

**IS A LITTLE BIT OF SEX AS GOOD AS A LOT?**

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**TR 93-1**

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keywords: segregation, recombination, facultative sexuality,  
Rivulus marmoratus, selfing hermaphrodite

running head: A LITTLE BIT OF SEX

Abstract.--Few of the costs and benefits that have been suggested for sex can be measured quantitatively. One cost which can be measured is the cost of producing males (or the "50% loss due to meiosis"). Some animals avoid much of this cost by reproducing asexually most of the time, but occasionally reproducing sexually. Others avoid the cost through regular self-fertilization, occasionally interrupted by outcrossing. Models show that these savings may be had with little loss in benefits. In particular, for some models which show that evolution is faster with sexual than with asexual reproduction, the rate of evolution is nearly as fast when only a fraction of reproduction is sexual and the rest is asexual. We describe two such models in detail. One is the segregation model of Kirkpatrick and Jenkins (1989a), which was modified to apply to facultative sexuality by Hedrick and Whittam (1989). The other is the recombination model of Eshel and Feldman (1970), which we modify to apply to facultative sexuality. We give some examples that illustrate a variety of ways in which animals may reduce the effort devoted to producing males, or to sexual reproduction. While some examples are clear and well known, others are less clear and deserve further study.

The costs and benefits of sexual reproduction are old problems in evolutionary biology (Ghiselin 1974; Williams 1975; Maynard Smith 1978; Bell 1982; Michod and Levin 1988). These problems are still of great interest, largely because of the suggestion that sexual organisms experience a cost of producing males that asexual organisms do not (Maynard Smith 1971, 1978; Williams 1975). If a sexual organism could effectively double its reproductive output by being asexual, then any argument in favor of sex would have to demonstrate a two-fold advantage in each generation. Some sexual species, including many fish and birds, do not pay a two-fold cost of producing males because males help in raising the young. There are a number of other costs of sex, including the difficulty of finding mates and the fact that sexual reproduction may take much longer than asexual reproduction (Bell 1982; Daly and Wilson 1983; Lewis 1987). Some of these costs apply to species that do not have separate sexes.

There are a number of ideas about what the benefits of sex might be (Bell 1982), but most of these are qualitative. One might ask of particular models for the advantage of sexual reproduction whether the advantage holds without diminution if sex is only occasional or is facultative. In some cases the answer is, "yes, almost." Recently, Hastings (1992) has pointed out that Sewall Wright asserted in a paper written in 1939 that frequent asexual reproduction with occasional sexual reproduction would provide the benefits of both (Provine 1986). Thus, the idea that occasional or

facultative sexual reproduction might be advantageous is not new, but attempts to model this advantage quantitatively seem to be quite new.

Several models (Bell 1988; Hedrick and Whittam 1989) suggest that most of the advantage of sexual reproduction may hold even when sex occurs only occasionally. These models assume that sex occurs facultatively, with a certain proportion of the population reproducing sexually in each generation. Facultative sexuality may be very rare, but Kirkpatrick and Jenkins (1989b) found that, at least for one model, the results also hold in the case of cyclic parthenogenesis.

We outline three models which suggest that the benefits of sex may be obtained with little cost if animals reproduce sexually only upon occasion. One of these models, based on Muller's ratchet (Muller 1964, Haigh 1978), has been explained at length (Bell 1988; see also Chao 1992), and we do not repeat the details here. We do provide the details of two other models. (1) One is the segregation model of Kirkpatrick and Jenkins (1989a), which was modified by Hedrick and Whittam (1989) to consider the effect of facultative sexuality. Hedrick and Whittam did not discuss their model in detail, and our calculations cast some doubt on the generality of their conclusions. (2) The recombination model of Eshel and Feldman (1970) was devised to compare the relative advantages of sexual and asexual reproduction. Eshel and Feldman

did not consider the possibility of facultative sexual reproduction, but we will do so here.

We list a number of examples of animals that save much of the cost of sex, and we suggest that a combination of occasional bouts of sexuality with frequent asexual reproduction may explain some anomalous observations on the genetic structure of seemingly clonal species.

MODELS SUGGESTING THAT A LITTLE BIT OF SEX IS ALMOST AS GOOD AS A LOT

#### A model involving segregation

Kirkpatrick and Jenkins (1989a) considered a simple one-locus, two-allele model to compare the rate of incorporation of beneficial homozygotes into populations that are either sexual (have segregation) or asexual (have no segregation). They showed that if the mutation rate is low when considered in terms of the population size and the rate of selection, then sexual reproduction might substantially increase the rate of incorporation of beneficial mutations. They suggested that if enough mutable loci are available, then this advantage of sex might be great enough to overcome the cost.

Hedrick and Whittam (1989) pointed out that the benefit of sex

adduced by Kirkpatrick and Jenkins (1989a) would be relatively undiminished if sex were only facultative. Here we will describe a model that produces results similar to those of Kirkpatrick and Jenkins and of Hedrick and Whittam. Their papers did not give mathematical details. We will give the details here.

Assume that at one locus of a diploid species there are genotypes:  $\underline{AA}$ ,  $\underline{Aa}$ , and  $\underline{aa}$ , having frequencies at time  $t$  equal to  $p_{11}(t)$ ,  $p_{12}(t)$ , and  $p_{22}(t)$ , respectively, and having fitnesses equal to  $W_{11}$ ,  $W_{12}$ , and  $W_{22}$ , respectively. Think of  $\underline{A}$  as the original, wildtype allele, and of  $\underline{a}$  as a beneficial mutant. Assume that the mutation rate from  $\underline{A}$  to  $\underline{a}$  per allele per generation is  $\underline{m}$ , and that the rate of back mutation is negligible. Genotypes, their frequencies, and their fitnesses are given in the following table:

(Put Table 1 here.)

In this model, genotype frequencies are changed in each generation by three processes: (1) mutation, (2) reproduction, with a certain proportion of reproduction being sexual, and (3) selection.

(1) Mutation will change genotype frequencies from  $[p_{11}(t), p_{12}(t), p_{22}(t)]$  to  $[q_{11}(t), q_{12}(t), q_{22}(t)]$  using the following equations (which suppress the dependence on  $t$ ):

$$q_{11} = p_{11} - 2mp_{11} - m^2p_{11}$$

$$q_{12} = p_{12} + 2mp_{11} - mp_{12}$$

$$q_{22} = p_{22} + mp_{12} + m^2p_{11}.$$

(2) We assume that some fixed proportion of the population,  $s$ , (with the same proportion for each genotype), will reproduce sexually by random mating, while the remainder will reproduce asexually. Reproduction will change genotype frequencies from  $[q_{11}(t), q_{12}(t), q_{22}(t)]$  to  $[r_{11}(t), r_{12}(t), r_{22}(t)]$  using the following equations (which suppress the dependence on  $t$ ):

$$r_{11} = (1 - s)q_{11} + s(q_{11}^2 + q_{11}q_{12} + .25q_{12}^2)$$

$$r_{12} = (1 - s)q_{12} + s(2q_{11}q_{22} + q_{11}q_{12} + q_{12}q_{22} + .5q_{12}^2)$$

$$r_{22} = (1 - s)q_{22} + s(.25q_{12}^2 + q_{12}q_{22} + q_{22}^2).$$

(3) Selection will change genotype frequency from  $[r_{11}(t), r_{12}(t), r_{22}(t)]$  to  $[p_{11}(t+1), p_{12}(t+1), p_{22}(t+1)]$  using the following equations:

$$p_{11}(t+1) = W_{11}r_{11}(t)/D$$

$$p_{12}(t+1) = W_{12}r_{12}(t)/D$$

$$p_{22}(t+1) = W_{22}r_{22}(t)/D,$$

where  $D = W_{11}r_{11}(t) + W_{12}r_{12}(t) + W_{22}r_{22}(t)$ .

We have done a number of simulations, plotting the increase in the overall frequency of mutant (a) alleles, given by

$$f(t) = .5p_{12}(t) + p_{22}(t)$$

against time, t, for different sets of parameters. We have followed Kirkpatrick and Jenkins (1989a) in assuming that the fitness of the heterozygote (Aa) is intermediate between that of the homozygotes. In fig. 1, we illustrate two simulations, both of which assume that  $\underline{W}_{11} = .90$ ,  $\underline{W}_{12} = .95$ , and  $\underline{W}_{22} = 1.00$ . In both figures, the populations start with  $\underline{p}_{11} = .999$  and  $\underline{p}_{12} = .001$ . In both fig. 1A and 1B, it is impossible to distinguish the curves for pure sexual reproduction ( $\underline{s} = 1.0$ ) and for facultative sexual reproduction with the proportion of reproduction that is sexual equal to one tenth ( $\underline{s} = 0.1$ ).

(Put fig. 1 about here.)

Curves are drawn for the proportion of reproduction that is sexual ( $\underline{s}$ ) decreasing by powers of ten. Thus, from left to right, we have  $\underline{s} = 0.1, 0.01, 0.001, \dots$ . The simulations differ only in that the mutation rate is  $\underline{m} = 10^{-9}$  in fig. 1A, while  $\underline{m} = 0$  in fig. 1B. In both cases, the effect of a little bit of sex ( $\underline{s} = 0.1$  or  $\underline{s} = 0.01$ , say) is almost the same as a lot ( $\underline{s} = 1$ ). For smaller proportions of sexual reproduction,  $\underline{s}$ , the rate of increase of

mutant alleles will be slowed, but when this proportion decreases far enough, the effect of further decreases diminishes in fig. 1A, while further decreases in  $\underline{s}$  continue to decrease the rate of incorporation of beneficial double mutants in fig. 1B. Fig. 1B closely resembles the figure that Hedrick and Whittam (1989) included in their paper, suggesting to us that they assumed that  $\underline{m} = 0$ . However, setting the mutation rate equal to zero makes it impossible for mutations to accumulate in asexual populations and exaggerates the advantage of sexual over asexual reproduction.

#### A model involving recombination

An old explanation for the advantage of sex is that recombination hastens evolution by bringing together beneficial mutations that occur at different loci in different individuals (Fisher 1930; Muller 1932; Eshel and Feldman 1970; Bell 1982). Eshel and Feldman (1970) used a two-locus haploid model with two alleles at each locus to investigate the relative rates of incorporation of beneficial double mutants for sexual and asexual reproduction. If genotypes  $\underline{AB}$  (wildtype),  $\underline{Ab}$  and  $\underline{aB}$  (single mutants) and  $\underline{ab}$  (double mutant) have fitnesses,  $\underline{W}_{11}$ ,  $\underline{W}_{12}$ ,  $\underline{W}_{21}$  and  $\underline{W}_{22}$ , respectively, with  $\underline{W}_{11} < \underline{W}_{22}$  and  $\underline{W}_{12} = \underline{W}_{21}$ , if all single mutations have the same small rate, and if double mutations are impossible, then we can compare sexual and asexual reproduction by comparing the rates at which a population that begins with only the  $\underline{AB}$  genotype will incorporate beneficial double mutants,  $\underline{ab}$ . The

beneficial double mutants are incorporated faster for asexual reproduction if  $\underline{W}_{11}\underline{W}_{22} > \underline{W}_{12}\underline{W}_{21}$  [the "super-multiplicative" case (Eshel and Feldman 1970)], while sexual reproduction permits faster incorporation if  $\underline{W}_{11}\underline{W}_{22} < \underline{W}_{12}\underline{W}_{21}$  (the sub-multiplicative case). The genotypes, their frequencies, and their fitnesses are given in the following table:

(Put Table 2 here.)

We modify this (Eshel and Feldman 1970) model to consider the possibility of facultative sexuality, in which a certain proportion of reproduction is sexual, while the rest is asexual. For each generation we first consider (1) mutation, then (2) recombination, with a fixed proportion of reproduction being sexual, and then (3) selection.

(1) Assuming that all single mutants (forward and backward) are equally likely, with rate  $\underline{m}$  for individual mutations, and that two mutations within a generation are impossible, we have that the  $\underline{p}$ 's go to  $\underline{q}$ 's under mutation according to the following equations (suppressing the dependence on  $\underline{t}$ ):

$$q_{11} = (1 - 2m)p_{11} + mp_{12} + mp_{21}$$

$$q_{12} = (1 - 2m)p_{12} + mp_{11} + mp_{22}$$

$$q_{21} = (1 - 2m)p_{21} + mp_{11} + mp_{22}$$

$$q_{22} = (1 - 2m)p_{22} + mp_{12} + mp_{21}$$

(2) Assuming that proportion  $s$  of reproduction is sexual, with random mating, and that proportion  $1 - s$  is asexual, then  $q$ 's go to  $r$ 's under reproduction according to the following equations (suppressing the dependence on  $t$ ):

$$r_{11} = (1 - s)q_{11} + s(q_{11}^2 + q_{11}q_{12} + q_{11}q_{21} + .5q_{11}q_{22} + .5q_{12}q_{21})$$

$$r_{12} = (1 - s)q_{12} + s(q_{12}^2 + q_{11}q_{12} + q_{12}q_{22} + .5q_{11}q_{22} + .5q_{12}q_{21})$$

$$r_{21} = (1 - s)q_{21} + s(q_{21}^2 + q_{11}q_{21} + q_{21}q_{22} + .5q_{11}q_{22} + .5q_{12}q_{21})$$

$$r_{22} = (1 - s)q_{22} + s(q_{22}^2 + q_{12}q_{22} + q_{21}q_{22} + .5q_{11}q_{22} + .5q_{12}q_{21}).$$

(3) Finally, under selection, the  $r$ 's at time  $t$  go to the  $p$ 's at time  $t+1$  according to the following equations:

$$p_{11}(t+1) = W_{11}r_{11}(t)/D$$

$$p_{12}(t+1) = W_{12}r_{12}(t)/D$$

$$p_{21}(t+1) = W_{21}r_{21}(t)/D$$

$$p_{22}(t+1) = W_{22}r_{22}(t)/D,$$

where  $D = W_{11}r_{11}(t) + W_{12}r_{12}(t) + W_{21}r_{21}(t) + W_{22}r_{22}(t)$ .

Fig. 2 illustrates the incorporation of beneficial double mutants in populations in which various proportions of reproduction are sexual. In both figures  $W_{11} = 0.90$  and  $W_{22} = 1.00$ . It is seen in fig. 2A (a sub-multiplicative case,  $W_{12} = 0.98$ ) that evolution is faster for sexual reproduction, and the rate of evolution is nearly as fast when some reproduction is sexual as when all

reproduction is sexual. On the other hand, fig. 2B (a super-multiplicative case,  $\bar{W}_{1,2} = 0.91$ ) shows that evolution is slower for sexual reproduction, and that the rate is nearly as slow when some reproduction is sexual as when all reproduction is sexual.

(Put fig. 2 about here.)

Another way to look at the rate of evolution is to plot the time that it takes to incorporate a particular proportion of beneficial double mutants into a population as a function of the proportion of reproduction that is sexual. In Fig. 3 we plot the number of generations until the frequency of double mutants reaches 0.80 against the proportion of reproduction,  $\underline{s}$ , that is sexual for several values for the fitness of the single mutants, assuming that the fitness of wildtypes is 0.90 and the fitness of double mutants is 1.00. In each case the population begins with all wildtypes, and the mutation rate is  $\underline{m} = 10^{-6}$  per allele per generation. It is seen that if more than a small proportion of reproduction is sexual then the time to achieve 80% double mutants is almost the same as when all reproduction is sexual. However, for a very small proportion of sexual reproduction, the time to achieve 80% double mutants may be quite different from the case in which all reproduction is sexual. Whether it is faster to achieve 80% beneficial double mutants with asexual or sexual reproduction depends on the fitnesses of the single mutants.

(Put fig. 3 about here.)

Recombination models for the advantage of sex have been discounted (Bell 1982), largely because attention has been concentrated on the case in which asexual reproduction is favored (the super-multiplicative case). Much less attention has been paid to the case in which sexual reproduction is favored (the sub-multiplicative case). Using Eshel and Feldman's (1970) model, our analysis shows that if sex is good, a little bit of sex is almost as good; while if sex is bad, a little bit of sex is almost as bad.

#### A model involving Muller's ratchet

A model for the disadvantage of asexual reproduction is Muller's ratchet (Muller 1964), which causes the minimum number of deleterious mutants in any individual in an asexual population to tend to increase with time. In any population subject to deleterious mutations, the average number of mutations per individual will tend to reach a balance between the mutation rate and selection. The basic idea is that mutations, most of which are deleterious, occur by chance and, without selection, the average number of deleterious mutations in the population will continue to increase. However, selection will tend to eliminate less fit individuals that have more mutations. If environmental conditions remain unchanged, then eventually an equilibrium will be reached at which the force of mutation would match the force of selection.

A mathematical treatment of the ratchet was given by Haigh (1978), who showed that in an infinitely large asexual population with a large number of loci subject to uniformly deleterious mutations with multiplicative fitnesses, the equilibrium distribution of the number of mutations will be Poisson with a mean equal to  $\underline{m}N/\underline{r}$ , where  $\underline{m}$  is the per locus mutation rate,  $N$  is the number of mutable loci, and  $\underline{r}$  is the selection coefficient for each mutation. For a finite population, there is a chance that there will be no individuals without mutations, and selection can only operate on individuals with at least one mutation. Assuming that the probability of a back mutation is low, then after the no-mutation class has disappeared, the fittest class will consist of individuals with one mutation. The average number of mutations per individual will increase to a new equilibrium and remain until, by chance, that one-mutation class will disappear, and the fittest class will consist of individuals with two mutations. This process will continue, with the number of mutants in the fittest class increasing in time.

The ratchet can be overcome by sex if population size is moderate (Bell 1988), because sex produces individuals with no mutations to make up the fittest class. Bell raised the question of how much sex (that is, what rate of recombination) is necessary to overcome the ratchet, and showed with a rough calculation that, for quite large populations, the ratchet could be overcome with a very low recombination rate. This is interesting because Bell was

concerned with ciliates, which have quite large populations and reproduce sexually only upon occasion (Nanney 1980).

#### EXAMPLES OF ANIMALS WITH SMALL AMOUNTS OF SEXUAL REPRODUCTION

##### Cyclic or facultative parthenogenesis

Obligately parthenogenetic reproduction is quite widely distributed among metazoa. There are even species of unisexual vertebrates (Dawley and Bogart 1989). These species arise from hybridization between sexual species. While recent evidence suggests that some of these hybrid species are very old (Hedges et al. 1992), they remain closely connected to their sexual parent species. In fact, there is the suggestion (Hedges et al. 1992) that there may be "leakage" of paternal genes into gynogenetic salamanders, which means that they may have some outcrossing. Despite the wide taxonomic distribution of parthenogenetic or unisexual species, their numbers are not large (Hebert 1987a). This suggests that obligate parthenogenesis arises quite frequently, but is not particularly successful evolutionarily.

On the other hand, cyclic parthenogenesis is found in only a few taxa, but these contain many species [about 15000 (Hebert 1987a)]. That is, cyclic parthenogenesis may arise infrequently, but when it does it is very successful. In cyclic parthenogens, there is a regular alternation of sexual and asexual reproduction,

with sexual reproduction often signalled by seasonal changes. Other animals, including free-living protozoa (Nanney 1980), regularly reproduce asexually, but occasionally reproduce sexually, generally in response to some environmental signal.

There also seems to be increasing evidence of some sexual reproduction among parasitic protozoa (Tibayrenc et al. 1991b; Hurst et al. 1992). Parasitic protozoa are important disease agents, and the issue of their sexual reproduction has been approached from two opposite points of view. Tibayrenc et al. (1990, 1991a,b) start from the assumption, based on laboratory observations, that parasitic protozoa are sexual, or are at least capable of sexual reproduction, and they try to show that parasitic protozoa have a clonal population structure by showing that gene frequencies are not in Hardy-Weinberg equilibrium. Hurst et al. (1992), on the other hand, start with the assumption that parasitic protozoa are fundamentally asexual, and then they try to show that parasitic protozoa sometimes reproduce sexually (that is, they have "covert sex") by giving evidence that populations are sometimes in Hardy-Weinberg equilibrium.

The occurrence of asexual reproduction in parasitic protozoa seems to be established (Tibayrenc et al. 1990, 1991a,b), but the question remains whether some recombination occurs, at least occasionally, in all parasitic protozoa, as might be expected on theoretical grounds (Hurst et al. 1992). If recombination is

universal in parasitic protozoa, its frequency and the circumstances of its occurrence remain to be determined in many cases.

### Selfing and sex

There are some species of animals that consist largely of hermaphrodites that seem to reproduce by selfing. We are particularly interested in the killifish, Rivulus marmoratus, a small fish [generally < 50 mm total length (Huebner et al. 1985)] that lives in mangrove swamps around the Caribbean, often in the burrows of land crabs (Taylor 1989). The fish can live under very harsh conditions, tolerating high levels of salt, high temperatures and low levels of oxygen. They can escape the worst conditions by leaving the water and moving overland, and they can survive out of water for some time if they are able to stay wet. Fish often find themselves isolated from others. Under that circumstance, asexual reproduction would certainly be convenient.

R. marmoratus populations consist largely of hermaphrodites (Harrington 1961), but males are sometimes found [about 1% in Florida, but from 10-25% in Belize (Davis et al. 1990)]. The reproductive role of R. marmoratus males is not clear. Hermaphrodites apparently fertilize eggs internally, and males lack an intromittant organ. Hermaphrodites do sometimes lay unfertilized eggs, and these eggs may be fertilized by males, as

has been demonstrated once in the laboratory (Harrington and Kallman 1968). Males have been observed attempting to mate in the field (Kristensen 1970), but a recent laboratory experiment has shed doubt on this observation (Turner et al. 1992).

These fish are interesting ecologically, and they are easy to keep in the laboratory. Further work should show whether they are a species that reproduces primarily by selfing but that has occasional bouts of sexual reproduction.

The tadpole shrimp, Lepidurus arcticus, seems to be another example of a selfing hermaphrodite (Beaton and Hebert 1988). Populations consist largely of hermaphrodites, with a small proportion of males (3%). Genetic studies suggest a clonal population structure, and as in the case of R. marmoratus, the role of males in reproduction is not clear.

A genus related to the tadpole shrimp are the brine shrimp, Artemia, some populations of which reproduce sexually, others asexually. Parthenogenetic populations occasionally produce males, but again, the role of these males in reproduction is not clear (Browne 1992).

The soil nematode, Caenorhabditis elegans, which has become an important animal for genetical research, is generally a selfing hermaphrodite, but populations include a few males (Hodgkin and

Barnes 1991, discussed by Godfray and Harvey 1991). The fertility of hermaphrodites is greatly limited by the necessity of producing sperm, and a hermaphrodite can increase its fertility two- or three-fold by mating with a male. This advantage of mating raises the question of why so few males are produced (Partridge and Harvey 1992, commenting on van Voorhies 1992). We do not propose an answer to this question, but we suggest that the key to understanding lies in the natural history of the animals.

#### CAN OCCASIONAL SEX EXPLAIN THE GENETIC DIVERSITY FOUND IN CLONAL SPECIES?

Allozyme studies of natural populations of Rivulus marmoratus suggest a clonal population structure (Vrijenhoek 1985). However, there is some variability among clones, and recent work using DNA fingerprinting has shown extreme clonal diversity (Turner et al. 1991). Turner et al. (1991) have asserted that this variability ultimately must be due to mutations. We suggest that this variability may be due to occasional outcrossing between clones.

Widespread clonal diversity is observed among obligately parthogenetic cladocera (Hebert 1987b), but this diversity may be explained by the involuntary recruitment of novel genotypes from related cyclic parthenogens. The obligate parthenogens may produce males as well as females. If the males mate with females from a sexual species, then half of the offspring become obligate

parthenogens, but with genes contributed by both parents (Innes and Hebert 1986; Hebert 1987b).

Parasitic protozoa also have a clonal population structure (Tibayrenc et al. 1991b), with a variety of wide-spread clones. The variability among clones is of practical importance, since defences against one clone might be ineffective against another (Tibayrenc et al. 1991b). While sex has been suggested as a mechanism that hosts might use to provide variability necessary to combat parasites (Hamilton et al. 1990), it is possible that sex is also a mechanism that helps provide parasites with the variability that makes it difficult for their hosts to combat them.

## CONCLUSION

The benefits of sex may be obtained almost without diminution when the costs of sex are reduced because sex occurs only every few generations, or with small probability in each generation. Sexual reproduction occurs only occasionally in cyclic parthenogens, and facultative sexuality may occur in many cases in which sex is difficult to observe ["covert sex" (Hurst et al. 1992)], as has been suggested for parasitic protozoa (Tibayrenc et al. 1991b), and as we suggest for Rivulus marmoratus.

Several questions remain to be answered:

(1) How general is the theoretical principle that a little bit of sex is almost as good as a lot? Other models include one that Hastings (1991; see also 1992) has proposed for germline selection based on under-dominance. In this case it might actually be better to have many mitotic generations between meiotic ones. That is, some beneficial changes might be possible that would be impossible with either pure sexual or pure asexual reproduction.

(2) How generally does sexual reproduction occur occasionally or facultatively? Kirkpatrick and Jenkins (1989b) answered Hedrick and Whittam (1989) by claiming that facultative sexuality is rare. However, they also mentioned that they had showed that Hedrick and Whittam's result held for cyclic parthenogenesis as well as for facultative sexuality.

(3) Are there other cases in which the cost of sex is reduced without the benefits being reduced commensurately? Parasitic wasps often show brother-sister matings which permit the evolution of female-biased sex ratios. That is, inbreeding permits the cost of producing males to be reduced. Are the benefits of sex thereby reduced in proportion to the reduction in cost, or are the benefits maintained without diminution?

(4) How do we obtain information about the existence of sexuality in what seem to be clonal organisms? For example, does clonal diversity provide evidence of outbreeding between clones, or is it evidence of an unusually high mutation rate?

It is an interesting theoretical possibility that organisms

showing occasional or facultative sexual reproduction may obtain most of the advantage of sex without paying much of the cost. With this possibility in mind, biologists may look for and find evidence of sexual reproduction in seemingly clonal organisms.

**ACKNOWLEDGMENTS**

We thank J. Ball, J. Bogart, T. Crease, P. Hebert, D. Lynn, R. McLaughlin, A. Nunez and S. Stewart for reading and commenting on this paper. This paper was written while RFG was on leave from the University of Minnesota-Duluth, visiting the Institute of Ichthyology at the University of Guelph.

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TABLE 1

## NOTATION FOR THE SEGREGATION MODEL

Genotype:	<u>AA</u>	<u>Aa</u>	<u>aa</u>
Frequency:	<u><math>p_{11}(t)</math></u>	<u><math>p_{12}(t)</math></u>	<u><math>p_{22}(t)</math></u>
Fitness:	<u><math>W_{11}</math></u>	<u><math>W_{12}</math></u>	<u><math>W_{22}</math></u>

NOTE.--The mutation rate from wildtype A to mutant a per allele per generation is  $\mu$ , and the probability of back mutations is zero. In each generation, the proportion of reproduction that is sexual is  $s$ .

TABLE 2

## NOTATION FOR THE RECOMBINATION MODEL

Genotype:	<u>AB</u>	<u>Ab</u>	<u>aB</u>	<u>ab</u>
Frequency:	<u><math>p_{11}(t)</math></u>	<u><math>p_{12}(t)</math></u>	<u><math>p_{21}(t)</math></u>	<u><math>p_{22}(t)</math></u>
Fitness:	<u><math>W_{11}</math></u>	<u><math>W_{12}</math></u>	<u><math>W_{21}</math></u>	<u><math>W_{22}</math></u>

NOTE.--The mutation rates from wildtype allele A to mutant a and back equal  $\mu$  per allele per generation. In each generation, the proportion of reproduction that is sexual is  $s$ .

## FIGURE LEGENDS

FIG. 1.--Rate of incorporation of beneficial mutant alleles for a segregation model with facultative sex. The population begins with 99.9% wildtype homozygotes and 0.1% heterozygotes. The fitnesses of wildtype homozygotes, heterozygotes and mutant homozygotes are  $\underline{W}_{11} = 0.90$ ,  $\underline{W}_{12} = .95$  and  $\underline{W}_{22} = 1.00$ , respectively. Viewing the curves from left to right, the proportion of reproduction that is sexual is  $\underline{s} = 10^{-1}$ ,  $10^{-2}$ , ...,  $10^{-6}$ . A, The mutation rate is  $\underline{m} = 10^{-6}$ . The curve for  $\underline{s} = 10^{-1}$  is indistinguishable from pure sexual reproduction,  $\underline{s} = 1$ , while the curve for  $\underline{s} = 10^{-6}$  is indistinguishable from that for pure asexual reproduction. B, The mutation rate is zero. The curve for  $\underline{s} = 10^{-1}$  is indistinguishable from pure sexual reproduction,  $\underline{s} = 1$ , but unlike B, the curve for  $\underline{s} = 10^{-6}$  would be clearly distinguishable from that for pure asexual reproduction. FIG. 1B closely resembles that given by Hedrick and Whittam (1989).

FIG. 2.--Rate of incorporation of beneficial double mutants for a recombination model with facultative sex. The population begins with all wildtype homozygotes. In each case the fitnesses of wildtypes and beneficial double mutants are  $\underline{W}_{11} = 0.90$  and  $\underline{W}_{22} = 1.00$ , respectively, and the fitnesses of single mutants are equal ( $\underline{W}_{12} = \underline{W}_{21}$ ). A, This is a "sub-multiplicative" case ( $\underline{W}_{11}\underline{W}_{22} < \underline{W}_{12}\underline{W}_{21}$ ), with  $\underline{W}_{12} = 0.98$ , and sexual reproduction incorporates beneficial double mutants more rapidly than asexual. From left to right, the

proportion of reproduction that is sexual is  $\underline{s} = 1, 2^{-2}, 2^{-3}, \dots, 2^{-15}$ . The plot for  $\underline{s} = 2^{-1}$  is indistinguishable from the case of pure sexual reproduction. B, This is a "super-multiplicative" case ( $\underline{W}_{11}\underline{W}_{22} > \underline{W}_{12}\underline{W}_{21}$ ), with  $\underline{W}_{12} = 0.91$ , and asexual reproduction is favored over sexual. From left to right, the proportion of reproduction that is sexual if  $\underline{s} = 2^{-8}, 2^{-6}, 2^{-5}, \dots, 2^{-1}, 1$ . The curves for  $\underline{s} = 2^{-7}$  and for  $\underline{s} = 2^{-8}$  are indistinguishable from each other and from the case of pure asexual reproduction.

FIG. 3.--Number of generations until the frequency of beneficial double mutants reaches 80% for the recombination model. The number of generations is plotted against the proportion of reproduction that is sexual,  $\underline{s}$ . In each case the population starts with all wildtypes, the mutation rate is  $\underline{m} = 10^{-6}$ , and the fitnesses are  $0.90 = \underline{W}_{11} < \underline{W}_{12} = \underline{W}_{21} < \underline{W}_{22} = 1.00$ . The curves differ in the fitness of single mutants,  $\underline{W}_{12}$ , which takes values 0.99, 0.97, 0.95, 0.93 and 0.91.

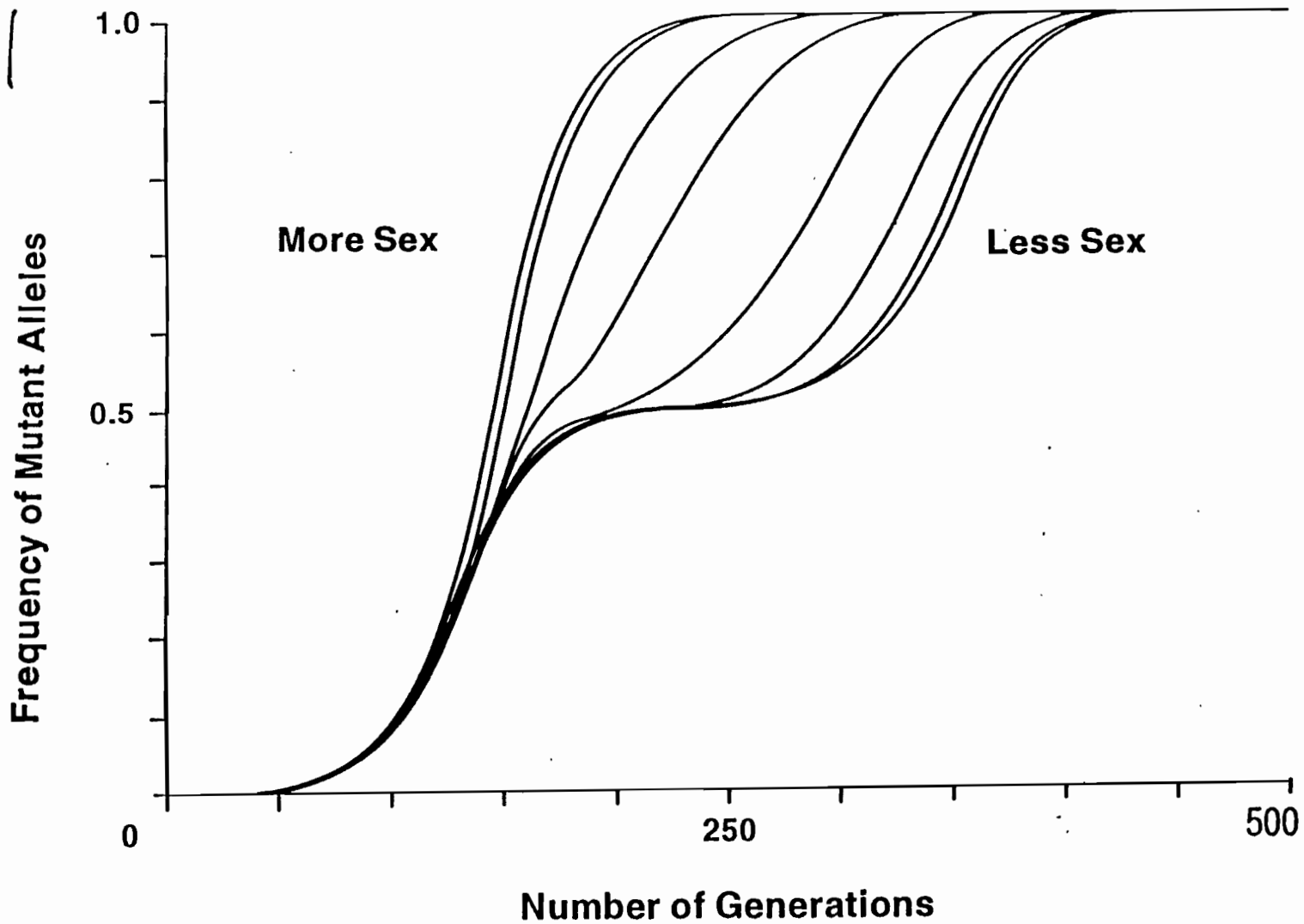
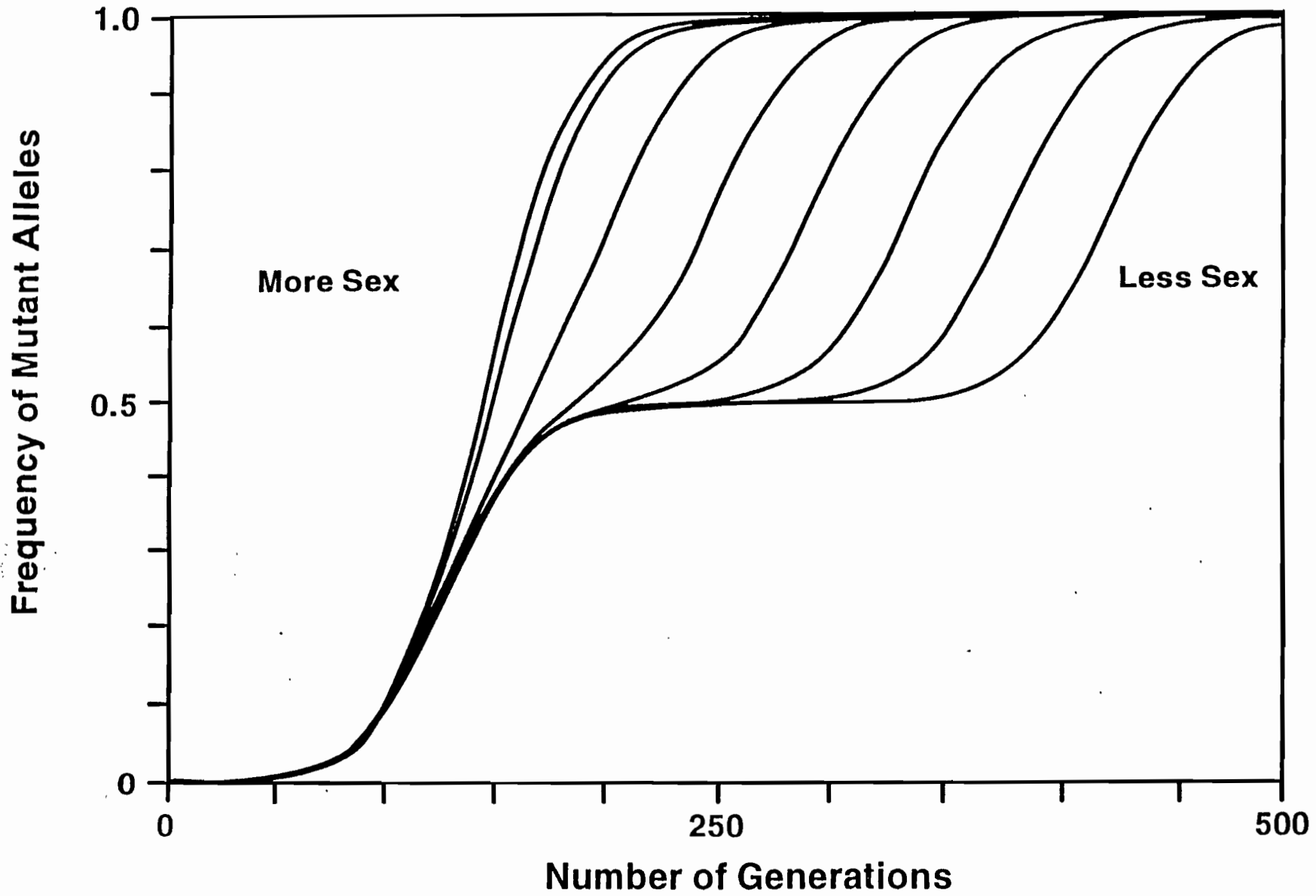


FIG 1.--RATE OF INCORPORATION OF BENEFICIAL MUTANT ALLELES FOR A SEGREGATION MODEL WITH FACULTATIVE SEX.

A. THE MUTATION RATE IS  $\mu = 10^{-6}$ .



B. THE MUTATION RATE IS  $\mu = 0$ .

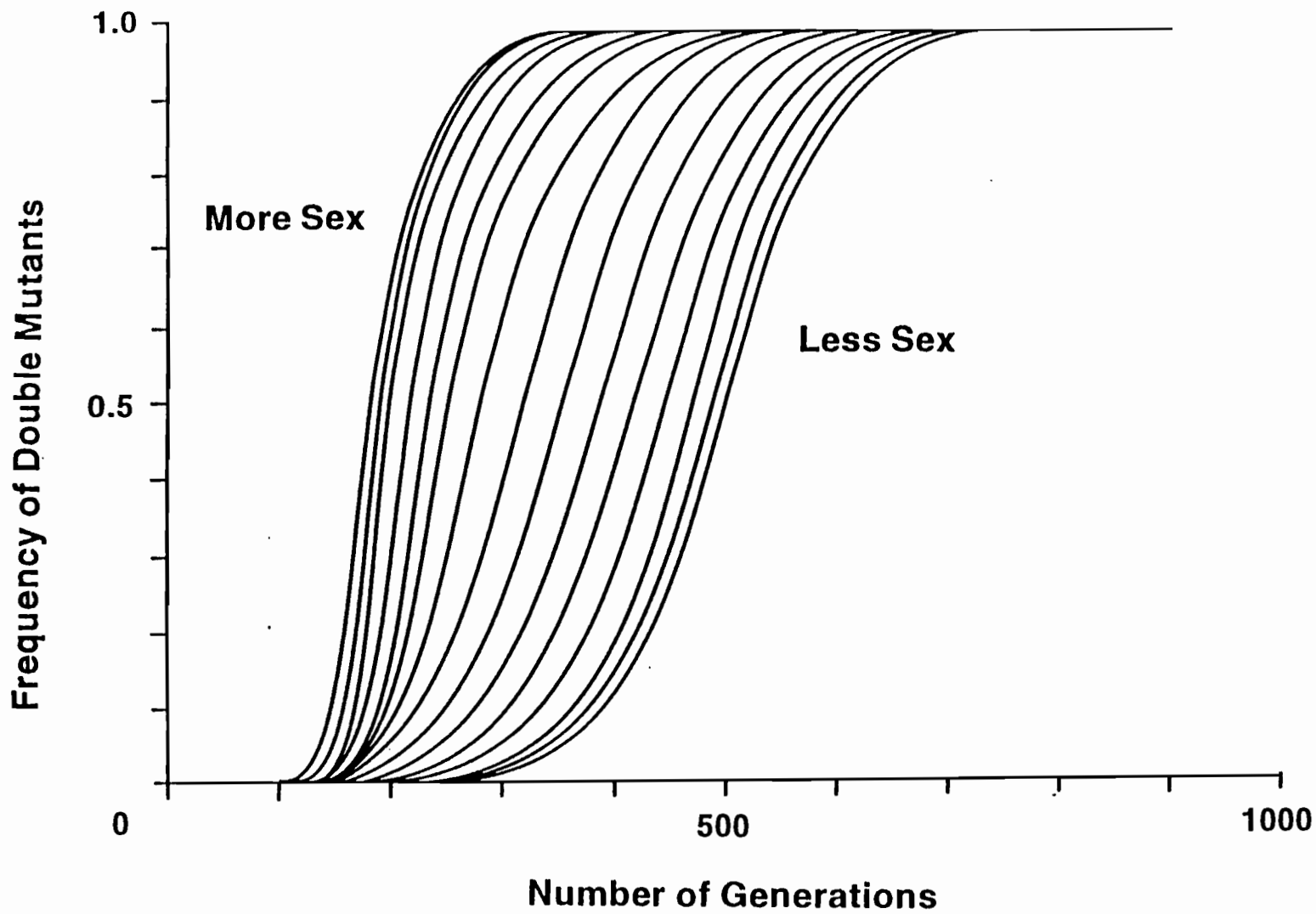
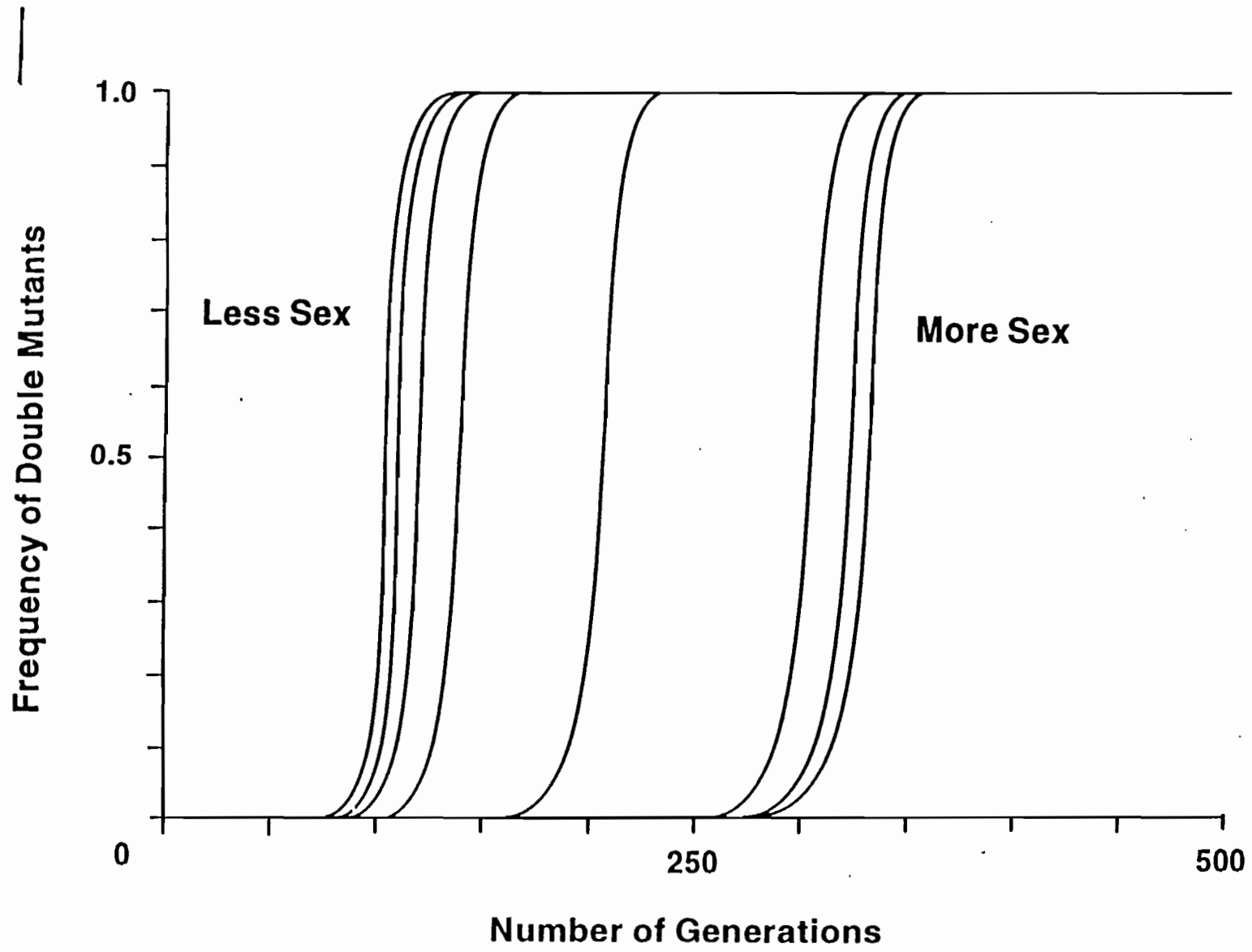


FIG. 2.--RATE OF INCORPORATION OF BENEFICIAL DOUBLE MUTANTS FOR A RECOMBINATION MODEL WITH FACULTATIVE SEX.

A. THE "SUB-MULTIPLICATIVE" CASE



B. THE "SUPER-MULTIPLICATIVE" CASE

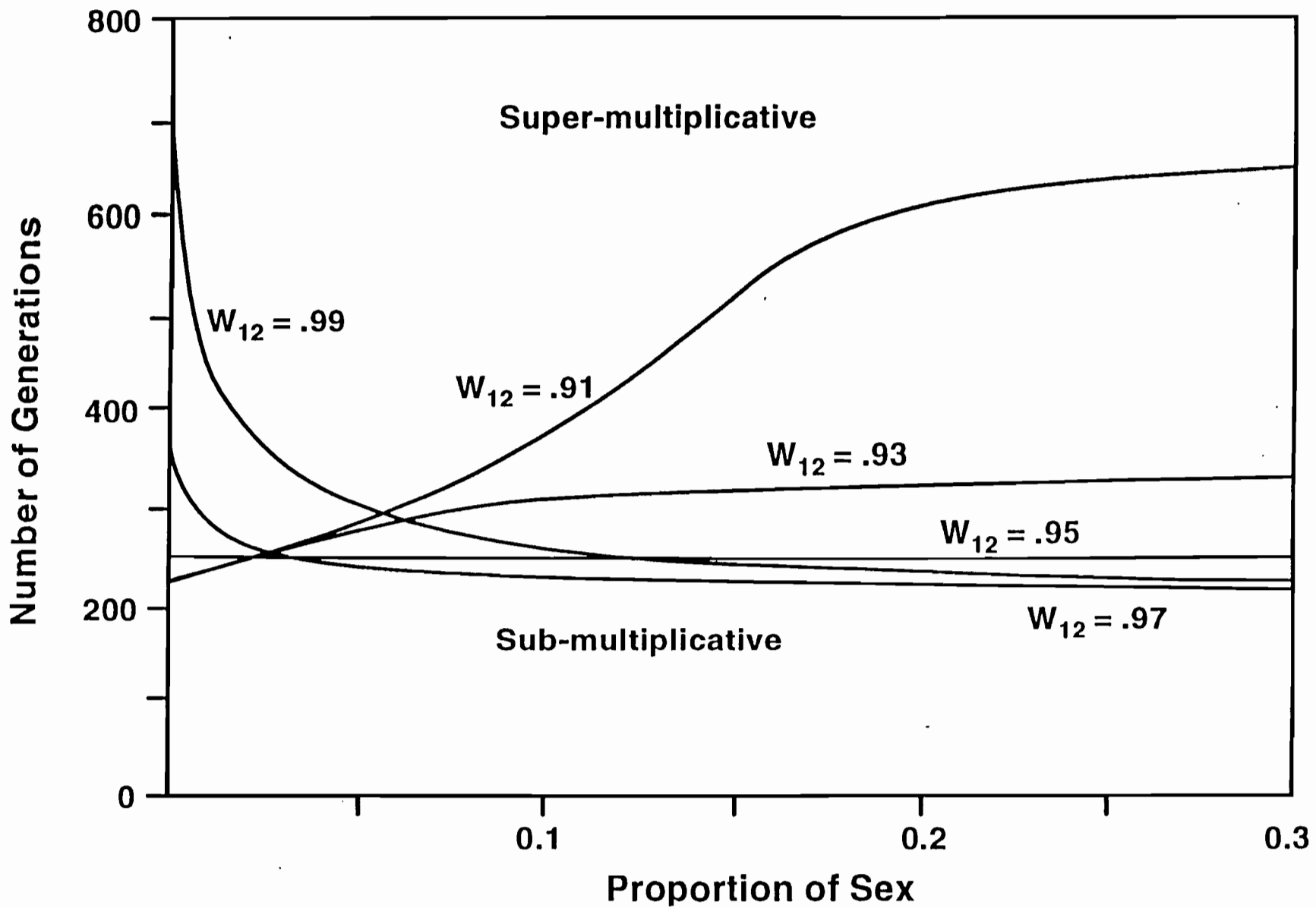


FIG. 3.--NUMBER OF GENERATIONS UNTIL THE FREQUENCY OF BENEFICIAL DOUBLE MUTANTS REACHES 80% FOR THE RECOMBINATION MODEL.

## Segregation model

```

A:NATSEXMU.BAS Line 1      Col 1      Insert Indent Tab
3 screen 12
4 window(0,2)-(1,0)
5 defdbl w,s,p,q,d,r
7 m = .000000001
10 W0 = .9
20 W1 = .95
30 W2 = 1
40 S = 1.0
45 for j=1 to 8
46 s=.1*s
50 PRINT "Proportion of sexual reproduction =";S
60 P0 = .999
65 P1 = .001
70 P2 = 0
71 for i = 1 to 500
72 q2 = p2 + m*p1 + m*m*p0
74 q1 = p1 + 2*m*p0 - m*p1
76 q0 = p0 - 2*m*p0 - m*m*p0
110 r0 = (1 - S)*q0 + S*(q0*q0 + q0*q1 + .25*q1*q1)
120 r1 = (1 - S)*q1 + S*(2*q0*q2 + q0*q1 + q1*q2 + .5*q1*q1)
130 r2 = (1 - S)*q2 + S*(.25*q1*q1 + q1*q2 + q2*q2)
200 D = W0*r0 + W1*r1 + W2*r2
210 P0 = W0*r0/D
220 P1 = W1*r1/D
230 P2 = W2*r2/D
240 R = .5*P1 + P2
250 IF INT(I/2) = I/2 THEN pset(i/500,r),4
300 NEXT I
310 next j
400 end

```

# Recombination model

```

A:HAPSEX.BAS   Line 1   Col 1   Insert Indent Tab
5 screen 12
6 window (0,0)-(1,1)
10 W0 = .9
20 W1 = .98
30 W2 = .98
40 W3 = 1
50 for j=0 to 15
55 s=2^(-j)
60 M = .000001
70 P0 = 1
80 P1 = 0
90 P2 = 0
100 P3 = 0
200 FOR I = 1 TO 1000
210 Q0 = (1 - 2*M)*P0 + M*P1 + M*P2
220 Q1 = (1 - 2*M)*P1 + M*P0 + M*P3
230 Q2 = (1 - 2*M)*P2 + M*P0 + M*P3
240 Q3 = (1 - 2*M)*P3 + M*P1 + M*P2
250 R0 = (1 - S)*Q0 + S*(Q0*Q0 + Q0*Q1 + Q0 *Q2 + .5*Q0*Q3 + .5*Q1*Q2)
260 R1 = (1 - S)*Q1 + S*(Q1*Q1 + Q0*Q1 + Q1*Q3 + .5*Q0*Q3 + .5*Q1*Q2)
270 R2 = (1 - S)*Q2 + S*(Q2*Q2 + Q0*Q2 + Q2*Q3 + .5*Q0*Q3 + .5*Q1*Q2)
280 R3 = (1 - S)*Q3 + S*(Q3*Q3 + Q1*Q3 + Q2*Q3 + .5*Q0*Q3 + .5*Q1*Q2)
300 D = W0*R0 + W1*R1 + W2*R2 + W3*R3
310 P0 = W0*R0/D
320 P1 = W1*R1/D
330 P2 = W2*R2/D
340 P3 = W3*R3/D
400 IF INT(I/2) = I/2 THEN pset(i/1000,P3),12
500 NEXT I
510 next j
520 end

```