanism of this type which can contribute to the maintenance of genetic variability in a population when the selective values are inversely related to the genotypic frequencies (for a review see Ayala and Campbell¹ and Clarke²). As pointed out by Kojima and Yarbrough³, one of the major advantages of this type of balancing selection is the almost total absence of genetic load at equilibrium.

Wright and Dobzhansky⁴ demonstrated that the relative fitness of a genotype may be a function of its relative frequency. Many examples are available where the fitness of a genotype or a species is inversely related to the frequency of the genotype or the species^{3,5-8}. At the same time, it has become increasingly clear that frequency-dependent fitness may play a major role in the maintenance of the numerous genetic polymorphisms existing in natural populations. Frequency-dependent mating success can be measured by regression of the logarithm of the ratios of mated individuals on the logarithm of the ratios at which the individuals are present. A survey of the published literature on mating success at different frequencies indicates that a linear frequency-dependent function fits the observed results well. Such a function also provides for statistical tests of significance. Moreover, it gives information on how strong the frequency dependence is and on the frequencies at which stable or unstable equilibria may exist⁹. Anderson¹⁰ presented an algebraic model for selection by the mating advantage of rare genotypes. In accordance with the results of recent experiments, the selective advantage is formulated as inversely proportional to the genotype frequency.

Frequency-dependent selection provides a means for maintaining genetic variability within populations without incurring a large genetic load. There is a wealth of experimental evidence for the existence of frequency-dependent changes in genotypic fitness among a wide variety of organisms. Examples of traits which have been shown to be subject to frequency-dependent selection include the self-incompatibility alleles of plants, chromosomal rearrangements in *Drosophila*, visible

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mutations, enzyme variants and rare male mating advantage in *Drosophila*. It has been shown in various *Drosophila* species that mating success of male genotypes is often dependent on their frequency in the population. This frequency-dependent mating effect seems to be relatively unimportant in females. According to Nunney¹¹, if frequency-dependent sexual selection is acting on one sex to maintain a polymorphism, then at genetic equilibrium deviations from Hardy-Weinberg ratios are not expected but an analysis of the occurrence of specific matings may reveal the selection.

The well-known rare male mating advantage (or minority male mating advantage) which is an example of negative frequency-dependent selection, occurs when two types of males are present in unequal proportions and the number of females inseminated by minority males is significantly greater than those expected on the basis of their relative frequency. This interesting phenomenon and some of its evolutionary implications have been widely discussed in *Drosophila*. The rare male effects have been reported when *Drosophila* males differ at single loci affecting external somatic traits¹²⁻¹⁴, when males come from different laboratory strains¹⁵, or are of differing karyotypes¹⁶⁻¹⁸, or if they carry different isozyme variants¹⁹.

In *D. melanogaster*, rare (or minority) male mating advantage was discovered for the first time by Petit in 1951. A similar phenomenon was observed by Lee Ehrman in 1966 in *D. pseudoobscura*. Since its discovery in *Drosophila*, rare male mating advantage has become a subject of special interest and has been found to be of common occurrence in *Drosophila*^{7,20-24}. The present review documents the results of various studies on rare male mating advantage in several species of *Drosophila*, other insects and vertebrates. Few cases of rare female mating advantage have also been described. Furthermore, different mechanisms to account for the rare male effect proposed by various workers have also been discussed.

Rare male mating advantage in *Drosophila*

Male sexual fitness has been proved to be an important fitness component in *Drosophila*^{25,26} at least under some conditions. An important consequence of rare male mating advantage is that it promotes outbreeding because an occasionally visiting male from another population tends to be favoured by the females^{27,28}. Mating behaviour of *Drosophila* species consists of species-specific action patterns which are accompanied by orientation movements²⁹. During courtship the *Drosophila* male provides the female with a variety of stimuli (visual, olfactory, tactile and auditory) which function to inform the female of the species identity of the male and to stimulate the female beyond its acceptance threshold

for accepting the male in copulation³⁰. One interesting and reportedly widespread factor bearing on mating success involves frequency-dependent sexual selection, where males in the minority with respect to males having other genotypes on rearing conditions have been observed to mate more frequently than expected based on their low proportions in mating chambers²⁰. Rare male mating advantage has so far been reported in *D. melanogaster*, *D. pseudoobscura*, *D. persimilis*, *D. immigrans*, *D. pavani*, *D. gaucha*, *D. tropicalis*, *D. willistoni*, *D. equinoxialis*, *D. funebris*, *D. ananassae* and *D. bipectinata*.

In 1951, Petit³¹ discovered rare male mating advantage in *D. melanogaster* by employing wild type and Bar eye mutant flies. It was demonstrated that Bar males were at a disadvantage in competition for mates when they were more common than the wild type in the population of competing males. This is an example of one-sided rare male mating advantage in favour of the wild type males when present together with the mutant males. In 1954, Petit³² used white-eyed and wild type flies and tested rare male mating advantage. The results showed the presence of rare male effect but this was again one-sided. Petit¹² studied the influence of several genetic and environmental factors like temperature, age and nutrition on rare male mating advantage. In this case, rare male effect was found to be generally one-sided. Alvarez *et al.*³³ studied density and frequency-dependent selection on the singed locus of *D. melanogaster*. In this study, an experiment of direct competition between wild type and mutant larvae at different frequencies and at two densities was carried out. At the higher density, the results showed that when the frequency of either of the two genotypes is low, its viability increases; when the frequency of either of these genotypes is high, its viability decreases. These results suggest the existence of a frequency-dependent selection mechanism in which an inverse relationship between frequency and adaptive value is established. It also demonstrates the important effect of density on frequency-dependent selection.

Markow *et al.*³⁴ tested rare male mating advantage among various *D. melanogaster* genotypes. Regression analysis gave one significant slope out of seven, suggesting that in the present study frequency-dependent advantages are not as common or as strong as reported for *D. pseudoobscura*. Markow³⁵ tested rare male mating advantage in coisogenic strains of *D. melanogaster*. Experiments were carried out to see if rare male mating advantage could be detected when males differ at only one locus. Markow found absence of rare male mating phenomenon in her study. No deviation from expected types of mating was observed. Paterson and Merrell³⁶ reported rare male mating disadvantage in *D. melanogaster*. The wild type males showed a significant rare male mating advantage with both wild type and white eyed females. However, the white-eyed males showed an

unusual type of frequency-dependent mating, as rare male mating disadvantage. The white-eyed males were less successful in mating when they were rare than when they were common. Different storage conditions can also bias the outcome of rare male experiments^{37,38}. It has been shown that fluctuations in mean sexual vigour of the males caused by sampling errors might result in a spurious rare male mating advantage³⁹. Markow suggests a significant behavioural difference between males chosen from different places in a storage container. Males closer to the top may be more active and therefore successful in courting. Pot *et al.*⁴⁰ found no rare male effect for alcohol dehydrogenase genotypes in *D. melanogaster*. Now the question arises, how small can a difference for a particular character between types of males competing for females be in order to give rise to a rare male effect. But first an important issue must be raised with respect to genetic background. If for instance, different mutants are used by taking two laboratory strains, their genetic background will probably differ. Sometimes such a different genetic background is used deliberately, the mutant only being used as a marker⁴¹. The use of coisogenic strains (wild type and *se* mutant strains are genetically similar except the *se* locus) devised to further diminish differences in genetic background is described by Markow³⁵. In this case she did not find a rare male effect for the mutant *sepia* competing with wild type in *D. melanogaster*.

Knoppien⁴² tested rare male mating advantage in *D. melanogaster* for strains raised at different temperatures. The results suggest that there is no evidence of rare male mating advantage for strains reared at different temperatures. Magalhaes and Rodrigues-Pereira⁴³ tested frequency-dependent mating success among mutant ebony of *D. melanogaster*. Measurements of the mating success of wild type and ebony strains of *D. melanogaster* with different frequencies have shown a frequency-dependent effect in both cases, but with a negative correlation for the wild type and positive correlation for the ebony strain. Petit and Nouaud⁴⁴ tested rare male effect by using white-eyed mutant of *D. melanogaster*. They found one-sided rare male mating advantage in favour of wild type males when present together with white-eyed mutant of *D. melanogaster*. By using multiple-choice test and single-female test, rare male mating advantage is also found in *D. melanogaster*^{45,46}. Rasmuson and Ljung⁴⁷ found no evidence for rare male mating advantage in *D. melanogaster* at low and high densities. The rare male mating advantage in *D. melanogaster* is also influenced by the sex ratio^{48,49}.

Tardif and Murnik¹⁵ tested rare male mating advantage for genetic background in *D. melanogaster*. They found rare male effect in all three cases, but in one case it was only one-sided. Rare male mating advantage in *D. melanogaster* has been tested by many workers for

different factors like mutants, allozymes, etc. and they have found no evidence of rare male mating⁵⁰⁻⁵². The mating success of the carriers of a genotype is sometimes dependent upon the frequency of the genotype relative to other genotypes in the same space. The phenomenon originally discovered by Petit in *D. melanogaster* was subsequently found in two other species, *D. pseudoobscura* by Ehrman and *D. persimilis* by Spiess. Ehrman *et al.*⁵³ discovered an interesting phenomenon while studying mating success of different inversion karyotypes of *D. pseudoobscura*. They found both types of males to be equal in mating success when present in equal numbers. However, at an unequal ratio for both types of males, the rare type of male was found to mate much more than expected for its frequency by chance, irrespective of genotype. This type of effect is known as two-sided rare male mating advantage. Salceda and Anderson⁵⁴ found rare male mating advantage for inversion karyotypes in natural populations of *D. pseudoobscura*. Rare male mating advantage for inversion karyotypes has been shown to occur in a natural population of *D. funebris*⁵⁵. Ehrman *et al.*⁵⁶ demonstrated the existence of rare male mating advantage in *D. pavani/D. gaucha* by employing wild type and yellow body mutant strains of these two sibling species characterized by random mating. Investigations of factors important in the rare male mating advantage have shown that the relative proportions of types of females present is of little influence^{12,18}. The importance of olfactory cues in the rare male effect associated with gene arrangements in *D. pseudoobscura* has been reported^{57,58}. Although the loci responsible for the difference in olfactory stimuli have not been identified, it is also unknown how differences at a single locus, whether external somatic markers or isozymes, function at sensory level to bring about the rare male effect. Ehrman *et al.*¹⁹ studied rare male mating advantage at an enzyme locus in *D. pseudoobscura*. There is evidence that the *Amy* locus and others for which it serves as a marker have an effect on the mating behaviour which include some degree of rare male mating advantage. Ehrman¹⁷ studied frequency-dependent mating success in *D. pseudoobscura* by direct observation in Elens-Wattiaux mating chamber using individuals of three karyotypes: AR/AR, AR/CH and CH/CH. In each chamber two karyotypes were represented with frequencies 10:10, 2:18 or 18:2. The males of the heterokaryotype AR/CH tend to have an advantage in mating compared to the homokaryotypes, provided both kinds of males are equally frequent, i.e. the ratio is 10:10. This advantage is further increased when the heterokaryotype is a minority, the ratio 2:18 when the homokaryotype, AR/AR or CH/CH is a minority (18:2) it is equally or more successful than the heterokaryotype in securing mates. Among females, the mating success is independent of frequency, or the minority females have sometimes a slight advantage.

Does rare male mating advantage occur in nature? There is some evidence that it is operating in natural populations. First, it was shown by Ehrman¹⁴ in *D. pseudoobscura* that rare male mating advantage can occur in a large room, so that it is probably not an artifact due to the usually small mating chamber. There are many factors, genetic and otherwise, which affect rare male mating advantage in *Drosophila*. Many examples have already been given by Ehrman¹⁶ in *D. pseudoobscura*, where she found the rare male effect for strains of different geographic origin, for mutants compared with wild type, for different karyotypes and also for different temperatures of rearing. But rare male effect was not found for wing clipping¹⁶.

Recent work has raised questions concerning the reality of the rare male mating advantage, pointing out that it could be a statistical artifact of marking flies for behavioural observation or of experimental bias in collecting males. Anderson and Brown⁵⁹ designed an experiment to test rare male mating advantage for three inversion karyotypes in *D. pseudoobscura* that avoids the sources of bias. The mating success of the male homokaryotypes ST/ST and CH/CH, relative to that of the heterokaryotype ST/CH, was frequency-dependent. Both ST/ST and CH/CH males displayed a statistically significant mating advantage at low frequency on comparing with their mating success in the mid-range of karyotypic frequencies. Both male homokaryotypes also showed a significantly greater mating success at high homokaryotypic frequency than at intermediate frequencies. The heterokaryotypes not only failed to show a rare male mating advantage but actually suffered a mating disadvantage at low frequency. These results suggest that rare male mating advantage is not always an experimental or methodological artifact but does occur in laboratory populations of *D. pseudoobscura*. It may occur for some genotypes but not for others. However, it may be only one of the several forms of frequency-dependent mating behaviour operating in a population.

Frequency-dependent male sexual selection is influenced by a number of factors: aging of the females, previous copulation with one of the types of males and previous exposure to other flies⁶⁰⁻⁶². Two types of effects are conceivable:

- (i) A change in frequency dependence of mating success.
- (ii) A change in differential mating success which is equal for all frequencies.

Both types of effects may simultaneously contribute to alter selection. A clear distinction between these two factors however, is not made by these authors. It seems that rare male mating advantage is weakened or absent if older females are used. An important finding is that previous copulation of a female with a male of a certain type changes the attitude of that female in favour of that

type of male, when she mates for a second time (see Pruzan *et al.*⁶³), probably irrespective of the frequency of that type of male. This means that an initial advantage of rarity of some types of males can be enlarged when the female has the opportunity to mate more than once⁶⁰.

In addition to morphological mutants, allozyme variants have also been tested for their ability to elicit a rare male mating advantage. Positive results were obtained for the amylase locus in *D. pseudoobscura* by Ehrman *et al.*¹⁹ but only at intermediate ratios of types and not at extreme ratios. Ehrman⁶⁴ tested rare male mating advantage in *D. pseudoobscura* karyotypes for density effect. Rare male mating advantage was found for both high and low density. In the case of low density the effect was quite weak than at high density. Fontdevila and Mendez⁶⁵ tested rare male mating advantage in *D. pseudoobscura* for allozymes but no rare male mating effect was found. Ehrman⁶⁶ found that *D. pseudoobscura* females prefer to mate with males that are rare among those courting them. Females appear to obtain information about the frequencies of different kinds of males by means of air-borne olfactory cues, probably lipids (especially in the case of arrowhead males). Sexual isolation is present when potential mates meet but do not mate; the isolation mechanism is an interpopulational usually interspecific phenomenon. In contrast, frequency-dependent mating advantage favouring less abundant kinds of males are at least in *Drosophila* species, intrapopulational and intraspecific⁷. Ehrman⁶⁷ tested sexual isolation versus mating advantage of rare males in *D. paulistorum* and found that frequency-dependent reproductive success, i.e. the mating advantage of rare *Drosophila* males is rarely expressed when substantial sexual isolation is present between the populations being tested. If the degree of sexual isolation changes with changing frequencies, unequal frequencies most often tend to increase isolation between the populations. It is apparent that sexual isolation takes dominance over frequency-dependent advantage; frequency-dependent mating is only expressed or expressed most vigorously when the sexual isolation either does not exist or exists only weakly⁶⁶.

In several species of *Drosophila*, certain males mate more frequently when they are less abundant than when they are in a majority. The mating advantage may be artificially induced by the use of a 'double chamber' technique, even when there are no differences in the actual frequencies of the competing males⁶⁸. Ehrman¹⁶ tested rare male evidence in geographic strains of *D. paulistorum* and found no evidence of rare male mating advantage. Ehrman⁶⁷ studied rare male mating advantage in *D. immigrans* for geographic origin. The rare male mating advantage was found for four cases but was only one-sided. Ayala⁹ reanalysed the data of Ehrman⁶⁹ by the regression method and found no effect of rare male mating advantage in *D. immigrans*. Adams

and Duncan⁷⁰ tested rare male mating advantage in *D. immigrans* for geographic origin. They found rare male effect in two out of six cases. Spiess and Spiess⁷¹ confirmed the effect of nongenetic properties in rare male effect on *D. persimilis*. They tested rare male effect for geographic origin and different temperatures of rearing. They found rare male mating advantage in all cases. Ehrman and Petit⁷² studied rare male mating advantage in three species of *Drosophila* – *D. willistoni*, *D. tropicalis* and *D. equinoxialis*, for geographic origin. They found rare male effect in most cases but not always two-sided. Knoppic²³ reanalysed the data by Ehrman and Petit⁷² and obtained similar results. Ehrman⁶⁴ found no effect of rare male mating advantage in *D. willistoni*.

D. ananassae is a cosmopolitan and domestic species. This species is unique as it possesses many genetic peculiarities⁷³. Singh and Chatterjee⁷⁴ studied rare male mating advantage in *D. ananassae* by using wild type and sepia and cardinal mutants. In all the experiments female-choice technique was employed. Experiments were conducted at nine different ratios. The results show that both types of males are equally successful in mating when present in the same ratio. They are more successful in mating when in a minority. This advantage disappears when the males become common. Singh and Sisodia⁷⁵ found evidence for rare male mating advantage in *D. bipectinata*. Wild type and cut wing mutant flies were used in the experiment. It is evident from their results that the mating percentage of both types of males remained high when they were in a minority. However, the mating advantage of both types of males was lost when their ratio in the mating chamber increased. Thus the males which show an advantage when in a minority were less attractive when they become common in the mating chamber.

Rare female mating advantage in *Drosophila*

Although much less common than rare male mating advantage, there are few examples of rare female mating advantage in *Drosophila*. Fontdevila and Mendez⁶⁵ found rare mating advantage for females but not for males in *D. pseudoobscura* with respect to different genotypes at esterase-5 locus. In this species, Ehrman *et al.*⁷⁶ also observed rare female mating advantage and the effect was quite large. Rare female mating advantage has also been reported for allozymes and some mutants at the singed locus in *D. melanogaster*⁵⁰. Ayala and Campbell¹ reanalysed the data of Ehrman⁶⁴ and established the occurrence of rare female mating advantage in *D. pseudoobscura* though it appeared much weaker than the rare male effect in the same experiment. Ehrman and Petit⁷² tested rare female mating advantage by employing different geographic strains of *D. willistoni*, *D. tropicalis* and *D. equinoxialis*. Their results showed the

presence of rare female mating advantage in all cases for *D. equinoxialis*; though its occurrence was doubtful in few cases for *D. willistoni* and *D. tropicalis*. Knoppic²³ reanalysed the data of Ehrman and Petit⁷² by applying K_M (now known as the cross product ratio, it was first used by Petit³¹ to study the frequency dependence of mating success–male sexual fitness) which also showed clear cut evidence for rare-female mating advantage in *D. equinoxialis*. Cereghetti *et al.*⁷⁷ measured frequency-dependent sexual activity in *D. melanogaster*. A rare female advantage exists not only for wild type flies but even for white-ebony mutant flies; both mated much more frequently when they were rare than all other frequencies. In their experiments, rare type mating advantage was found with both sexes.

Fewer examples of rare genotypes mating advantage are known in females than in males but they exist. The data of Ehrman⁶⁴ and Spiess⁷⁸ were reanalysed by Ayala and Campbell¹ employing log regression method. It was found that there is a significant inverse relationship between female input and output frequencies of karyotypes in *D. pseudoobscura*¹. This finding shows that rare female mating advantage is obscured by the blockage of female receptivity⁶⁵. Ehrman⁶⁹ has reported that rare female effect is only expressed in early matings in different strains of *D. immigrans*. Ehrman and Petit⁷² reported very illustrative cases of rare female mating advantage in the *D. willistoni* species group. However, the results of Fontdevila and Mendez⁶⁵ differ from those of Ehrman and coworkers in that females are mostly responsible for the rare effect in mating selection. Females are responsible for recognizing not only the presence of different male genotypes but also their relative proportions¹⁸. It has also been suggested that the discriminating cues may be specific odours associated with pheromones released by flies^{57,79}. However, the complete process of recognition has not been understood in its physiological details. It has been pointed out by Fontdevila and Mendez⁶⁵ that sexual selection in female may play a more important role than sexual selection in male and it is known that females are the discriminating sex. The results of Fontdevila and Mendez⁶⁵ show no female preference for either male genotype. On the other hand, rare male genotypes mate more often than expected. It has been suggested that the main reason for not detecting rare female mating advantage is that females mate only once and when most of the females have mated their mating numbers are a reflection of their input numbers. Males can mate repeatedly and some rare males can participate in mating more often than expected⁶⁵.

Rare male mating advantage in other species

This unique phenomenon has also been shown in parasitic wasp, flour beetle, ladybird beetle, housefly, guppy

fish, sunfish and cricket²³. Thus rare male effect is known to occur in species other than *Drosophila* although a limited number of them have been tested. Sinoock⁸⁰ observed rare male mating advantage in flour beetle *Tribolium castaneum* but the experimental approach prevented the difference between a rare male effect and frequency-dependent progeny production to show up with the rare type favoured. Grant *et al.*^{27,81} reported the occurrence of rare male mating advantage in parasitic wasp *Mormoniella vitripennis*. Rare male mating advantage in nature has been shown for ladybird (beetle) *Adalia bipunctata*^{82,83} and possibly for milkweed beetle⁸⁴. The rare male effect has been shown for sex-linked colour mutants of the guppy fish *Poecilia reticulata*^{85,86}. The rare male effect has been proved to be a natural outcome of the some type of behavioural polymorphism in field crickets⁸⁷ and sunfishes⁸⁸. There are some additional examples of rare type mating advantage which are still not very clear and require further investigation in butterflies^{89,90}, moth⁹¹, geese¹⁶, sheep⁹² and even humans⁹³. The possibility of negative frequency-dependent sexual selection has been suggested in monogamous species, e.g. the Arctic skua^{94,95}.

Eanes *et al.*⁸⁴ studied frequency-dependent mating success in natural populations while analysing enzyme polymorphism in the milkweed beetle. They found evidence for rare male effect in three out of the twelve cases analysed and these authors also discussed some of the difficulties in studying frequency-dependent mating success in populations. Although Muggleton⁸² found rare male effect for different morphs of the ladybird in a natural population, Brakefield⁹⁶ was not able to repeat Muggleton's results. The negative frequency dependence of male mating success has been found for some sunfishes and field crickets^{87,97,98}. The nature of the rare male mating advantage may depend on the mode of reproduction. Male mating success was determined by the number of siring of the brood in the guppy fish^{85,86}. Bryant *et al.*⁹⁹ tested rare male mating advantage in housefly *Musca domestica*. They found rare male effect and suggested that it might be an artifact due to bias as a result of alternate marking (wing clipping) or fluctuations in mean sexual vigour caused by sampling errors.

Mechanisms underlying rare male effect

The rare male mating advantage may be of two types: (i) one-sided rare male mating advantage, and (ii) two-sided rare male mating advantage. Frequency dependence of male mating success is easily observable when the two types of males competing for females differ greatly in their mating behaviour. It is because of the difference in the effects of their mating behaviour on mating success under varying frequency. A number of mechanisms have been suggested to account for rare

male mating advantage for the cases in which one type of male has a greater mating success than the other. According to DeBenedictis¹⁰⁰, a one-sided minority mating advantage will result when the females exercise preference for one type of male over another type at ratios constant over frequencies, while males do not discriminate. If one type of male is sexually more active than the other, a one-sided rare male mating advantage in favour of the more vigorous type can be explained on the basis of male-male competition⁹⁹. Kence and Bryant¹⁰¹ found one-sided rare male mating advantage when one type of male is more vigorous than the other. It is likely that one male can take advantage from courtship stimulations of the other male when both males court the same female simultaneously. The vestigial mutant of *D. melanogaster* provides an example of this type of interaction. The mutant male shows a greatly impaired courtship behaviour and consequently much reduced mating success. The mutant male can be as successful as the wild type male, if the wild type male is present to warm up the female to the advantage of male¹⁰². In *D. melanogaster*, wild type males when present together with white-eyed mutants also show an example of one-sided rare male mating advantage. The mutant male does not circle around the female while courting and remains mainly at the rear side and hardly moves around. Therefore, competition for space around the female for the wild type males will be mainly intragenotypic rather than intergenotypic producing a one-sided rare male mating advantage in favour of the wild type males⁷².

Ehrman¹⁶ provided some examples of differential male mating success in which wild type males were more vigorous than mutant males. When regression analysis of these experiments was done, it indicated a two-sided rare male effect. This case could be explained as a one-sided rare male effect when the model of Bryant *et al.*⁹⁹ is applied. A two-sided rare male mating advantage has been found very often between strains not showing much difference in mating behaviour. Ehrman¹⁰³ tried to show how a *Drosophila* female knows which types of males are rare. The females do not have to carry out the difficult task of discriminating between rare and common males and constant mating preferences are sufficient to explain the observed frequency dependence¹⁰⁴. Ehrman¹⁶ found that in some of her experiments rare male effect disappeared when rare males in the mating chamber were the common males in an adjacent chamber from which air was passed into the mating chamber. This observation led to the interpretation that olfactory stimuli from the adjacent chamber in which males were common prevented the discrimination of rare males in the mating chamber. However, there was inconsistency and ambiguity in the results of some of these experiments. The possible behavioural mechanisms which might give rise to such mating preferences were discussed by O'Donald¹⁰⁴. Variation in mating threshold of females

was suggested to be the main cause for such mating preferences. The females with low mating threshold would mate more readily with preferred males and also more readily than the females which mate randomly. The general level of stimulation of females is enhanced due to the presence of other courting males and thus females are stimulated to mate more readily. There will be decrease in the proportion of preferential matings with increasing density. According to O'Donald¹⁰⁴, the mating preference would be density-dependent but not frequency-dependent. Magalhaes and Rodrigues-Pereira⁴³ analysed frequency-dependent mating success of wild type and ebony strains of *D. melanogaster*. Frequency-dependent effect was found in both cases but with a positive correlation for the ebony strain and negative correlation for the wild type. The wild type males are more active than mutant males. The competition should be lower when the frequency of wild type genotype is also lower. In that situation mating success is higher for both types of males. When the more active type increases in frequency, the competition is strong resulting in reduction of mating success of both types of males.

Since females of *Drosophila* have this discriminating ability, it was proposed that females choose the males in a frequency-dependent manner favouring the rare type of males in mating^{16,18}. The way in which rare male experiments are conducted cannot distinguish between the two possibilities: (a) the females prefer to mate the rare type of male, (b) the rare type of male compensates for its rarity by becoming more sexually active. Ehrman and Spiess¹⁸ proposed the sampling and habituation hypothesis to account for rare male mating advantage. According to this hypothesis, the nature of cue is different for different male types. The females become conditioned against mating with the males that first court them during their unreceptive period after eclosion. Since these males would usually be the more frequent type, the rare male type would gain mating advantage when the females become sexually active as they are able to break through the habituation by its slightly different cues. The sampling and habituation hypothesis has been supported by the work of Averhoff and Richardson^{105,106} who studied the role of pheromones in mating behaviour of *D. melanogaster*. They found an increase in heterogamic matings due to inbreeding of few generations. Further, intrastain courtship and mating was hampered as a result of inbreeding. The sexual behaviour of males of an inbred line could be stimulated by the presence of females of another inbred line. The males vigorously courted females of another line. Thus genetic variation existed for pheromones while subsequent inbreeding caused genetic uniformity among flies with respect to these pheromones. Genetically similar males and females do not sexually excite each other probably because of habituation to their own phero-

mones^{105,106}. However, polymorphism with respect to pheromones in *D. melanogaster* was found for males but not for females making habituation as proposed by Averhoff and Richardson¹⁰⁵ less probable¹⁰⁷. The suggestion that a novel odour can break habituation to the ordinary odour is in agreement with the sampling and habituation hypothesis¹⁸. Smith¹⁰⁸ presented evidence for novel odour which can break the habituation in *Lasioglossum zephyrum* (the guard bee). What mediates this frequency-dependent behaviour? Evidence has been presented for the influence of an air-borne factor of olfactory nature^{18,104,109,110}. However, the vibrational cue may also play a role in rare male mating advantage¹¹¹.

The actual cause of rare male mating advantage is not yet fully understood. There is no single mechanism responsible for it. Probably a combination of specific mechanisms is responsible, and the set of mechanisms operating in one species may be different from those in other species. If the rare male mating advantage is true, the most probable explanation is that females are able to recognize that two types of males are present and change their receptivity in favour of rare males^{17,18}. Ehrman, Petit and others have carried out a series of experiments to know the sensory basis of this recognition^{18,44,57,58,64,66,68,104,112}. Ehrman¹¹³ also concluded that sexual isolation among strains of *D. paulistorum* adversely affects minority mating advantage. Thus two different pheromones, one for sexual isolation and the other for minority recognition, might be required for the olfactory cue basis of the rare male mating advantage. Petit and Nouaud⁴⁴ found the role of auditory signal rather than odour responsible for minority recognition in *D. melanogaster* and they argued that the difference in their results (auditory) and those of *D. pseudoobscura* (pheromonal) could be due to the involvement of two different species. Averhoff and Richardson¹⁰⁵ concluded that pheromones were responsible for genotypic recognition in their experiments with *D. melanogaster* and Dal Molin²⁸ found odour (but not pheromones) as the basis of olfactory cue in the rare male mating of *D. melanogaster*. Petit and Nouaud⁴⁴ also concluded that rare male mating advantage occurred through competition for space around the female in conjunction with female conditioning to male signals. On the other hand, Spiess and Kruckeberg⁴⁶ suggested that such conditioning (specially habituation) was not operating in their studies with *D. melanogaster*, but it was observed that females tend to reject males of the first courting type. These discrepancies among experiments, both within and between species demonstrate that if rare male effect exists at all, a number of causative factors may be involved. Anderson and McGuire¹¹⁴ found statistically significant difference in mating success of a given genotype between two laboratory population cages although very careful precautions were taken to keep all the factors equal in both cages. However, they could not

trace the effect but suggested that minor environmental fluctuations between the two cages were responsible for the difference. Because mating success of a given genotype in *Drosophila* is dependent on many factors, it seems difficult to keep all the factors constant in any experiment dealing with mating success^{26,115,116}.

Evolutionary significance of rare male effect

From the viewpoint of population genetics, when a rare type has a higher Darwinian fitness than the common type, selection is balancing and may lead to a protected polymorphism. Initially the rare genotype will increase in frequency if there are no other selective forces operating against it but as soon as the rare type becomes more common, its advantage disappears which may lead to stable equilibrium. Among the different models which have been proposed to explain the high level of genetic variability at single loci in natural populations, the classical heterozygote advantage model (or the over dominance model) has been used often. According to this model, the heterozygote has a higher fitness than the corresponding homozygote. There is occurrence of a genetic load since it has been argued that there is a limit to the degree of genetic variability a population can maintain under this model. Contrary to this, negative frequency dependence or rare male mating advantage may represent a way of maintaining a high level of genetic variability without any genetic load at equilibrium. This could be of considerable evolutionary significance as it plays an important role in the maintenance of high level of genetic polymorphism found in natural populations.

Because the evolutionary implications of this phenomenon are potentially important, the rare male mating advantage has become a subject of special interest since its discovery in *Drosophila*. It seems that a number of gene and chromosomal polymorphisms in *Drosophila* are maintained by such frequency-dependent selections which could be of considerable evolutionary significance since it has been argued that there is a limit to the degree of genetic variability a population can maintain under the classical heterozygote fitness advantage model¹¹⁷. Thus as a result of frequency-dependent selection, a balanced polymorphism can be maintained by sexual selection in the absence of heterosis in the heterozygotes. If this phenomenon is at all widespread in natural populations, it may play a considerable role in maintaining genetic diversity. An interesting outcome of the rare male advantage is that an occasionally visiting male from another population is favoured by the females, thus promoting outbreeding.

Conclusion

The present survey on rare male mating advantage in the genus *Drosophila* shows that it occurs in several species

of *Drosophila*. It has also been shown to occur in certain other insects and a few vertebrate species. Rare male mating advantage has been suggested to be a natural outcome of behavioural polymorphism in field crickets and sunfishes. Apart from *Drosophila*, rare male mating advantage has been documented for other species, though a limited number of species have been subjected to this kind of study. Most of the tests have been performed under laboratory conditions and in a few cases it has been demonstrated to occur in natural populations. If this phenomenon is widespread among organisms, it would be of special evolutionary significance as a mechanism for maintaining genetic polymorphism in natural populations without genetic load at equilibrium, and also for promoting the exchange of genes among different populations.

Since its discovery in *Drosophila*, rare male mating advantage has become a subject of special interest. Because evolutionary implications of this phenomenon are potentially important, explanations regarding the mechanism underlying the rare male effect have been sought. There have been several attempts to account for the rare male mating advantage as an artifact of the experimental approach. Because mating success of a given genotype in *Drosophila* is dependent on many factors, it seems difficult to keep all the factors constant in any experiment dealing with mating success. Only a few studies on rare type mating advantage in nature have been carried out, but some positive evidence has been obtained. Thus rare male mating advantage is not an artifact of experimental approach. According to the sampling and habituation hypothesis of Ehrman and Spiess, the nature of the cue is different for different male types. The females become conditioned against mating with the males that first court them during their unreceptive period. As these males are of the more common type, the rare males are successful in mating as they are able to break through the habituation when the females become sexually active. Rare male mating advantage can also occur when the two types of males differ greatly in mating behaviour, one male type being more vigorous than the other. It is also possible that one male type can take advantage of the courtship stimulation of another male type when both forms are courting the same females. It has also been demonstrated that compensation as well as simulation of the rare male effect is possible with the male odour as a causative agent and thus olfactory cues are important. Experiments have shown that rare male mating advantage is influenced by age of the females and previous mating experience. Earlier studies employed the direct observation method to determine the mating preference between flies confined to a small space. It was first shown by Ehrman that this phenomenon can occur in a large room so that it is probably not an artifact due to the small mating chambers. The cause of rare male effect is not yet resolved

fully and indeed it is likely that there is no single mechanism responsible for it. Probably a combination of specific mechanisms is involved and there may be interspecies differences with respect to the sets of mechanisms underlying the rare male effect. More sophisticated experiments are needed to understand the mechanism of rare male effect.

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ACKNOWLEDGEMENTS. Financial support from CSIR, New Delhi in the form of Research Associateship to S.S. is gratefully acknowledged. We also thank the anonymous reviewer for helpful comments on the manuscript.

Received 17 September 1999; revised accepted 30 October 1999