AN HYPOTHESIS TO ACCOUNT FOR THE MAINTENANCE
OF SEX WITHIN POPULATIONS

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ABSTRACT: An hypothesis is presented to explain the maintenance of sex on the basis of individual selection. Frequency-dependent selection by the biotic component of the environment produces linkage disequilibrium of varying sign, thus selecting for recombination.
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Two approaches to the problem of the evolutionary significance of sexual reproduction have been taken. The question of whether or not sex facilitates faster evolution was the first considered (Fisher, 1930; Muller, 1932) and has received the most attention. Felsenstein (1974) and Thompson (1976) have presented lucid reviews of the history of ideas on this question. This approach to sex is group-selectionist, as the benefits of sex, if any, accrue only over relatively great spans of time.

The second approach is directed to the question, Why is sex retained within populations? It must be remembered that sexual reproduction entails a two-fold cost of meiosis (Maynard Smith, 1971), a recombinational load for well-adapted genotypes, through homogenization with the gene pool of the population (Lewontin, 1971; Williams, 1975) as well as subsidiary costs, such as production of nectar (Solbrig, 1976). Williams (1975), especially, has championed the view that the adaptive value of sex must be sought at the level of the individual. In support of this, he cites the existence of species in which both sexual and asexual reproduction occur. Maynard Smith (1976) points out that rates of recombination, which is somewhat analogous to sex, are variable and selectable in natural populations.

The models which have been proposed to account for the maintenance of sex and recombination within populations fall into two distinct categories (Felsenstein and Yokoyama, 1976). One set of models (Williams and Mitton, 1973; Williams, 1975; Stroebeck et al., 1976; Felsenstein and Yokoyama, 1976) is based on the effect found by Hill and Robertson (1966), that genetic drift in finite populations produces random linkage disequilibrium. Sex breaks down this linkage disequilibrium, and increases the probability that a favored genotype will be produced.

An alternative explanation was proposed by Maynard Smith (1971) and developed further by Charlesworth (1976). They found that recombination may be favored if temporal variation in the environment produces selection for linkage disequilibrium of varying sign. For example, if genotypes AB and ab are selected in some generations, and Ab and aB in others, recombination may be advantageous. The conditions that maximally favor recombination include high variance in the linkage disequilibrium selected in alternative environments, and temporal variation of the environment of intermediate period, with respect to generation time. Both Maynard Smith and Charlesworth believe that selection of this type is probably rare in natural populations, and therefore that this mechanism for the maintenance of recombination may not be biologically realistic.
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Here I propose a mechanism that provides some biological realism for the models of Maynard Smith and Charlesworth. Most theoretical studies of the adaptive significance of sex (e.g., Levins, 1965; Williams, 1975; Maynard Smith, 1976) assume that selection takes place in the context of an abiotic, unresponsive environment. However, it may often be that the biotic component of the environment - competitors, predators, and, especially, diseases, pests and parasites - exerts greater selection pressure. Most organisms are probably under intense pressure to escape, in one way or another, this biotic component of the environment. Two escape routes are open, in space and in time. Escape in space is the strategy of fugitive species. Sexual reproduction, with attendant genetic change, may allow escape in time.

Levin (1975) has proposed that pest pressure selects for high rates of recombination in plants, which facilitates production of novel genotypes, uniquely adapted to escape present pest pressure. My hypothesis differs from Levin's in that sex and recombination are advantageous not to produce novel genotypes as such, but to produce rare genotypes, of which novel ones are a subset, within a population.

Clarke (1976) has recently reviewed the evidence that frequency-dependent selection by parasites may account for a great deal of genetic polymorphism in natural populations. In his view, parasites or diseases hit hardest those genotypes that are most common within a population. Fitness of a genotype is thus negatively correlated with its frequency or abundance, and this brings about stable genetic polymorphisms. I believe that precisely the same mechanism, frequency-dependent selection, makes sexual reproduction advantageous, possibly enough so to overcome the two-fold cost of meiosis.

Consider an asexual prey species with two variable loci. It consists of four genotypes, $\underline{AB}$, $\underline{Ab}$, $\underline{aB}$, and $\underline{ab}$, each of which is attacked by a specific enemy (predator, parasite, etc.). With frequency-dependent selection by enemies, common genotypes are at a selective disadvantage. Under a wide variety of conditions, each asexual genotype and its enemy will undergo numerical fluctuations in a stable limit cycle (May, 1973). These numerical fluctuations of individuals of prey genotypes can be transformed to fluctuations in the frequencies of different genotypes within the prey species. Fitness of a genotype may be defined as the antilog of the slope of frequency as a function of time. The sum of these frequencies is unity; therefore these fluctuations of frequencies are necessarily out of phase. Because the biology (intrinsic rate of increase, migration rate, etc.) is likely to vary among the different enemy species, the periods of the prey-predator cycles are also likely to vary among genotypes. The conditions that the prey-predator cycles be out of phase and of unequal periods ensure that various pairs or sets of genotypes are selected in different generations. Thus the selected, optimum sign and magnitude of the linkage disequilibrium varies temporally, and recombination is favored.

The enemies must perceive or react to the different genotypes as distinct entities. For instance, consider an herbivorous insect with two variable loci, one determining which of two host plants is selected for oviposition by the female, and one governing whether the larvae feed in the sun or in the shade. Parasites may perceive this insect as four distinct species, and specialize on them as such. Although the loci may have intrinsically multiplicative fitnesses, the response of the parasites imposes independent stable limit cycles and variable linkage disequilibrium, as discussed above. Sex and recombination will be favored in this insect.

In natural populations, a given species is probably confronted with many species of enemies that vary in their intrinsic rates of increase, migration rates, virulence, foraging tactics, etc. The prey species, or any genotype of

it, can be attacked, through both genetic and numerical response of an enemy, from any one of many directions. The dynamical behavior of such multi-species systems and its effect on linkage disequilibria among various loci in the prey species must be terribly complex. It is my guess that sex and recombination reduce the effect of the currently most potent enemies.

Finally, it is worth considering briefly those situations in which sexuality is not favored by the mechanism proposed here. Keep in mind that asexual reproduction avoids the two-fold cost of meiosis, preserves adaptive combinations of genes, and obviates investment in structures and energy used in sexual reproduction.

1. In areas at the periphery of a species' range, or in climatically variable environments (e.g. the temperate zone), pest populations may not be able to survive continuously. Because they cannot genetically or numerically track the target species, selection for sex is reduced in these populations.

2. Populations that colonize a new area, such as a continent or an island, have escaped in space from pest pressure. In this case, frequency-dependent selection for sex vanishes. However, this escape in space is probably only temporary, as the original pests may eventually colonize the area, or the native biota may adapt to the colonist (cf. taxon cycle, Ricklefs and Cox 1972). If such a species does abandon sexual reproduction, it may ultimately be devastated when pest pressure resumes.

3. For fugitive species or weeds, asexual reproduction may be a permanently suitable strategy. Populations of such species are generally short-lived and scattered unpredictably in space. Pests, if there are any at all, may exterminate local populations. But rapid extinction is the fate of such populations in any case, and the selection pressure exerted by pests may be insufficient to overcome the benefits of asexuality.

4. Hybrids between species are a quantum jump in genotype space from their closest relatives. This may release them from biotic selection for long stretches of time. However, a pest species itself may somehow make a jump in adaptation, thereby resuming selection for sexuality. If the hybrid is asexual, it may be in deep trouble. I would expect hybrids, and asexual species in general, to be affected by a relatively small variety of diseases, parasites, pests, etc., one or more of which may be very abundant.

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