All of the 20 or so published efforts to explain the evolutionary origin and maintenance of sexual reproduction (see bibliography) appear to be either incomplete or wrong. The following is just an effort to say a few useful things. It's incomplete too, but I hope it isn't wrong.

That sexual reproduction sometimes has short-term advantages to individuals is demonstrated by the existence of populations (e.g., of aphids) that continue to reproduce asexually for one or more generations then return for one or a few generations to sexuality (Williams and Mitton, 1973). One needs only to assume that such species occasionally produce individuals that fail to return to sexual reproduction or begin an increase in the proportion of asexual generations. Although these possibilities may not actually have been demonstrated in a species of this kind, both seem virtually certain to occur now and then. White (1964), for instance, remarks that nearly every insect species studied carefully now and then reproduces parthenogenetically.

Only species evidently capable of continuing asexual reproduction are relevant to the above argument, which is the reason for restricting the example to species that reproduce alternately asexually and sexually, each for one or more generations. Some species may have been sexual so long, or in such a fashion, that it would be difficult to return to asexuality. Monozygotic twins (e.g., in humans) or quadruplets (e.g., North American armadillos) and other instances of polyembryony (e.g., many larvae are produced from a single egg in numerous insect parasites living in large hosts) are cases of asexual reproduction not all of which could be continued indefinitely.

Conjugating ciliates recombine their genotypes and continue as individuals, presumably modifying their phenotypes and dividing later asexually. But most sexual organisms, like ourselves, use their phenotypes to produce gametes, which are themselves products of a meiotic recombination during gametogenesis, and to place those gametes into a genotype that is additionally novel because the other half of it comes from another organism. Thus, short-term advantages of sexual recombination to individuals are usually represented by effects on their descendants. I suggest that the usual advantage of sexual recombination may be usefully described as the value to parents of placing their gametes into better genetic environments. Since the nature of the superior genetic environment may be partly or completely unpredictable to the sexual parent (because the ecological environment is unpredictable), we may expect the parent to evolve to produce a greater or lesser superfluity of genetically diverse offspring as a result of a history in which some of the offspring so produced have failed, compared to asexual genotypes, while others have proved superior. The unpredictability of winning combinations and the relative success of the collections of winning combinations that represent entire progenies of individual parents (sets of parents), compared to the success of broods produced by asexual genotypes, are the factors determining whether or not sexual recombination will be maintained. Sexual reproduction has been described as the better method of <u>producing</u> a superior genotype, asexual reproduction as the better method of <u>maintaining</u> a superior genotype.

As I noted in lecture, the advantages of parthenogenesis over sexuality are threefold: (1) truer reproduction (maintenance of a superior genotype); (2) doubled reproductive rate (every offspring has babies); and (3) no expenditure of energy, or risk-taking, in locating a mate and mating. These are the advantages that recombination must overcompensate when sexuality prevails in a species that occasionally produces parthenogenetic individuals (there is another issue, termed the "cost of meiosis," discussed under group selection below).

<u>An Aside:</u> I hope you recognize that diploidy, the evolution of dominance and recessiveness, heterosis, and linkage are all intricated with the evolution and maintenance of sexuality. Additionally, I believe that the significance of genetic variability in sexual populations will be understood somehow as a part of the clarification of the functions of sexual reproduction. Maynard Smith (<u>In</u> Williams, 1971) refers to the importance of sexuality as a combiner of parts of genotypes, each genotype adapted to a different environment, the combination leading to genotypes superior in other (new) environments. How many different environments are there to be considered when one is attempting to answer the question: How much genetic variability can selection explain? I suggest that the answer may be derived by

multiplying the number of individuals in a population times the number of loci per individual times the average number of alleles per locus. For acknowledging that environments, in selective terms, include ecological, physiological, and genetic aspects (Williams, 1966) means acknowledging that every copy of every allele may be in a unique environment. If this idea catches your fancy you might like to consider for what purposes it is legitimate to average the effects of those environments, as the calculations of population genetics necessarily do, and for what purposes it is not legitimate (Is it legitimate, for example, when one is trying to see how much genetic variation can be explained by selection alone?). This is part of what was implied by my statement in the Melbourne paper that ". . . heredity cannot be totally eliminated as a variable in any given circumstance by considering only one or a few loci." (p. 108). For anyone who wishes to pursue this set of problems I can loan a rough draft of a brief manuscript.

The central importance of sexuality and sex ratio selection in understanding the evolution of behavior, and the relationship of these phenomena to the above issues, seem to me the basis for a legitimate argument that if one wishes to become a behaviorist he should not only study the physiological and ontogenetic backgrounds of behavior, but even more important and perhaps first of all, he should become an expert on natural selection and the complex genetic mechanics produced by it.

Back To Sexuality: In compering sexual and asexual genotypes as competitors one cannot measure simply the collective value of a brood in the sexual line to determine the fitness of the parent. Also involved is how different is the average fitness of the brood members from the rest of the population -- or, more specifically, from that of potential mates. A set of offspring enormously superior to the asexualy genotype(s) might, on this account, be limited to producing a set of grandchildren inferior to the asexual genotype(s) (and the problem of what to measure and when to measure it to determine what it is, after all, that selection is maximizing once again rears its ugly head). This is a hazard of specialized sex (meaning loss of the ability to become quickly asexual when a superior genotype is produced); and to some extent it binds together the members of a sexual population and gives a special importance to the average fitness of sexual genotypes. The average fitness of genotypes in sexual populations has little significance except when there are asexual genotypes (or the members of a very similar sympatric species -- an ecological competitor) to compete with. If there are no asexual genotypes, then unless fitness differences involve some kind of "absolute" values (i.e., they refer to differential survival) rather than the relative fitness of individuals in competition with one another (i.e., differential reproduction) it will be the variance in fitness that determines the rate of evolution. Situations involving the above "absolute" and "relative" fitness values are roughly equivalent to Wallace"s (1968) "hard" and "soft" selection, which he used to explain why genetic load is a misleading concept when it involves arithmetic which implies that, for example, the fitness of a population is lowered when it acquires a beneficial allele because of the "genetic deaths" necessary to remove the old deleterious allele by selection -- see also Brues, 1968; Wallace, 1970, in the bibliography on genetic load). But if there are competing asexual genotypes, the more fit sexual genotypes will be hurt in their competition with the asexual genotypes by having only inferior genotypes with which to recombine. One way out of the dilemma is selective mating. If phenotypes produced by superior genotypes possess the ability to restrict their matings to other superior genotypes, they need not be dragged down all the way by the average fitness of the entire sexual population. Selective mating, however, increases the cost of mating (see above).

The general retention of a meiotic process during gametogenesis which increases the recombining effects of the total process of zygote formation increases the diversity of progeny, reduces their similarities as individuals to the parental genotype, and (because of the nature of meiosis) increases the chance element in the makeup of the genotypes of offspring. The widespread existence of meiotic gametogenesis and cross-fertilization in combination not only emphasizes the pervasiveness of environmental change and its unpredictability, but also suggests a prevalance of negative heritability of fitness between generations. It suggests, in other words, that genotypes successful in one time and place are not likely to be sucessful in the habitat of the next generation. This situation seems best examplified by species in which alternate generations live in different habitats, hosts, or seasons. The effects of selection and adaptation in the one location reduce likelihood of success in the next.

This simple environmental situation, however, is probably a poor candidate as the reason for maintenance of sexuality. The sexual process in general is characterized by random segregation of genetic elements during meiosis, deviations from randomness evidently chiefly involving aspects of linkage increasing the likelihood that full complements and co-adapted complements of the genetic machinery are delivered to each meiotic product. Such randomness implies unpredictability in the environment more than it does change.

If the environment of a species simply cycles between narrow, predictable alternatives (e.g., winter-summer, crowded-uncrowded, migration favored -- migration disfavored) an alternative route to adaptation exists: construction of a genotype capable of utilizing environmental indicators to produce the appropriate one of two (or a few) phenotypes. In fact, all studies indivicate that this is the route taken in such circumstances. As an example, I have indicated (Alexander, R. D. 1968; Quart. Rev. Biol.) that in no case among the thousands of insect species that (1) inhabit temporary environments (migration-favored alternating with migration-disfavored) and (2) contain within the species both long-winged individuals that tend to fly and short-winged individuals that cannot fly, has a single species been demonstrated to possess alternate alleles responsible for the prevalence of the two phenotypes. Instead the phenotypes are triggered by environmental conditions. The extreme examples are probably migratory locusts+aphids in which the phenotypic variations are so great that different adults have often been described as separate species.

Thus, it is the unpredictable aspect of environments that must represent our main focus in understanding maintenance of sexuality. I hope you understand when I add that something similar has to be involved in our efforts to understand the evolution of phenotypes, in general, and of ontogenetic plasticity of all kinds, including learning and culture (more on that in another ditto).

Maynard Smith's idea (In Williams, 1971) that the recombining of genetic elements adapted to different subsets of a species' environment rather than the recombining of new mutations (e.g., Fisher, 1958) is the principal reason for the maintenance or sexuality has intriguing implications. If correct it means that the environments of species, while both changing and unpredictable, are nevertheless in some important sense simply changing from state to state within some kind of predictable limits. It suggests that particular environmental states recur in different times and places, with the correlations among times, places and states unpredictable (as far as the organisms are concerned). Perhaps this state of affairs is predictable from the heterogeneity of species' environments, since the only genotypes available for recombination will by definition be those that are adapted to some past part of the environment of the environment, and the only ones successful in the next generation will be those whose adaptation happened to be to a part of the environment that will be repeated, at least to some degree or in some sense. I don't know how to test this set of questions, but I suppose one should begin with a thorough analysis of Maynard Smith's disagreement with Fisher. I haven't succeeded in that regard yet.

The relative rarity of asexual reproduction, given the frequency with which parthenogenetic trends begin, especially in insects, and the virtual absence of total asexuality, suggests that the advantages of sexuality in fact involve attributes of environments that are essentially universal throughout time and space; and the obvious candidate is unpredictability. Phenotypes may be described as buffers of flexibility and plasticity by which genotypes improve their reproductive success in varyingly changeable and unpredictable environments (or, in another view, by which they stabilize the environments of their genotypes for varying periods to take advantage of optimal times for reproduction or multiplication). The universality of phenotypes (there seem to be no naked genotypes) also attests to the importance and the pervasiveness of environmental unpredictability and heterog neity. It is a consideration of some interest to me that, barring sexual reproduction having been favored consistently for so long that returns to asexuality have become quite difficult, the retention and continued exaggeration of sexual recombination through all of the three mechanisms of recombination (1) meiotic gametogenesis, (2) cross-fertilization, and (3) outbreeding -- even in organisms with the most plastic of phenotypes, such as trees and humans -- indicates that phenotypic plasticity has rarely if ever been a total success in coping. If it had, we should have become

asexual. Or maybe (you take it from here . . .). The extent to which maximizing numbers of descendents and maximizing likelihood of representation in some distant generation jibe, like the existence of phenotypes and the rarity of conjugation without multiplication, may also attest to the changing nature of life's environments throughout its history.

I have written above mostly about the maintenance of sexual reproduction. I can't add to what Williams (1966 and Maynard Smith (1971) have said about its possible origins. I didn't explain all of Fisher's arguments because I don't understand them all. I didn't analyze and summarize Maynard Smith's and Crow and Kimura's papers (See Williams, 1971) because I think they're wrong in some important regards, and I can't figure out whether or not I'm right. I didn't even go systematically through Williams and Mitton's (1973) paper with you, mostly because it seems unnecessarily complex and maybe sometimes irrelevant.

But I haven't convinced myself that I'm right. This topic is a fine one for an essay by someone really caught up with it and I am convinced that the time is ripe for a well-written, carefully reasoned, summarizing and clarifying publication. One of you might be capable of developing it. And here is a written promise that a paper publishable in a refereed journal on a topic this difficult and important and relevant to the course alone yields an A grade.

(It seems curious to me that selective mating should be so obvious and prominent at the behavior or individual level in sexual organisms and so non-evident at the meiotic and gamete level.)

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