

INBREEDING AND THE PARADOX OF SEX: A RESOLUTION?

William M. Shields

Department of Environmental and Forest Biology
State University of New YorkCollege of Environmental Science and Forestry
Syracuse, New York 13210

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ABSTRACT: The paradox that sex appears to benefit species, while harming individuals, rests on the assumption that sex is equivalent to outbreeding (random mating in large, $N_e > 10,000$, populations). Inbreeding (random mating in a small, or nonrandom mating in any size, population) may reduce or eliminate the costs of sex while maintaining an advantage over asexuality, if the faithful transmission of successful parental genomes to progeny is favored in particular environments. Relative to outbreeding, inbreeding will reduce the cost of meiosis owing to the increased relatedness of mates. It will also ameliorate recombinational load by facilitating greater fidelity (though not perfection) in the transmission of successful and coadapted allele combinations at interacting loci. Relative to asexuality (apomixis or ameiotic parthenogenesis), inbreeding is less likely to suffer a mutation accumulating "ratchet", and thus inbred progeny are likely to suffer lower mutational loads than similar asexual families. Analysis of the species distribution and frequencies of occurrence of asexuality, inbreeding, and outbreeding in the higher plants is consistent with the hypothesis that sex may have evolved and currently may be maintained by individual selection as an evolutionarily conservative rather than a progressive reproductive tactic.

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Sexual reproduction is defined as the recombination or exchange of parental genetic material during progeny production. In diploid eukaryotes sexually produced offspring arise from the fusion of gametes (syngamy) that are recombination products of parental meiosis. Processes which lack syngamy and recombination are usually considered asexual. The ubiquity of sex, as defined, has produced a "kind of crisis" in evolutionary biology (Williams, 1975). The paradox of sex stems from a contrast between its easily demonstrated benefits for groups or species, and its apparent disadvantages for sexual individuals. On theoretical grounds, conflicting selective pressures are expected to be resolved most often in favor of individual adaptation (for review, see Maynard Smith, 1976a; but see Wilson, 1980). Thus the widespread occurrence of obligate sexuality has generated a lively discourse among evolutionary biologists (for reviews, see Ghiselin, 1974; Williams, 1975; Thompson, 1976; Maynard Smith, 1978).

Accepting the obvious, a number of schools have proposed a complex of often complementary hypotheses explaining sex as a truly biotic adaptation. Focusing on the effects of syngamy, the Fisher-Muller School (Fisher, 1930; Muller, 1932; 1958; Crow and Kimura, 1965; 1969; Kimura and Ohta, 1971) suggested that the primary function of sex was to increase the rate of adaptive evolution by increasing both the rate and probability of combining two independent and favorable mutants into a single individual. Focusing on the consequences of recombination, the "reassortment" (Thompson, 1976) school (Darlington, 1932; 1958; Dobzhansky, 1937; 1970; Lewis, 1942; Mather, 1943; 1953; Stebbins, 1950; 1957; Dodson, 1953; Mayr, 1963; Felsenstein, 1974) also suggested that sex functioned to increase evolutionary rates, but emphasized the increased genetic flexibility resulting from the generation of novel allelic combinations from variants already present in a group's gene pool. Reinforcing each other, both schools concluded that sex was ubiquitous because sexual species were: 1. less likely to go extinct, 2. more likely to speciate, 3. or both 1 and 2, owing to their increased flexibility and evolutionary potential relative to asexual species (see references above, also Stanley, 1975; Van Valen, 1975; Treisman, 1976). Fisher (1930, p. 50) went so far as to suggest that sex might be the only character "evolved for the specific rather than for the individu-

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al advantage". In his excellent review (from which my conceptual organization is derived), Thompson (1976) provided evidence that sex could be a biotic adaptation. However, his interpretation of the admittedly sparse experimental evidence (e.g., Thompson, 1977), suggested that sex might be a conservative factor that prevented a group from wastefully depleting its genetic variance by tracking unimportant environmental fluctuations, or important but temporary fluctuations too closely.

Dissatisfied with reliance on biotic adaptation and its implication of effective group selection in general, a third school (Williams, 1966; 1971; 1975; 1980; Maynard Smith, 1968; 1971a; 1971b; 1974; 1976a; 1977; 1978; Ghiselin, 1969; 1974; Williams and Mitton, 1973; Levin, 1975; Nyberg, 1975; Treisman and Dawkins, 1976; Felsenstein and Yokoyama, 1976; Glesener and Tilman, 1978; Hartung, 1981) explored the individual consequences of sex in search of advantages that would more than balance the obvious disadvantages.

With some drift, each of the schools followed an intuitive argument, first expressed in detail by Weismann (1891), that the crucial consequence of sex was the generation of genetic novelty. They were also unanimous in inferring from this that sex must function to meet changed or changing environmental conditions (see also Bonner, 1958). In the end, the primary differences between the various schools were in their detailed explanations of what kinds of novelties (mutational or recombinational) were important in maintain sex, who (individual or group) benefitted from these consequences, and when (immediately or in the future).

The entire problem of sex was attacked on a broad front by a host of investigators using comparative evidence, intuitive and mathematical analyses, and computer simulation, in order to determine what factors controlled the adaptive value of sex. Detailed results of these studies have fueled a series of comprehensive and synthetic reviews (e.g., Ghiselin, 1974; Williams, 1975; Thompson, 1976; and Maynard Smith, 1978). The details are not as important for the arguments developed here as are some of the general conclusions emerging from them. Instead of reviewing the details again, I will rely on the earlier work to summarize much of the pertinent evidence and consensus conclusions.

The growing consensus is that the conditions that would favor the Fisher-Muller explanation of sex are not likely to be frequent or efficient enough to maintain sex (fusion) as a strictly biotic adaptation. The primary difficulty is that what sex brings together more quickly, it breaks apart just as quickly (Thompson, 1976). Evidence for within-population genetic variance for recombination is unequivocal in contradicting any hypothesis on the maintenance of sex that relies solely on arguments of group benefit (Turner, 1967a; 1967b; Williams, 1975; Maynard Smith, 1978). So the extreme individual selectionists (Ghiselin, 1974) were probably correct in seeking individual benefits for sex that would more than balance individual costs. Though they have succeeded in producing a number of partial or potential answers, all such explanations are restricted by a lack of generality, a reliance on admittedly unrealistic assumptions, or on infrequent conditions as primary selective forces. In the end, they are unable, either singly or jointly, to explain the maintenance of sex in many regularly, or obligately, sexual organisms. Sex then, is a paradox, a contradictory thorn in the sides of those, including myself, who view natural selection as a process operating through the reproductive success of individuals (Williams, 1980).

DISADVANTAGES OF SEX

Syngamy.--The dual nature of sex allows an independent analysis of the detrimental consequences of both its normal component processes (syngamy and recombination). The primary disadvantage of syngamy can itself be viewed in two different ways, either as a significant ecological (Maynard Smith, 1978), or genetical (Williams, 1975; 1980) "cost" associated with biparental reproduction. Maynard Smith (1978, p. 2) succinctly described the former as, "the twofold disadvantage of producing males", while Williams (1975, p. 9) described the genetic cost as, "the 50% cost of meiosis". Maynard Smith argued that in a sexual species, with

equal numbers of males and females, sex is not an "evolutionarily stable strategy" (Maynard Smith and Price, 1973), being susceptible to invasion by parthenogenesis. In this situation, the putative value of parthenogenesis is an immediate increase in the relative fecundity of a parthenogenetic female. Such a female produces only daughters, but in numbers expected to equal the total output of a sexual female (whose progeny will consist of equal numbers of the sexes). Thus, the proportion of parthenogenetic females in a total "population" consisting of both sexual and parthenogenetic females will increase, actually doubling in the early generations when parthenogens are still rare. If there is to be a cost of producing males or investing in male function, then "males" must function solely as sperm donors. As both Williams (1975) and Maynard Smith (1978) have pointed out, the ecological cost will not usually apply in situations where male parental care is necessary to produce successful progeny (but, see below), nor, perhaps, to organisms with isogamous gametes and no clear distinction between the sexes (see also, Manning, 1976a). It also applies with less force to hermaphroditic organisms, if they can reduce their investment in male function without reducing reproductive success. Such asymmetric investment is expected to be most easily attained in self-fertilizing organisms (Maynard Smith, 1978), a prediction confirmed in selfing plants that often show predicted reductions in pollen investment (Cruden, 1977).

The genetic argument of a cost of meiosis implies that a major disadvantage of syngamy results from sexual parents discounting their genetic representation in descendants by 50% because they "share" offspring with unrelated individuals. A sexual parent produces haploid gametes that fuse with another individual's gametes to produce progeny. Half of each sexually produced offspring's genome is maternal, half paternal, so that a sexual female that produces 10 offspring can claim only 50% of their genes, or 5 offspring equivalents. In contrast, a parthenogenetic (or otherwise asexual) individual's offspring carry only their mother's genes. If she produces 10 offspring, they would equal 10 offspring equivalents, or twice the total genetic representation of a sexual female. Recently, Williams (1980) has suggested that this cost can be viewed in the context of inclusive fitness and kin selection. A sexually reproducing female invests in relatives (offspring) with lower relatedness ($r = 0.5$) than otherwise similar asexual females (parent-offspring $r = 1.0$). Inclusive fitness theories of kin selection (e.g., Hamilton, 1964a; 1964b; West Eberhard, 1975) suggest that beneficence, including parental investment, should, if possible, be dispensed preferentially to closer kin. This implies that sex can entail a genetic cost, in that individual donors are not maximizing the relatedness of their most direct beneficiaries.

Maynard Smith (1978) and others have suggested that the ecological and genetical costs of sex are the same problem. In most instances, they are indeed two sides of the same coin. Yet this practical equivalency does not imply a logical equivalency. For example, the genetic argument could apply with equal force to outbreeding hermaphrodites, even if they limited investment in male function obviating any ecological cost. Theoretically, an internally fertilized and cross-breeding hermaphrodite would be capable of reducing its investment in male function until its relative fecundity approximated that of an asexual individual (Maynard Smith, 1978, p. 40). The perhaps too stringent assumption in this case is that each individual is guaranteed one mating (but for an empirical example of such conditions, see Fischer, 1980). If true, there would be no competition for mates and asymmetric investment in sexual function would be evolutionarily stable (Maynard Smith, 1978).

Such individuals might produce 9 fecund progeny for every 10 produced by an otherwise equivalent asexual individual. This would occur, for example, with a transfer of 80% of initially male investment into female function, and result in a reduced 10% (vs. the normal 50%) ecological cost of sex. If such organisms outbred, they would produce 9 offspring with an $r = 0.5$, for 4.5 genetic offspring equivalents. When compared with asexuality's undiscounted 10 offspring equivalents,

the potential for a genetic cost in inclusive fitness to the sexual individual is readily apparent. The same point can be illustrated by the more realistic case of a monogamous species with extensive paternal care. Though such species, by definition, bear little or no ecological cost (Maynard Smith, 1978), but if they outbreed they will reduce their relatedness to progeny. In both cases, then, the ecological and genetic components are related but logically separable costs of sex.

Recombination.--The disadvantage of recombination is as easy to conceptualize as that of syngamy, but at present it is essentially impossible to quantify. The origins of the argument can be traced from Fisher (1930), and is perhaps best expressed by Maynard Smith (1978, p. 78), who notes, "More generally, one can simply say that since surviving individuals have genotypes of higher than average fitness, they only stand to lose, in a uniform environment, by producing recombinant offspring". The cost of recombination can be measured as a "load" (Williams, 1975) corresponding to the average reduction in progeny fitness resulting from the disruption of favored coadapted genomes during gametogenesis. The end result of sex is that demonstrably successful parents will, on average, produce less fit progeny because of the genetic differences between parents and young that sex generates. In essence, recombination reduces the heritability of fitness, so that there will be a lower correlation between the fitness of a parent and its offspring. In contrast, asexual reproduction theoretically permits a successful parent to transmit an exact duplicate of its successful genome to its progeny (Maynard Smith, 1978). In a uniform environment, then, natural selection is expected to favor individuals with reduced (or zero) recombination, because fitter parents will produce fitter offspring only in the absence of recombination. The argument implies that in a uniform environment, sexually produced progeny are more likely to be less fit than asexual progeny, increasing the already considerable theoretical disadvantage of sex (for review, see Williams, 1975; Maynard Smith, 1978).

A large measure of theoretical and observational evidence supporting this view of recombinational load has accumulated over the past 50 years (for review, see Maynard Smith, 1978, Ch. 5). Indeed, recombinational load has generally been proposed as a driving force behind the evolution of such diverse characters as, chromosome linkage groups in general (Fisher, 1930; Wright, 1931; Darlington, 1932; 1958), the reorganization of separate loci into closely linked supergenes (Ford, 1964; Turner, 1967b), and the maintenance of balanced chromosomal inversion polymorphisms in flies, especially *Drosophila* (Dobzhansky, 1937; 1970). In each of these instances, the characters are thought to have evolved specifically to reduce the levels of disruptive recombination. Following the logic of these arguments to their ultimate conclusion led to Turner's (1967a) seminal question, "Why does the genome not congeal"? Why does recombination (and syngamy) not give way to asexual reproduction?

ADVANTAGES OF SEX

The search for sex's advantages was facilitated by the occurrence of within-population variation in recombination, which automatically focused attention on sex's consequences for individuals. It was made even simpler by the "apparently unanimous" (Daly, 1978, p. 771; also, see Williams, 1975; Maynard Smith, 1978) conclusion that the primary consequence of sex, and therefore its function, was to increase the genetic diversity of one's offspring (so that siblings differed among themselves and from their parents) in response to changed or changing environmental conditions (but, see Manning, 1976b). Williams (1975, p. 7) stated the paradigm for investigating sex explicitly, "it is easier to reason from a set of premises to a valid conclusion if you know the conclusion in advance". Many followed his lead and the search for an explanation of sex became a search for the proper premises, that is for the initial conditions, and types and degree of environmental fluctuation that would favor sexual reproduction. Within this model two distinguishable (though

some believe that they are operationally identical) classes of models evolved. Ecological models focused on the consequences of varying environments and genetical models focused on the consequences of randomly generated linkage disequilibria in finite populations (the Hill-Robertson effect). Without entering the discussion of whether they are all subsets of a single model (e.g., Felsenstein, 1974; Felsenstein and Yokoyama, 1976) or truly independent (e.g., Maynard Smith, 1978), I will treat them separately.

Ecological Models: Varying Environments.--All the ecological models rely on environmental conditions which vary in a manner that offspring face qualitatively different environments than those faced by their parents. For the most general models of simple spatial and temporal variation, Maynard Smith (reviewed in 1978) has shown that if two or more loci are important in adapting an individual to a single state of any of an environment's variable features (e.g., features = temperature and rainfall, states = hot or cold, wet or dry), or if the states of different features are correlated (e.g., hot areas are wet, cold areas dry), then recombination will almost always be maladaptive (occasionally neutral). Only in the unlikely event that correlations between different features' states change sign from generation to generation (e.g., generation 1 = hot-dry, cold-wet; generation 2 = hot-wet, cold-dry) would selection favor increased recombination.

A second less general, but more plausible, model combines a specific pattern of dispersal and spatial heterogeneity in the environment to produce positive selection for higher recombination (Maynard Smith, 1968; Slatkin, 1975). This model requires two differentiated populations living in selectively different and geographically separated areas, each contributing migrants to a third ecologically unique area. If members of the two parent populations only meet in the third area, and if selection in that area favors a novel genotype which consists of alleles drawn from each parent population, then selection can favor recombination in the novel environment (Fig. 1). In the illustrated case, a linear habitat is sharply divided into a central novel region (linear extent = Z) in which haploid genotype Ab is favored, while the original environments favored the fixed genotypes AB and ab . If $Z > \delta / \sqrt{s}$ (where δ = average dispersal distance; s = selection intensity against the parental genotypes and alternative recombinants), there would be no selection on recombination. If $Z < \delta / \sqrt{s}$ (Case C), selection will favor increased recombination in the small central region but reduced recombination in the much larger parental regions. Finally, if $Z \approx \delta / \sqrt{s}$ (Case B), recombination will be neutral in the parental regions and positively selected in the novel environment. While this model does indicate that there are plausible conditions which would select for increased recombination, it is unlikely that such conditions occur frequently or widely enough to explain recombination universally. Maynard Smith (1978) also noted that it was equally easy to conceive of similar conditions which would favor reduced recombination (e.g., if two loci switch selective states at the same spatial location, or the states of different features are spatially correlated).

A third class of ecological models have developed from Williams' seminal discussions resting on an assumption that intense selection coupled with fluctuating environments could produce conditions favoring sexual reproduction in a wide variety of organisms (Williams and Mitton, 1973; Williams, 1975; 1980). Williams expressed the essentials of his argument in an elegant gambling metaphor. A heterogeneous, fluctuating environment may be viewed as consisting of a series of lotteries (patches), each having a single winning ticket (number) imposed by selection. An asexual parent, then, buys 100 tickets, only to discover that all have the same number. A sexual parent may be able to afford fewer tickets, owing to the cost of males (Maynard Smith, 1978), but each will have a different number, increasing the possibility that at least one of them will win one of the lotteries.

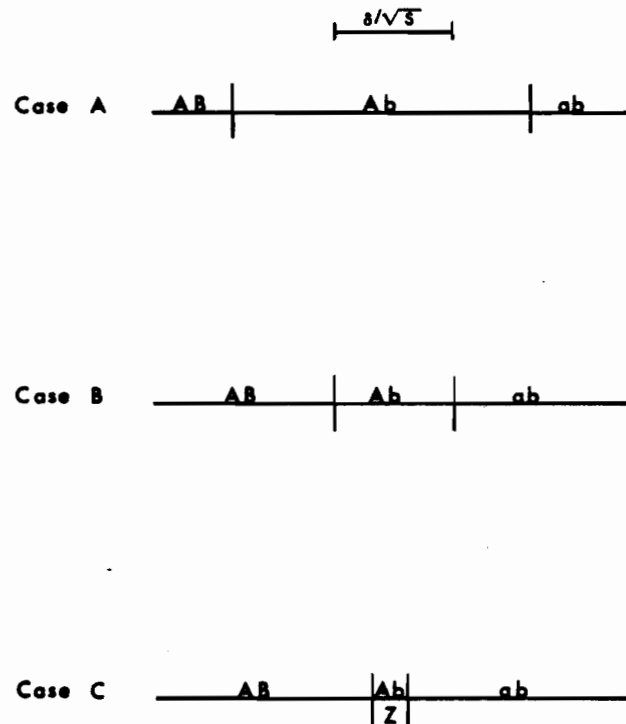


Fig. 1. Relation between characteristic dispersal distance (δ), selection (s) and the distance between environmental discontinuities (Z) which will determine the selective value of recombination in the central environment (from Maynard Smith's [1978] treatment, of Slatkin's [1975] model).

Expanding on a graphic model developed by Emlen (1973), Williams (1975) saw this advantage of sex as resulting from the production of progeny with a broader probability distribution of fitness potential than would result via asexuality. Given this difference, sex would be favored if selection were intense enough that only those progeny with extremely high fitness (sisyphian) genomes would be likely to survive (Fig. 2A). Decreased selection intensities would decrease the advantage of sex, until asexuality regained its former favor (Fig. 2B). The necessity of extreme selection intensities led Williams (1975) to conclude that the model was primarily applicable to organisms producing enormous numbers of progeny which could meet the selective pressure. Specifically, he concluded that his models could explain sex in high fecundity ($> 10^7$ offspring/female/lifetime), and perhaps some medium fecundity ($10^3 - 10^7$ OFL) organisms, but they could not explain sex in low fecundity species ($< 10^3$ OFL: including most of the vertebrates). Extending his gambling analogy, low fecundity organisms would not be expected to have a large enough stake (fecundity) to insure the production of sisyphian genotypes, and so for them sex appeared to remain maladaptive (Williams, 1980).

In a formal, mathematical simulation of Williams' basic model, Maynard Smith (1976b; 1978) detected the predicted trend. Sex produced an advantage only when

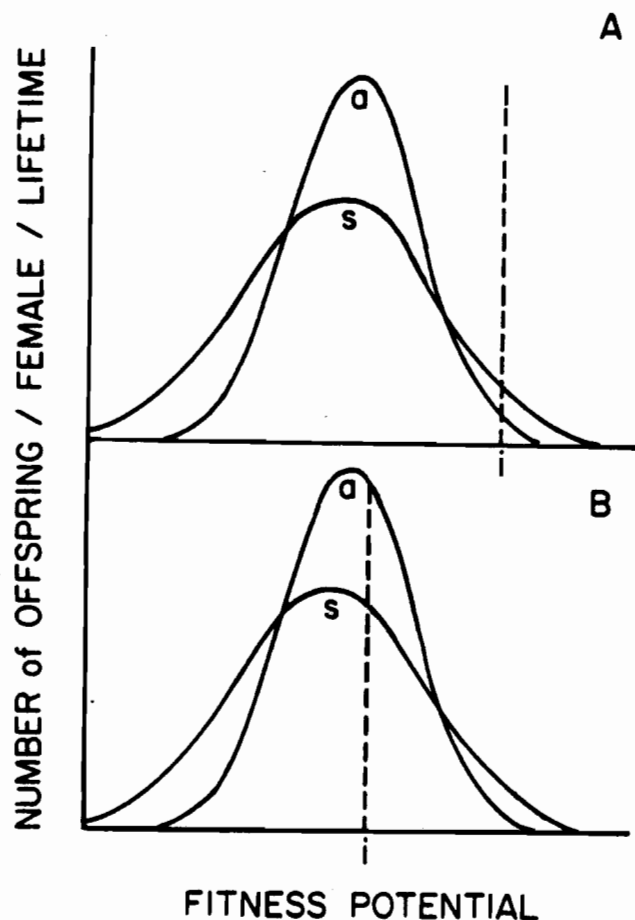


Fig. 2. The relationship between selection intensity (i) and the probability distribution of fitness potential associated with the progeny produced in a single female's lifetime via asexual (a), or sexual (s) reproduction. A. high selection intensity favors the more variable (sexual) progeny. B. low selection intensity favors the less variable (asexual) progeny (modified from Williams, 1975).

30-40 individuals competed for a single patch, implying that the parents contributing competing offspring to each patch produced many progeny. He also cautioned that his numerical results (lower than Williams' intuitive estimate) were possibly an artifact of the arbitrary conditions of his simulation (e.g., each patch consisted of 5 different selective features). More realistic conditions might increase the association between high fecundity and an advantage of sex, confirming Williams' conclusion that sex remained to be explained in the majority of low fecundity organisms.

Maynard Smith (1978) went further, questioning the applicability of Williams' "sib competition" model to many high fecundity organisms. He based his critique on what he perceived was both a crucial assumption, and a crucial weakness, of Williams' Elm-Oyster model: the necessity that sibs compete in environments that differ from that of their parents. If offspring were dispersed randomly into a heterogeneous environment, one to a patch, there would be no sib competition and the advantage of sex would disappear. Extending the gambling

metaphor, Maynard Smith (1978, p. 100) suggested that the comparison would be with an asexual parent buying 100 identically numbered lottery tickets, but entering them in 100 different lotteries (each with a different winning number) so that the asexual strategy is at no disadvantage. He concluded that the Elm-Oyster model is not as general an explanation as Williams had hoped, and indeed was not likely to apply even to its illustrative organisms. The elm because most seeds fall very short distances from their parent, the oyster because their dispersal is so vagrant that sibs are unlikely to compete in the same patches.

Williams (1975) offered yet another model, the cod-starfish hypothesis, which contained a kernel of an argument that might address Maynard Smith's objections (Williams explicitly noted that the cod-starfish model could apply to the elm and especially to the oyster), because it did not require sib competition for unitary patches in a heterogeneous environment. It does assume intense selection (and therefore still applies primarily to high fecundity organisms), and that the primary advantage of sex results from increased variability in progeny with a resulting increase in the number of offspring blessed with sisyphian genomes (Fig. 2). The novel approach of this model was a switch from a coarse to a fine-grained environment. Progeny were dispersed randomly throughout large expanses of parental habitat, rather than as sib groups into discrete and variable patches. Sib competition still occurred, but the arenas were no longer discrete subdivisions, but rather had expanded to the entire parental environment. Taken together the models imply that sex will have an advantage, regardless of the spatial structure of the environment, as long as selective conditions change over time, and if selection is intense enough to insure that only sisyphian genomes can expect success.

I have not presented much of the detail or supporting evidence that suggests that jointly, Williams' (1975) and Maynard Smith's (1978) models, along with those relying on similar logical structures (e.g., Levin, 1975; Glesener and Tilman, 1978; Bulmer, 1980; Hartung, 1981), do provide reasonable explanations of the maintenance of sex in environments which vary in plausible ways. They appear to be generally applicable to species with sufficient excess fecundity to afford the sexual gamble. But the paradox is not resolved for low and medium fecundity organisms, which, at least theoretically, cannot afford the gamble. Williams' (1975, p. 102) answer for them was that sex was "a maladaptive feature ... for which they lack the preadaptations for ridding themselves" (see also, Treisman, 1976; Williams, 1980). Maynard Smith's more "hopeful" conclusion was that the genetic, rather than the ecological, models offered a better hope for a general and universal (applying to low and high fecundity organisms alike) explanation for recombination (if not for syngamy).

Genetic Models: Linkage Disequilibrium and the Hill-Robertson Effect.--Recombination produces all of its consequences, both good and bad, through a single mechanism of reducing linkage disequilibrium. By definition, disequilibrium exists if gamete genotype frequencies do not reflect indepent assortment. In the simplest case of a two locus haploid genome with two alleles at each locus (the argument can be generalized to the diploid multilocus case), there are 4 gamete genotypes (AB, Ab, aB, ab). If the frequency of these gametes (genotypes) are g_{AB} , g_{Ab} , g_{aB} , g_{ab} , then D , a coefficient of linkage disequilibrium (Lewontin and Kojima, 1960; Lewontin, 1974) can be calculated by comparing the frequencies of coupling (AB, ab) and repulsion (Ab, aB) gametes by,

$$D = (g_{AB} \times g_{ab}) - (g_{Ab} \times g_{aB}) \quad (1)$$

If the loci are segregating independently (free recombination between them), and Hardy-Weinberg conditions apply, then the gamete frequencies will equal the cross-products of their constituent allelic frequencies and the population will be in linkage equilibrium ($D = 0$). A population of gametes in disequilibrium will contain an excess of coupling ($D > 0$) or repulsion ($D < 0$) gametes. Such a population, then, consists of gametes which carry, as a group, a nonrandom association of alleles, such that, for example, a gamete carrying A is more likley to carry B than b. Since the primary genetic consequence of recombination is to reduce such disequilibria, (i.e., the disruption of nonrandom allele associations), any ad-

vantages or disadvantages of recombination must stem from this effect.

Viewed in this manner, the disadvantage of recombination is obvious. One of the primary forces expected to produce linkage disequilibrium is natural selection (for review, see Lewontin, 1974). Whenever selection favors an individual because it possesses harmoniously interacting (i.e., coadapted) alleles, then adaptive linkage disequilibrium is a possibility because selection is expected to reduce the relative frequency of less favored "random" associations. Selection generates the nonrandom state we call adaptation, recombination alters that state, producing a significant depression in fitness (recombinational load) relative to tighter linkage that would have permitted a combination to pass from parent to offspring unchanged.

To demonstrate a potential advantage for recombination, then, it is necessary to demonstrate selectively disadvantageous linkage disequilibria which could profitably be reduced. The conditions responsible for such disequilibria must be non-selective, making chance factors likely candidates. In a masterful synthetic review of the consequences of recombination, Felsenstein (1974; Felsenstein and Yokoyama, 1976) suggested that all the models claiming an advantage for recombination (and sex), from Fisher and Muller, through Maynard Smith and Williams ultimately can be expressed in terms of the Hill-Robertson effect. Hill and Robertson (1966) discovered (via simulation) that randomly generated disequilibria coupled with linkage could limit a population's response to selection. They suggested that the decreased response resulted from linked alleles interfering with each other's selective increase and ultimately fixation. Given randomly generated disequilibrium, recombination has two potential advantages. On average, it is expected to, (1) increase the probability of fixing newly favored alleles (composer effect), and (2) decrease the probability of fixing newly disfavored alleles (editor effect). The alleles in question can "originate" in two distinct ways. In a changed environment, the selective value of some alleles, currently segregating at equilibrium frequencies, will change sign. In any environment, alleles with novel selective value will originate in every generation via random mutation. Such mutations can be either favorable or unfavorable, but the latter is far more likely. Thus the raw materials are normally present. If chance factors do produce nonrandom associations including such novel alleles, then linkage will reduce the efficiency of selection in producing adaptive evolution. The question remains, are these composer and editor effects, either independently or jointly, significant enough factors to outweigh the disruptive effects of recombination?

A novel favorable mutation, or a previously deleterious allele favored by a recently changed environment, initially occurs at relatively low frequencies. In a finite population, they are unlikely to occur with all the alleles segregating at other loci, and so will not be in linkage equilibria. At least part of the time such alleles are likely to originate in association with other less favored alleles. In such an association, they are less likely to increase in frequency and more likely to be lost as a result of drift, as the poor linkage relation interferes with positive selection on the novel allele (Hill-Robertson effect). The composer effect of recombination increases the probability that the newly favored allele will, sooner or later, become associated with the more successful genetic backgrounds available in the population. Complete linkage (or asexuality) limits all novel favorable alleles to their original associations. By shuffling the deck in every generation, recombination increases the likelihood that combinations of favorable alleles will get together. This argument applies whether the "population" in question is a local deme, or the population of progeny (sibs) produced by a single female. Therefore recombination's composer can be favored by both group and individual selection, as has been demonstrated by computer simulations (Felsenstein, 1974; Felsenstein and Yokoyama, 1976).

Maynard Smith and his colleagues (Strobeck et al., 1976; Maynard Smith, 1977; 1978) visualize the same process from a conceptually (but not mechanistically) different perspective. Emphasizing the utility of the concept of "gene" or "repli-

cator selection" (Dawkins, 1976; 1978), they view a gene for recombination as primarily affecting its own replication rate rather than its bearer's individual fitness. From this framework, the concept of "hitch-hiking" (e.g., Maynard Smith and Haigh, 1974; Maynard Smith, 1978) becomes useful. An allele which increases recombination will be associated with novel favorable allele combinations at other loci more often than an alternative allele for lower recombination. Positive selection will act to directly increase the frequency of such favorable combinations which will, therefore, indirectly increase the frequency of the high recombination allele. The latter increases by hitching a ride with the favorable combinations it helps produce. Computer simulation (Strobeck et al., 1976) has indicated that such hitch-hiking would only be important if the locus for recombination was tightly linked to the loci at which favorable combinations were produced.

Whether viewed from the perspective of hitch-hiking, the Hill-Robertson effect, or even the original intuitive arguments (e.g., Fisher, 1930; Muller, 1932), it is obvious that for the composer effect to be of major and general significance in maintaining recombination, favorable mutants must occur at fairly high rates. Maynard Smith (1978) concluded that such limitations made it likely that the composer effect of recombination might be a sufficient explanation of why the genome does not congeal completely, but it was inadequate as an explanation of why recombination occurred at the levels actually observed in nature. The composer was, at best, a partial answer to the question why sex.

A second consequence of recombination which Felsenstein (1974) explored in detail was the decreased likelihood that a group would accumulate and fix newly disfavored alleles owing to an automatic editor associated with the composer. The editor effect was the obverse of the composer, and also operated by reducing randomly generated linkage disequilibria. Rather than increasing the efficiency with which selection could operate on favorable alleles and combinations, the editor increased selective efficiency against deleterious alleles and combinations. Muller (1964, p. 8) introduced the problem by pointing out that an asexual species "incorporates a kind of ratchet mechanism, such that it can never get to contain, in any of its lines, a load of mutations smaller than that already existing in its at present least-loaded lines". More importantly, he also noted that such least-loaded lines could "become more heavily loaded by mutation". Expanding on Muller's original argument, Felsenstein (1974) concluded that owing to the greater genomic frequency of deleterious (vs. favorable) mutations, recombination's editor effect was possibly of greater importance than the composer effect.

One can illustrate both the ratchet and the editor which functions to prevent the ratchet by considering a population of individuals, each carrying a unique and newly arisen mutation. Any allelic combination which includes such a mutation will be in linkage disequilibrium with alternative genotypes generating the Hill-Robertson effect. At times, and by chance, even an otherwise most favored genome will contain a novel and deleterious mutant. Such a genome's positive selective value will interfere with the selective elimination of any deleterious mutants associated with it. If individuals within such a population reproduced asexually, then the deleterious mutants would tend to accumulate in the group's gene pool (via the ratchet), so that succeeding generations of individuals would carry them in ever increasing numbers (Fig. 3A) at an every increasing cost in fitness. If two of the novel mutants are actually favored (e.g., A and B in Fig. 3A) but arise in different individuals, they cannot be brought together into a single individual unless one recurs in an individual which carries the second from a previous ancestor. Asexuality's lack of a composer is entirely due to its inability to reduce linkage disequilibria between such favorable mutants. In this case, immediate fitness is not reduced, but a potential for increasing fitness is missed.

With sex, recombination would reduce the linkage disequilibria associated with novel mutations, so that both the composer and the editor would be more and the ratchet less likely to operate. Depending on mutation rates (see below), recombination can produce offspring carrying fewer, more, or an equal number of muta-

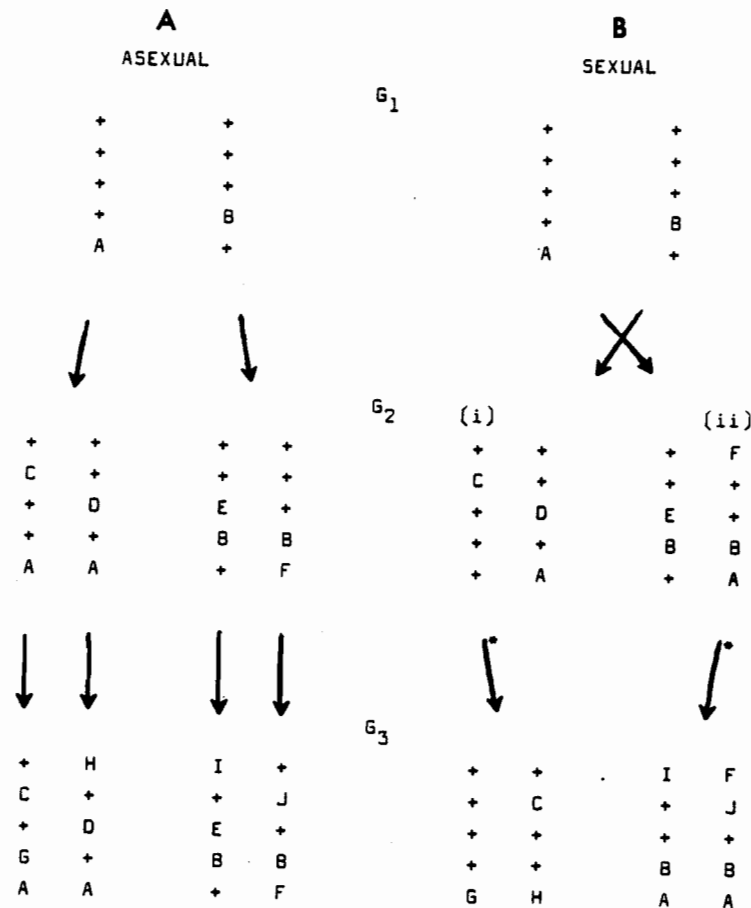


Fig. 3. A comparison of asexual and sexual reproduction illustrating, A., the ratchet effect of asexuality, and B., the editor (i) and composer (ii) effects of recombination. Each haploid genome is the product of replication (asexual) or recombination of replicated parental genomes (sexual) over three generations (G). Progeny produced in the third generation via sex are the product of interbreeding (*) between two individuals loaded with a single mutant (i.e., more than one zygote is present in each class of sexual progeny), while selection only permits one class (either i or ii) to survive and reproduce (for further details, see text).

* tions as each parent. If these mutations are generally deleterious, sex can limit, or even reduce a group's mutational load, by reassorting independent parental mutations into a single "waste" gamete or individual (ii in Fig. 3B), that can then be eliminated by natural selection. Complementing this process, a second gamete or offspring (i in Fig. 3B) will be produced which will be selectively favored owing to its reduced mutational load (Muller, 1964). This editing process can continue, generation after generation, obviating the ratchet, and helping to maintain the lowest mutational load consistent with the characteristic mutation rates and selection intensities operating in the group.

If two favorable mutations (A and B, in Fig. 3B) have originated in two different individuals, then the "waste" gamete of the editor becomes the favored individual

(ii in Fig. 3B). Under such conditions recombination will have brought novel favorable mutations together into a beneficial association. In either case, recombination does possess a potential advantage over asexuality, and its capacity to edit and compose simultaneously affirms the view that sex is a more flexible strategy than asexuality.

To explore the importance of sexuality's editor and asexuality's ratchet, Maynard Smith and Haigh (in Maynard Smith, 1978, Ch. 3) have initiated quantitative studies of the factors likely to control their operation. These included the rate of deleterious mutations arising in a genome per generation (U), the average selection coefficient against such mutations (s), and the size of the population. Their admittedly preliminary results very roughly ("within an order of magnitude") indicated that for progeny produced asexually, if $U/s < 1$, the ratchet would not operate (i.e., deleterious mutations would not accumulate so that recombination would be unnecessary), if $U/s > 10$, the ratchet would operate in all but very large populations, and if $U/s > 20$, the ratchet would always operate. Similar analyses suggested that for sexual groups the editor would operate as long as roughly, $U < 1$ (though increasing individual fecundity would increase the threshold U needed to induce the ratchet), but that it would only be useful if "the majority of deleterious mutations are only slightly deleterious" (s is small, Maynard Smith, 1978, p. 36).

Maynard Smith's (1978, p. 36) compelling summary conclusion concerning the theoretical consequences of recombination's editor effect was "... for a given error rate per site per replication, the maximum amount of essential genetic material in the genome which can be reproduced without steady deterioration is substantially greater for a population with genetic recombination". Although this is couched in terms that could be misconstrued as group benefit, and has been explicitly simulated in such a framework (Felsenstein, 1974), the advantage also applies to a female which produces a "population" of progeny in her lifetime, since her individual success is measured by comparing her population of progeny with the populations produced by others. A female which reproduces sexually, then, may benefit by producing some offspring with a reduced load of deleterious mutations when compared to the average load carried by all the offspring produced by her asexual competitor.

Though limited, there is empirical support for the hypothesis that asexuality can incorporate a ratchet, resulting in an asexual group's steady accumulation of harmful mutations with an associated reduction in fitness. The most extensive studies have involved heterogonic species that normally alternate sexual and asexual generations. When such a species is experimentally prevented from engaging in sexual reproduction (e.g., conjugation in protozoa, syngamy and recombination in arthropods) a gradual early, and then later an accelerating decline in vigor, fertility, or some other fitness component usually accompanies the forces asexuality (for reviews, see Geddes and Thompson, 1914; Wright, 1977, Ch. 5). The end result is often the extinction of entire asexual stocks (reproducing exclusively by fission or parthenogenesis). This characteristic pattern of declining vigor associated with ultimate extinction led Wright (1977, p. 147) to conclude that as an explanation of the observed decline, "that of gradual accumulations of unfavorable mutational effects seems preferable in the case of decline under parthenogenesis". In the only comparable study of a vertebrate, Leslie and Vrijenhoek (1978; 1980) presented indirect evidence based on genetic comparison of clones of the obligate parthenogenetic fish, *Poeciliopsis monacha-lucida*, "suggesting that deleterious genes may accumulate in genomes sheltered from recombination".

Though far from conclusive, the combined weight of the theoretical considerations and the data supporting them, suggests that for a variety of organisms the ratchet may be the most harmful consequence of asexuality. This implies that the editor may be the most important beneficial effect of sex and recombination. If true, the often mentioned association between obligate asexuality and higher risks of extinction (e.g., Stebbins, 1950; 1971; Dobzhansky, 1970; Stanley, 1975; Maynard Smith, 1978) may not result from asexuality's lack of genetic flexibility or evolutionary potential. Rather, an asexual group may court extinction because it is actually un-

able to prevent maladaptive evolutionary change, as its ratchet steadily accumulates deleterious mutations and reduces the group's, and its constituents, level of adaptation. This view is consistent with the common association of polyploidy and asexual reproduction observed in nature (Stebbins, 1950). Despite the higher mutation rate expected in a polyploid (owing to their increased number of loci), higher ploidy could shield a genome from the phenotypic effects of accumulating mutations for longer durations. The resulting reduction in polyploid extinction rates, relative to diploids, would increase the relative proportion of polyploids in the total pool of asexual species.

Together, then, the ecological and genetic models of the evolution and maintenance of sexual reproduction have clearly succeeded in outlining the problem. Just as clearly, all of their partial and potential answers to why sex, whether considered singly, or in concert, have failed to explain sex in all of its manifestations (see also, Williams, 1975; 1980; Maynard Smith, 1978). While many consider Williams' sibling competition and progeny diversification models reasonable explanations of the maintenance of sex, they can only apply to relatively high fecundity organisms ($> 10,000$ offspring per female per lifetime) which can afford the gamble of sex. For most low fecundity organisms, including the *Drosophila* flies and the many vertebrates studied most extensively by population biologists, the occurrence of sexual reproduction remains a puzzling anomaly.

INBREEDING AND SEX: A RESOLUTION?

Until recently (e.g., Maynard Smith, 1978; Shields, 1979; Williams, 1980), discussions of the problem of sex either implicitly or explicitly equated sex with biparental outbreeding (random mating in large, $N_e > 10,000$, populations). Current representations of the cost of syngamy, whether measured in males produced or as a genetic cost of meiosis, are presented in a calculus which obviously relies on an assumption of perfect outbreeding. For example, only if mates have zero alleles identical by descent would the cost of meiosis equal 50%. Most of the theoretical treatments of recombination have also assumed large, random mating (= outbreeding) populations. For whatever reasons, the relativity of relatedness, the continuous nature of inbreeding, the operation of inbreeding via either genetically positive assortative mating or random mating in limited populations, and the absolute impossibility of perfect outbreeding, have failed to enter discussions of sex except in the most rudimentary fashion.

In this case inbreeding can be defined as random mating in small ($N_e < 1000$) populations, with decreasing population size increasing inbreeding intensity. The genetic consequences of inbreeding are expected to occur whether inbreeding takes the form of incest or random mating in finite demes. Indeed, it is possible to view regular full-sib incest as random mating in an effective population of two (Allen, 1965; Crow and Kimura, 1970). By reconsidering sex in the context of regular inbreeding, I have developed an alternative view of sex's evolutionary causes and consequences. In low fecundity organisms, inbreeding sex may be an individual adaptation functioning to increase the probability that successful parental genomes are more faithfully transmitted to progeny. In this framework sex would be a conservative rather than a progressive evolutionary force.

COST OF SYNGAMY

Genetic Costs.--In a perfectly outbreeding species, the cost of meiosis will be a 50% loss in genetic representation in offspring that are shared with an unrelated mate. In terms of inclusive fitness and kin selection, it is obviously better to invest parental resources in progeny that are closer ($r = 1.0$, asexual) than more distant ($r = 0.5$, outbreeding) relatives. But as Williams (1980) has also noted, asexuality is not the only mechanism which will increase r between a parent and its offspring. Since relatedness is an increasing function of the level of

inbreeding (Jacquard, 1975), increasing the relatedness of parents will also increase relatedness between parents and their offspring. Obviously self-fertilizing organisms do not share offspring (parent-offspring $r \approx 1.0$). Less obvious perhaps, but nonetheless true, any level of fairly continuous inbreeding, whether nonrandom (e.g., full-sib mating) or random ($N_e < 1000$), will increase r , and given sufficient time is expected to approach the $r = 1.0$ characteristic of asexuality (Jacquard, 1974). In a regularly inbreeding species, there may be little or no genetic cost of meiosis, and any level of inbreeding will reduce any cost below that expected for outbreeders. If, in the earlier example of a crossfertilizing hermaphrodite, mates were related (e.g., siblings with an $r = 0.5$), then progeny would be more closely related to their parents ($r = 0.75$ vs 0.5 with outbreeding). This would yield a parent, 6.75 offspring equivalents vs. the 4.5 associated with wider outbreeding, and the genetic cost of sex would have been reduced considerably. As inbreeding intensity increased, the cost of meiosis would be expected to decrease, finally disappearing with continuous self fertilization or lesser inbreeding intensities.

Recently, Dawkins (1979) has criticized this view as a fundamental misunderstanding of kin selection. For argument, he assumes that a species is monogamous, and that a female has a choice of outbreeding (producing progeny with an $r = 0.5$), or mating with her brother (producing a 'super-child' with an $r = 0.75$). The error, he suggests, is failing to consider brother's reproductive success independent of sister. If both outbred, brother would produce a nephew or niece with an $r = 0.25$ for her, that when added to her own progeny ($r = 0.5$) would yield genetic representation equal to the single progeny of incest. Dawkins (1979, also see Bengtsson, 1978) did note that the proposed advantage of inbreeding of bringing "extra close relatives into the world", would apply to many polygynous species where incestuous matings would not deprive "brother" of opportunity for mating elsewhere.

Hidden in his critique is the assumption that the gene is the only replicator and primary unit of selection. Dawkins (1979) does suggest that the argument can be rephrased to "genes for inbreeding are propagated at the expense of genes for outbreeding, having a greater probability of getting into each child born". To a gene, it is irrelevant whether its transmission probability is 0.75 in one relative or $0.5 + 0.25$ in two. But the applicability of the criticism relies entirely on the gene selection view.

Consider the same situation, but make the perhaps more realistic assumption that the traits in question are controlled by genetic differences at two independent loci (e.g., sex = $AaBb$, asex = $AABB$) and the conclusion changes. The probability of a complex trait being transmitted will be the probability that both genes will be found in one of the progeny involved. For the sibling pair, the probability that the genetic substrate for a trait will be transmitted remains 0.75. For the outbreeding siblings, however, the total probability falls to 0.50, as male and female each have a 0.25 probability of transmitting the whole pair. As the genetic basis for a trait becomes more complex, with more loci controlling trait differences, the disparity in the genetic cost of meiosis between inbreeding and outbreeding, and therefore inbreeding's relative advantage would become more pronounced.

The "selfish gene" view has led to similar suggestions (Treisman and Dawkins, 1976) that there may actually be no genetic cost of meiosis. Their argument explicitly invokes the perspective of the sexual allele, without stating its implicit assumption of inbreeding. In short, Treisman and Dawkins (1976) suggest that if sex were controlled at a single locus homozygous for a sexual allele, then such an allele would suffer no cost of meiosis. Even in the event that a complex character like sex were controlled by a single locus, their model assumes inbreeding. The postulated homozygosity of the sexual allele produces a population with an $r = 1.0$ at the sexual locus. In this perfectly inbred group, at least from the perspective of the sexual allele, there would indeed be no cost of meiosis. Yet it would be the inbreeding, and not merely the gene selectionist view that actually eliminated the cost. Williams' (1975) argument of a 50% cost of meiosis would be valid in an outbred group, even from the perspective of single alleles. For example, if there were

multiple alleles, each capable of independently producing sexuality in either single or double dose (i.e., $S_1, \dots, S_n$), then true outbreeding with mates having no sexual alleles in common would be possible. In such a group, the cost of meiosis to each sexual allele would be 50% for as long as the outbreeding remained possible. As soon as inbreeding occurred, the cost of meiosis would begin to decline until complete fixation of one allele in a population eliminated the cost just as Treisman and Dawkins argued.

Ecological Costs.--Regardless of the relationship between the genetic cost of meiosis and the ecological cost of producing males, inbreeding apparently can affect the problem of investment in male function. Both Maynard Smith (1978) and Williams (1975; 1980) suggest that inbreeding sex will still entail an ecological cost if parents expend equal resources on male and female function. If males function solely in the fertilization of females, and if conditions are such that inbreeding will inevitably occur, then only sufficient sons need be produced to insure that all of a female's daughters will be fertilized. Since a single son will often be sufficient to inseminate all his sisters, any overproduction of males may lead to wasteful "local mate competition" (Hamilton, 1967; Alexander and Sherman, 1977), with closely related males competing among themselves for mating rights. Females which reduce such wasteful competition by biasing the primary sex ratio of their progeny in favor of more productive females are expected to be more successful. The female biased sex-ratios observed in many inbred or incestuous arthropods (especially Hymenoptera, for reviews, see Hamilton, 1967; 1972; Alexander and Sherman, 1977), and the decreasing male investment (measured by a pollen/ovule ratio) associated with increasing inbreeding intensities in hermaphroditic plants (Cruden, 1977) are consistent with a view that inbreeding coupled with sex-ratio adjustments can, and has in a variety of organisms, reduce or eliminate the ecological cost of syngamy. Thus, inbreeding may produce substantial reductions in both the genetic and ecological costs of meiosis relative to wider outbreeding.

INBREEDING AND EQUAL SEX RATIOS

Williams (1980, p. 374) has stated that even in inbred groups, if parents "continued to spend resources equally on the production of sons and daughters, they would be equally (as compared to outbreeders) wasteful of resources" (see also, Maynard Smith, 1978). The consensus his statement represents is that inbreeding per se generates female-biased sex ratios, and that the combination of inbreeding and female-biased sex ratio is a necessary condition for reducing the ecological costs of sex. Williams (1980) also concluded that since most vertebrates do not show biased sex ratios, they are not inbreeding and must be suffering the full cost of meiosis. If inbreeding is not the direct cause of unequal sex ratios, then an equal sex-ratio would not necessarily imply that a particular organism is outbreeding.

I (Shields, 1979) have also argued that if males function solely to fertilize females, and inbreeding is assured, then reduced investment in male function should, and apparently does, follow. If males have additional roles, beyond sperm donation, or parents cannot be sure that close inbreeding will occur, then equal investment may be the rule regardless of average inbreeding intensity. For example, there is a consensus (e.g., Williams, 1975; 1980; Maynard Smith, 1978) that if an organism mates monogamously, and males behave parentally (e.g., most birds), equal investment will be the rule regardless of the mating system.

What is apparently overlooked in such discussion is that parenting is only one of the potential roles a male may fill in order to insure successful reproduction. Regardless of the mating system or male parental disposition, if males compete among themselves for the control of resources necessary to raise offspring (e.g., nest sites, food, predator or weather refuges including hibernacula, for review see Emlen and Oring, 1977), then equal investment could be favored even in polygynous systems and in the absence of paternal care. Since females in such systems are likely to be incapable of defending resources against often larger and more aggressive males, the latter would be necessary for successful reproduction. This means that male invest-

ment would not necessarily be wasteful in a variety of mating systems. A crucial factor in determining the value of male investment, and therefore the ecological cost of sex, might not be the presence or absence of paternal care, but the occurrence of any form of male investment whether directed at obtaining mates or parenting.

Adaptive sex ratios may actually be determined by the degree of intrasexual competition for reproductive resources (including members of the opposite sex) combined with the patterns of competitor relatedness characterizing a particular organism. For example, if dispersal were extremely limited, by choice or low mobility, then the high relatedness of neighboring males would result in inbreeding, and independently in wasteful local mate competition (Hamilton, 1967; 1972). In such circumstances, it could pay to reduce male investment resulting in a female-biased sex ratio. Indeed, many of the parasitic hymenoptera parasitize hosts singly (for review, see Hamilton, 1967), while some mites actually mate within their mother's body (e.g., Elbadry and Tawfik, 1966). Either behavior almost guarantees full-sib incest and therefore limits potential male competition for mates to full siblings. It is such species that do show the expected female bias in primary sex ratios (e.g., 1:6 to 1:9 in an *Adactylidium* spp. mite, Elbadry and Twfik, 1966).

A question remains as to whether it is inbreeding per se or the sib competition that favors the biased sex ratios. One school has emphasized the importance of inbreeding (e.g., Hamilton, 1967; Williams, 1980; and especially Maynard Smith, 1978), and predicts that female biased sex ratios will always be associated with inbreeding. I (Shields, 1979) have suggested that the occurrence of less related males competing with sons for daughters might force a female to produce more sons than predicted by the average level of inbreeding alone in order to compete successfully and insure some male success. I concluded that inbreeding could, but not necessarily would, contribute to and be associated with biased sex ratios (also, see Alexander and Sherman, 1977). More recently, Taylor and Bulmer (1980), using various mathematical analyses and simulations more rigorously demonstrated that intrasexual kin competition rather than inbreeding actually controlled adaptive sex ratios. They suggested that whenever competition among sibs (or other close kin) of one sex was more intense than among members of the other sex, the sex-ratio should be biased away from the high competition sex. Symmetrically, they showed that even if competition were intense among same-sex kin, if the competition were of equal intensity in both sexes (e.g., in a finite, random mating, and completely inbred deme), the favored sex ratio would be unity. Taylor (1981) concluded that, "Sib-mating (or selfing in hermaphrodites) or more generally mating between relatives, often contributes to these (biasing) factors, but the inbreeding which results in itself, has no role in determining sex ratio".

The ecological cost of males, then, may be overrated as a problem in explaining the adaptive value of sex. For the many organisms in which some form of male investment is required for successful reproduction, potential costs could be small or nonexistent. In organisms with minimal paternal investment, the costs will apply, but only if population structure forces the two sexes to compete asymmetrically (e.g., Taylor and Bulmer, 1980; Taylor, 1981). These costs can be reduced by adjusting the ratio of investment in different sex offspring. Inbreeding will reduce the genetic costs of syngamy by increasing the relatedness of parents and their offspring, and may, but need not, be associated with documented biases in primary sex ratios. In the latter case the association is not likely to be directly causal.

RECOMBINATIONAL LOAD

In a sexual population recombination will generate a potential genetic load by breaking up associations of harmoniously interacting alleles at different loci. By reducing the nonrandom genotypic disequilibria generated by selection, recombination may produce a fitness depression relative to a more perfect asexual replication. The degree of potential recombinational load is expected to vary with inbreeding intensity (Shields, 1979; 1982). Theoretical analyses and computer

simulations of relatively intense or extreme inbreeding (e.g., Jain and Allard, 1966; Nei and Li, 1973; Li and Nei, 1974; Charlesworth, 1976; Charlesworth et al., 1977), as well as empirical study of animals (e.g., Allard and Wehrhahn, 1964) and especially plants (e.g., Allard et al., 1968; Weir et al., 1972; Hamrick and Allard, 1972; Schaal, 1975; Jain, 1976), all indicate that both random and non-random inbreeding can increase allelic correlations across loci, whether the loci are linked or not, and in the presence or absence of epistatic selection (for general review, see Allard, 1975). In the end, a major consequence of relatively intense inbreeding (and perhaps a primary function?) can be viewed as, "organizing the entire populational genotype into a sort of giant supergene...to increase the frequency in the population of genotypes which confers (sic) high fitness and hence to increase adaptation to the local environment" (Allard, 1975, p. 124).

For example, in an inbred group fixed at each of two interacting loci (e.g., both parents AABB), recombination can never disrupt the allelic associations across those loci. The problem becomes more complex in the more realistic case when a population is segregating at some, or even many, loci, and individual heterozygosity is being selectively maintained. If the favored genotypes at interacting loci are heterozygotes (e.g., both parents AaBb), intense inbreeding will increase the probability that A and a will be associated only with B and b, an association that has already proven itself in successful ancestors. Inbreeding, then, in combination with natural selection, would be capable of increasing the likelihood of producing favored AaBb genomes.

In contrast, wider outbreeding increases the field of allelic variability (e.g., $A_1A_2B_1B_2 \times A_3A_4B_3B_4$) generating a wider variety of progeny genomes. In some or all of these, allele combinations will be produced that have never been tested in successful ancestors, and so are likely to have a reduced probability of interacting well and a greater probability of generating a significant recombinational load.

What has been described here as recombinational load is also the major component of the outbreeding depression I have described elsewhere as cases where members of different populations of the same species show considerable depressions in fitness when they outbreed too widely (reviewed in Shields, 1982). Indeed, it is remarkable how closely related two mates can be, and still show significant outbreeding depression (e.g., plants 10 m apart showing reproductive incompatibility, Price and Waser, 1978). Sex, whether inbreeding or outbreeding, will theoretically produce a recombinational load in segregating populations. By limiting potential mates to close relatives, inbreeding can minimize this recombinational load. This will occur because the probability that alleles that are brought together in offspring have already proven their compatibility in a successful ancestor increases with inbreeding intensity. At a multilocus level, inbreeding tends to preserve successful and coadapted genomes, with the degree of preservation being positively correlated with the continuity and intensity of inbreeding. "By contrast, an outbreeder is ill-equipped by virtue of its mating system to perpetuate specific genotypes adapted to specific niches" (Allard, 1975, p. 124).

A similar point can be made phenotypically. Williams' (1975) and Emlen's (1973) suggestion that sex functions to increase the variance of the probability distribution of a female's progeny's fitness potential (Fig. 2) assumes that sex is equivalent to wide outbreeding. Continuous inbreeding tends to mimic the theoretical effects of asexuality by producing a family of progeny with a narrower distribution of fitness potential (Falconer, 1960). As the intensity of inbreeding increases, the genotypic (and presumably phenotypic) resemblance between parent and offspring is expected to increase. Should environmental factors interact with a species biological properties to induce low selection intensities (e.g., Fig. 2), then inbreeding might be favored over outbreeding, and for the same reasons as asexuality.

Inbreeding, will ameliorate, and can eliminate, all of the disadvantages of sexual reproduction. If it is continuous and intense enough, it will reduce, and can eliminate, the genetic cost of meiosis, and if there is one, the ecological cost

of producing males. It will also reduce the degree of recombinational load, i.e., minimize the probability of outbreeding depression. With a single exception it can do everything that asexual reproduction does. If fitness potential and adaptation depend in any measure on any form of heterotic selection, then sex, whether inbreeding or outbreeding, will entail a segregational load. Segregation implies that any heterozygous locus will invariably produce progeny which are homozygous for its constituent alleles. Since such homozygous segregants are defined as less fit than their heterozygous parents, sex entails a fitness depression owing to their production (Wallace, 1968; 1970; Dobzhansky, 1970; Crow and Kimura, 1970). Given inbreeding's genotypic consequence of reducing zygotic heterozygosity (Crow and Kimura, 1970), segregational loads are likely to be greater for an inbreeder than an outbreeder. This is one of the theoretical components of inbreeding depression. As it is, only asexual reproduction is capable of transmitting diploid heterozygous genomes without a segregational load. Given this, and the fact that asexuality appears to do everything that inbreeding does, only more efficiently, the question remains why would asexuality not replace sex, even if the latter were inbreeding? If we equate sex and inbreeding for the sake of argument, then we are no longer limited to discussion of sex's traditional function of generating variable progeny in changed or changing environments. Since that argument necessarily assumed outbreeding, the question evolves to: is there a potential function of sex, compatible with the consequences of inbreeding, that predicts the occurrence of sex in place of asexuality in appropriate organisms or environments?

INBREEDING VERSUS ASEXUALITY: A QUESTION OF FIDELITY

Traditionally, and with little disagreement (e.g., Mather, 1973; Williams, 1975; Maynard Smith, 1978), the major advantage of asexual reproduction has been considered its copying fidelity. In one form or another, individual, kin, or group selection was viewed as favoring a balance between an enhancement of immediate fitness (via asexuality), and the flexibility required to meet future environmental flux through genetic change (via sexuality). Given a set of information (a DNA blueprint) that has controlled the development and activity of an individual) that has met the environmental challenge by surviving and reproducing more successfully than individuals with alternative blueprints, what is an appropriate strategy for maintaining that adaptive edge for that individual's descendants? In stable and uniform environments, a reproductive mechanism that permitted precise duplication of a successful blueprint should be favored. Previous workers (e.g., Stebbins, 1950; Williams, 1975; Maynard Smith, 1978) have suggested that this is precisely the consequence, and one of the potential benefits, of asexual reproduction. The logic of their arguments led to a necessary reliance on an assumption that sex (= outbreeding) must be associated with environments which varied in ways that prevented successful genomes in one generation from being successful in the next. Without that assumption, it followed that many organisms would be reproducing asexually, a conclusion at odds with much of the evidence (Williams, 1975; 1980; Maynard Smith, 1978).

If, for the moment, we assume that there are a broad range of environments and associated conditions that would favor precise replication of successful parental genomes (e.g., uniform and stable environments), then the usual inference would be that organisms in such environments should be asexual (e.g., Williams, 1975). For a variety of conditions that conclusion would be wrong. That it remains a consensus can perhaps be attributed to a failure to consider the reproductive consequences of mutation, and the usually hidden, and perhaps blinding, assumption that sex is synonymous with outbreeding.

Sex versus asexuality.--Reproduction can be divided into two component processes, (1) replication of parental DNA, and (2) fusion and transmission of replicated DNA during progeny production. Whether asexual or sexual, reproduction's components of replication and production are usually spatially and temporally independent. For a wide variety of organisms, mutation might be an inevitable biochemical consequence of replication (for review, Bernstein, 1977; Bernstein et al., 1981). For such

organisms replication itself could never transmit successful parental genomes with perfect precision. Asexuality would endow offspring with perfect copies, but of imperfectly replicated parental genomes, and so would not transmit the successful genome, but one altered by an unspecified number of novel mutations. In the face of significant mutation pressure, asexuality would be incapable of transmitting parental genomes with perfect fidelity. Asexuality's ratchet would cause the assimilation of such mutations in every generation (given a sufficient mutation rate), making the production of progeny genetically identical to their parents impossible. Because of the ratchet, the process might also be cumulative, so that any difference between an initially successful ancestor and a particular set of its lineal descendants, would increase with each bout of reproduction separating them (Fig. 3A). Ever equitable, asexuality would distribute this parental mutation load into all of an individual's progeny, with each offspring suffering, on average, equivalent fitness reductions.

With respect to recent mutation, sex should be capable of greater fidelity, though not perfection, in transmitting successful parental genomes. Recombination is expected to edit parental mutations into waste gametes or progeny (Fig. 3B, ii). Simultaneously, some progeny would be produced that in the extreme would resemble their parents at all but their own newly mutated loci (Fig. 3B, i). This conservative aspect of sex should theoretically apply regardless of the relatedness of mates (Felsenstein and Yokoyama, 1976; Bernstein, 1977; Shields, 1979; Bernstein et al., 1981).

Recently, however, Heller and Maynard Smith (1979) have argued that selfing, and by implication lesser levels of inbreeding, may suffer a ratchet similar to asexuality's. Their argument, while valid, is questionable in this context because it depends on special conditions. In their analysis, selfing suffers a ratchet, if and only if, the deleterious mutations in question are fixed in homozygous condition in a finite diploid population. They suggest that the ratchet operates, "... because an individual homozygous for i mutations cannot, by selfing, produce offspring homozygous for fewer mutations" (Heller and Maynard Smith, 1979, p. 290, emphasis added). Because of the small population size associated with selfing ($N_e = 1$), such conditions may occur with some frequency in selfers. Yet the ratchet will also operate in any size population regardless of inbreeding or outbreeding intensity as long as the loci in question are fixed in the entire population.

While their models are interesting, they may be less important to a comparison of sex and asexuality. I have (Shields, 1979) argued that sex can edit deleterious parental mutations immediately (i.e., in the generation) after their origin. In contrast, given a sufficient mutation rate asexuality is powerless. For example, if one mutation will definitely originate in every individual in every generation, then each of those mutations will be transmitted to all of an asexual individual's progeny, which will also add their own personal mutations. In the absence of recombination, selection cannot effectively eliminate such mutations except by extinguishing an entire line. If each mutation is somewhat deleterious whether alone in haploid species, or in heterozygous condition in diploids, then sex would have an immediate benefit (for similar arguments and conclusions, see Bernstein, 1977; Bernstein et al., 1981).

Since novel mutations are almost invariably going to be present in parents as members of heterozygous loci, recombination can edit, regardless of inbreeding intensity. In Heller and Maynard Smith's (1979, p. 289) words, even in selfers, "no ratchet operates on the heterozygous loci, because by selfing a heterozygote can give rise to a normal homozygote". I would add that if an ancestral locus were normally maintained in heterozygous condition by selection (e.g., A_1A_2), then a selfer newly loaded at that locus (e.g., A_1A_1) could not transmit the ancestral heterozygote. Selfing would still maintain the perhaps more important interlocus associations (A_1 with rest of the genome). However, relatively intense inbreeding, coupled with cross-fertilization, would permit maximum editing efficiency and maintenance of interlocus associations. If mates are close kin, but members of different nuclear families (i.e., possess no common parents), then the parental mutations each

carries will have arisen independently. The likelihood of two independent mutations at the same locus in two parents is low, so parental heterozygotes are more likely to be reconstituted while editing parental mutations.

This reduced fidelity may be at least part of the reason for the relative rarity of selfing and other forms of extreme incest in nature. Based solely on genetic considerations editing is more efficient and less wasteful when mates are close but non-family kin (e.g., first cousins, Shields, in press). Similar considerations may explain the relative rarity of automictic forms of sexual reproduction. Automictic forms that result in complete homozygosity (e.g., embryonic doubling, or premeiotic doubling and fusion of sister chromatids) cannot transmit adaptive heterozygotes at all. The other forms of automixis (e.g., fusion of primary pronuclei, or secondary nonsister chromatids) at best mimic the effects of selfing (i.e., some recombination potential with significant segregational loads, for review, see White, 1978, p. 287-8).

Sex will obviate the ratchet, minimizing mutational loads, while asexuality is incapable of doing the same in the face of significant, but not unrealistic, mutation pressure (Bernstein, 1977; Bernstein et al., 1981). With respect to the variation potentially generated by mutation, sex can reproduce successful parental genomes more faithfully than asexuality. This will be as true of extreme inbreeding as it is of any level of outbreeding. The hypothesis that sexual reproduction in the form of inbreeding may serve to preserve adaptation by increasing the resemblance of progeny and their parents is consistent with the "reasonably well established" generalization "that the frequency of recombination tends to be higher in selfing or inbreeding species or varieties than in related outbreeding ones" (Maynard Smith, 1978, p. 120, see also Stebbins, 1950; Darlington, 1958; Grant, 1958; Charlesworth et al., 1977). Given the obvious terminological differences, perhaps the true association is between increased inbreeding intensity and increased levels of recombination (usually estimated by recombination indices = number of chromosomes + number of chiasmata per genome, see Darlington, 1958). As the continuity and intensity of inbreeding increase, reaching a maximum at obligate selfing, the field of allelic variability available for recombination is expected to decrease. This could reduce to nil the probability of disrupting extant coadapted allele complexes. At the same time, mutation will continue unabated, so that increasing recombination, by increasing crossover opportunities, will increase the efficiency of both editor and composer with wholly beneficial consequences. If, on the other hand, inbreeding intensity were reduced, then the probability of disrupting coadapted complexes would increase, unless the level of recombination also declined. The observed correlation, then, is compatible with a primary function of inbreeding of preserving that which has proven itself.

Inbreeding Versus Outbreeding.--Wide outbreeding is even more likely to produce progeny with genomes significantly different from their successful ancestors than is asexuality. Though the editor would operate, minimizing mutational loading, the fixed genetic differences between mates would generate a diversified progeny. Few or none would be expected to closely resemble either of their parents. The cost of such diversification would be a significant recombinational load (outbreeding depression), that could outweigh any benefits gained via the editor (Fig. 3).

For example, if the ancestral and coadapted portion of an individual's genome were indicated by pluses (e.g., Fig. 3B), then outbreeding would entail mating (+) individuals with others carrying alleles from different complexes (e.g., minuses, so + - - + a, Fig. 3B). Parental mutations could be edited, but the resulting progeny would carry potentially maladapted mixtures of pluses and minuses never before associated in a successful individual. To continue the blueprint analogy, outbreeding would be like taking two different blueprints, cutting them into pieces, and reassorting them into entirely novel combinations. While the new structures might function, they would not be likely to resemble the originals in any but a cursory way.

If conditions existed that favored relatively faithful transmission of parental genomes, then inbreeding could be favored over both asexuality and outbreeding. In-

breeding's favor would stem from its versatility, as it reduced (or eliminated) the disadvantages associated with both asexuality and outbreeding, and managed to gain their respective benefits. By reducing the field of allelic variability available for recombination, it would reduce or prevent the disruption of coadapted genomes. By reducing effective population size, and reducing the number of different individuals in a deme's ancestry, inbreeding would produce a family of genetically homogeneous (and not necessarily homozygous, Shields, 1979 and in press) individuals. The homogeneity would only become apparent upon inspection of the large ancestral genome (all loci except those with recent mutations), at which all deme members are expected to carry similar arrays of previously associated alleles. For this ancestral genome, that which recombination broke apart, syngamy would reunite, since true novelties would be unavailable. Of course, if there were segregating loci in such a deme, even intense inbreeding would entail some diversification of progeny. By limiting the field of recombination, inbreeding cannot produce exact duplicates of parental genomes, but it will reduce the number of expected differences and most importantly the probability that such differences will entail untried associations of alleles likely to produce outbreeding depression. Inbreeding would not be expected to produce perfect reproductive fidelity, but it would do a more efficient job than outbreeding which, by definition, is a diversifying influence.

In the same inbreeding population recombination would act to reduce the detrimental gametic disequilibria generated by the occurrence and transmission of rare deleterious mutations. The editor increases the potential efficiency of selection against such mutations with immediate benefit. Since most mutations are likely to be deleterious (Fisher, 1930), the effect of the editor may be a primary function of recombination, especially when it is associated with mating of relatively close kin (also see, Daugherty, 1955; Felsenstein, 1974; Manning, 1976b; Bernstein, 1977; Bernstein et al., 1981).

As an added bonus, and perhaps a secondary function, inbreeding sex also facilitates composition of novel but favorable allele combinations with greater frequency than asexuality, just as the Fisher-Muller school has long maintained. In contrast to outbreeding, the limited field of alternative alleles in potential mates associated with inbreeding makes it less likely that, "... a successful combination of characteristics is attained in individuals only to be broken up in the next generation by the mechanism of meiosis itself" (Wright, 1931). In the end, fusion of related gametes, themselves the product of recombination of the previous generation's chromosomes, is a flexible, and yet a conservative process, "affording an opportunity for new departures and in tending to secure a holding fast of that which is good" (Geddes and Thompson, 1914; see also Grant, 1958; 1963; 1971).

The relative costs postulated to be associated with the alternative reproduction strategies (Fig. 2 and Table 1) suggest that if the mutational load of asexuality is greater than the combined segregational and recombinational load of sex, then sex can be favored by individual selection for its immediate benefits. Similarly, if inbreeding's greater segregational load is more than balanced by a reduced recombinational load relative to a specific level of outbreeding, then inbreeding will be favored. As with any system with costs and benefits, then, different conditions may favor different choices and different optimal levels of inbreeding or outbreeding for different species (for review, Shields, 1982 and see below).

WHY FIDELITY

If inbreeding does function to preserve successful genomes during reproduction, more specific predictions concerning who should inbreed are possible. Inbreeders should occur in environments in which successful parental genomes have a high probability of being successful in subsequent generations. Extending Williams' (1975) gambling analogy, if winning lottery numbers (i.e., well adapted, high fitness genomes) remain relatively constant from generation to generation, rather than

Table 1. The relative values of the genetic costs hypothetically associated with alternative reproductive strategies.

Potential Costs	Reproductive Strategy		
	Outbreeding	Inbreeding	Asexuality ¹
Cost of meiosis	high	low	none
Cost of males	high or none	low or none	none
Recombinational load	high	low	none
Segregational load	low	high	none
Mutational load	low	low	high

¹ Here asexuality is considered equivalent to ameiotic parthenogenesis or apomixis as most forms of automixis do include some capacity for recombination (see text for further discussion).

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changing haphazardly, then it will benefit a current winner to bequeath to its progeny ticket with numbers as similar to its own as possible. What have been called uniform, constant, or stable environments would be expected to favor inbreeding. Characterized by improbable spatial homogeneity and temporal stability, such environments are expected to be rare. However, these only generate sufficient and not necessary conditions for inducing or maintaining inbreeding's favor.

Overlooked in the search for changing environments that might favor progressive (i.e., sexual) reproduction is the selective relevance of the stability or constancy of the association between particular genomes and environments. Adaptation to ecological conditions need not be limited to allelic substitution in response to every environmental fluctuation. One common alternative appears to be the fixation of complex epigenetic systems that adaptively respond to environmental flux phenotypically rather than genetically. Characters like developmental and genetic homeostasis, switch genes controlling phenotypic expression in heterogeneous environments, canalization, and experiential modification of behavior (learning), all permit and promote development of favored phenotypes in the face of considerable environmental perturbation (for review of genetic "buffering", see Lerner, 1954; Waddington, 1957; Wright, 1977; for review of learning, see Mason, 1979; Pulliam and Dunford, 1980).

The distribution of adaptive epigenetic systems suggests a possible phylogenetic trend, with the higher complexity that results in genetic independence of ecological (both biotic and abiotic) change being associated with a more advanced state (e.g., vertebrates). An ideal example of a complex adaptive system might be the vertebrate immune response. If a heritable genetic response were required to deal with every change in potential pathogens, most vertebrates would have lost the war to their parasites long ago. Owing to their short generation times and large population sizes, the average bacteria or virus is constantly generating genetic novelty. Because of their longer generations and much lower fecundity, the average vertebrate host could not possibly respond with genetic changes in the germ plasm to every novel pathogen. Such a race would be expected to go to the reproductively swifter pathogen. Given this challenge, the favored strategy appears to have been the evolution of a genetically complex but phenotypically plastic immune system (e.g., Jerne, 1974; Burnet, 1975).

When the immune response, or other complex epigenetic systems are considered, a genome might be considered a compilation of information gathered by all of its ancestors. Whether an environment is constant or fluctuating, homogeneous or heterogeneous, predictable or not, in an ecological time frame, if it has been associated with a particular lineage for sufficient evolutionary time, then the in-

formation carried in each of the lineage's genomes should be current and vital to adaptation in that environment. If such lineage-environment associations are relatively stable, then parent-like genomes will usually have higher probabilities of success in offspring generations. Only radical ecological changes producing states beyond the historically normal range of variability are likely to reduce intergenerational correlations enough to favor radical genetic changes in response. Such radically changing environments are as improbable as perfectly constant ones (Maynard Smith, 1978).

The relatively slow pace of phylogenetic evolution, the stability of basic developmental processes and body plans across large taxonomic groups, and the occurrence of remarkable protein similarities between otherwise divergent groups are all consistent with the view that genomes especially at the regulatory level may change slowly on an evolutionary time scale (for reviews, see Mayr, 1963; Simpson, 1967; Gould, 1977). Such a thesis implies that at any point in time the vast majority of living organisms are the products of relatively stable lineage-environment interactions. If true, conservative reproductive mechanisms should approach universality in nature. While this may sound novel, it may only be a restatement of the fact that the organic world is not one giant panmictic breeding unit. Instead, it is divided into more or less isolated and genetically different interbreeding groups variously designated species, subspecies, or populations. Even outbreeding, when defined as species-wide panmixis, is a relatively conservative process, when compared with the potentially more progressive, though rarely practiced, interspecific or intergeneric interbreeding.

PREDICTIONS AND EVIDENCE

Given that reproduction should be conservative, two questions emerge, (1) how conservative, and (2) how is the conservatism to be achieved? As stated, the argument implies that the favored level of conservatism will be controlled by the stability of a given lineage-environment association. This suggests that if either the environment or the lineage changes in a way that makes phenotypic tracking impossible, a less conservative reproductive process might be favored. I would suggest that this is exactly the case for many high fecundity organisms. First, such high fecundity ($> 10^5$ offspring/female/lifetime) organisms (e.g., marine invertebrates, some plants) are less likely to possess well developed buffering systems (Manning, 1976b). Thus, they are more likely to respond to environmental change with genetic change. Second, by producing enormous numbers of variable progeny, high fecundity parents increase the probability that the pool of competing individuals that includes their progeny will differ from the pool in which they themselves proved their worth. Thus, high fecundity may be associated with lineages that fluctuate in time regardless of environmental flux. An environment need not change radically, it need only generate conditions favoring high fecundity. The resulting association between intense selection and large numbers of variable progeny will tend to favor the more progressive outbreeding end of the sexual continuum owing to the associated production of sisyphian genomes (Fig. 2). I agree with Williams (1975; 1980; see also Bulmer, 1980) that the variable progeny, sib-competition models can explain the occurrence of outbreeding sex in high fecundity organisms. The actual decision about what constitutes "high" or "low" fecundity in the context of these models is arbitrary. My usage is a bit less conservative than Williams' (1975), but the point is the same. Less than 100 progeny is certainly low fecundity, greater than 10^7 is certainly high, somewhere between these values is a switch point that current models are unable to quantify.

If lineage-environment associations were more stable, then more conservative reproductive processes would be favored. If we assume that such stable associations are normally associated with low fecundity ($< 10^4$ OFL), then the more conservative processes (i.e., asexuality and inbreeding) would also be associated with low fecundity. In the absence of mutation and the ratchet, asexuality would be the ultimate

conservator, so we can refine this prediction. If the rate of mutation per genome per generation were low enough to prevent the ratchet, then low fecundity organisms should reproduce asexually. If, on the other hand, mutation rates were high enough to induce the ratchet, but low enough so that the ratchet did not operate in every generation, then a low fecundity organism could alternate bouts of asexual and sexual reproduction (i.e., a heterogonic strategy). Under such conditions, the number of asexual generations separating two sexual events, should be negatively correlated with mutation rates. Finally, if mutation rates were high enough to insure the ratchet's operation in every generation, then low fecundity organisms should inbreed in every generation (Table 2).

Table 2. Predicted associations among fecundities, mutation rates, and reproductive strategies.

Mutation Rate/ Generation/ Individual ¹	Fecundity	
	Low (< 10 ⁴)	High (> 10 ⁵)
Low	Asexual	Asexual
Medium	Heterogonic ²	Heterogonic
High	Inbreeding	Outbreeding

¹ Alternation of asexual and sexual generations, may be sporadic or cyclic.

² The mutation rate/generation/individual (M) is equal to the mutation rate/locus/generation (10⁻⁹ - 10⁻⁴) times the number of loci per individual (10² - 10⁵) and so theoretically can range from about 10⁻⁷ to 10 mutations/generation/individual. Any M greater than 1.0 would favor obligate sexuality, since all asexual progeny would accumulate mutations in every generation regardless of selection intensities.

MUTATION RATES AND REPRODUCTIVE STRATEGIES

To examine these specific predictions we need only investigate the association between expected mutation rates and mating strategies. At the allelic level mutation is a physicochemical event, and so absolute mutation rates may be a function of absolute time. If we assume that average mutation rates are normally minimized by natural selection (for reviews, see Williams, 1966; Maynard Smith, 1978), the decreasing generation time will decrease the number of mutations arising per generation. If we also assume that mutation occurs independently at different loci, then reducing the number of functional loci (i.e., decreasing genome size) will decrease the number of effective mutations per genome. Thus, minimal mutation rates per individual per generation are expected in organisms with small genomes and short generation time. The latter expectation is consistent with the observed per locus mutation rates of 10⁻⁹ to 10⁻⁶ per generation characteristic of prokaryotes and many unicellular eukaryotes with short generation times (< 48 h). The higher per locus mutation rates (10⁻⁶ to 10⁻⁴) observed in most higher eukaryotes with longer generation times (weeks to many years) are also in line with expectation (for reviews, see Dobzhansky et al., 1977; Wright, 1977).

In an elegant and somewhat overlooked paper (e.g., it is not cited in Maynard Smith, 1978), Manning (1976b) explored the phylogenetic distribution of asexuality and sexuality in an attempt to answer the question, "Is sex maintained to facilitate or minimize mutational advance"? He suggested that many groups had "evolved methods of making themselves independent of variations in the external environment", by employing, "both behavioural and physiological buffering mechanisms". Since such

organisms (primarily cephalopods, many insects, and especially the vertebrates) usually perceive the environment as fine-grained (Levins, 1968), their, in many cases, exclusive sexuality cannot be attributed to varying environments. He concluded that for these organisms, "the most important function of sex is to reduce the mutation load" (by obviating the ratchet). Since such organisms also have the largest genomes and longest generation times, they further support his argument and confirm my prediction regarding the association of sex and expected mutation rates. The exclusive sexuality in these fine-grained species is not entirely consistent with the view that sex functions primarily to meet the challenges of a varying environment.

In contrast, species that perceive their environments as coarse-grained (Levins, 1968) in space or time (including bacteria, protozoa, porifera, coelenterates, platyhelminthes, bryozoa, annelids and many plant species) show a reduced capacity for homeostatic buffering, and would, therefore, be more likely to respond to fluctuating environments genetically. If sex did function to meet the demands of such varying environments, then such species should be "predominantly sexual" (Manning, 1976b). They are not, most being predominantly asexual or heterogonic to varying degrees. For example, Manning (1976b) noted that while the bacteria often possess parasexual processes, asexuality is their more common reproductive strategy. I would add that as predicted, it is usual in prokaryotes for many asexual events to separate independent parasexual events (i.e., the ratio of asexual to sexual generations is high). The prokaryotes also have the smallest genomes and shortest generation times of the organisms examined. Similarly, many of the short generation protozoans appear to rely almost exclusively on asexuality, while many that engage in sex do so relatively infrequently (high asexual/sexual ratio). Heterogonic life histories in the eukaryotes also appear to be associated with relatively short generation times (< 2 weeks), while the asexual/sexual ratio also declines as predicted.

These broad comparative data on the phylogenetic distribution of asexuality and the frequency of its occurrence in heterogonic species are consistent with a hypothesis that the major factor controlling the occurrence of asexuality is mutation pressure. If a species can reproduce fast enough, relative to the size of its genome, then it can beat the mutational clock. That is, if some progeny can be produced with parental genomes unaltered by deleterious mutation, then asexuality will be favored over any sexuality with its reduced conservatism and increased segregational load. If, and perhaps this is more likely, mutation rates are intermediate so that deleterious mutants are assimilated, but at relatively low rates during the asexual portion of a species' life cycle (i.e., many but not all are loaded) then when the assimilated load reaches a sufficient level, sex and its editor can intervene, cleansing a family of its accumulated mutations. Only when mutation rates are high enough to drive the ratchet in every generation and load all the progeny produced by a female will the editor automatically balance sex's segregational load and exclusive sex finally replace asexuality. In answer to Manning's question, and consistent with my predictions, it appears that sex may be maintained to minimize mutational advance, that is to conserve parental genomes (for additional supporting evidence, see Manning, 1976b; Bernstein, 1977; Bernstein et al., 1981).

FECUNDITY AND REPRODUCTIVE STRATEGIES

If the genomic mutation rate is high enough to induce the ratchet in every generation, then sex may be a necessity in every generation. If an organism facing this mutational challenge does not have sufficient fecundity to afford the gamble of outbreeding, then it should employ the more conservative strategy of inbreeding. Organisms characterized by large genomes, long generation times, and low fecundity (e.g., many insects and plants, almost all of the vertebrates) should be inbreeding. Those characterized by high fecundity are expected to be outbreeding (Table 2).

I have reviewed the evidence for these associations in a variety of animals elsewhere (Shields, 1982). With very few exceptions, the relationships were as predicted. High fecundity animals (e.g., many marine invertebrates and fishes) dispersed vagrantly over very large distances and cross-fertilized with neighbors after settling, generating very wide outbreeding. Low fecundity animals generally dispersed philopatrically (moving small distances from their birthplace) and showed a variety of other characters (e.g., positive assortative mating with relatively close kin on the basis of signal dialects) consistent with a conclusion that they were inbreeding, and optimally, by random mating in small semi-isolated demes (for complete review, see Shields, 1979; 1982; and in press).

The crucial predictions were that based on genetic consequences alone, "Philopatry which is effective in producing relatively intense inbreeding should occur in, and only in, low fecundity organisms. Wider outbreeding resulting from vagrant dispersal should be characteristic of high fecundity organisms" (Shields, 1982). While the patterns of dispersal observed in animals are generally consistent with these predictions, the model is more general. The same predictions should be borne out by examining dispersal in the plants. Not only do the higher plants offer as wide a range of fecundity as animals, but, owing to their possession of two classes of potential propagules (seeds and pollen), they offer a wider range of possible associations between dispersal and mating strategies. Most adult plants are sessile hermaphrodites, so that individual (vs. gene) dispersal will occur primarily via diploid seeds. The mobility of pollen will permit adjustments in mating strategy independent of requirements for individual dispersal met by seed, since pollen's primary function will be mating and gene dispersal. Thus plants offer a stronger test of the hypothesis predicting a negative correlation between fecundity and inbreeding intensity because they can falsify it in more ways than was possible with animals (Table 3).

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Table 3. Predicted associations between fecundity and dispersal strategies for pollen and seeds of the higher plants (gymnosperms and angiosperms).

Fecundity		Dispersal Systems	
Low	Seed Philopatry +	or	Seed Vagrancy +
	Pollen Philopatry or Selfing		Selfing
High	Seed Philopatry +	or	Seed Vagrancy +
	Pollen Vagrancy		Pollen Philopatry or Pollen Vagrancy

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Given philopatric seed dispersal, plants can inbreed by limiting pollen dispersal. If, on the other hand, greater outbreeding is favored, a species with philopatric seed dispersal can still outbreed by dispersing its pollen vagrantly. Given vagrant seed dispersal, any pollen dispersal (either vagrant or philopatric) is expected to result in fairly wide outbreeding. This occurs because the seeds developing in proximity are likely to have been drawn from a wider area, so that near neighbors (and potential mates) are unlikely to be particularly close relatives. If a species is forced to disperse seed widely, while inbreeding is favored, then

the only effective mating system would be selfing (i.e., zero pollen dispersal). Of the six potential dispersal strategies available to plants, the three promoting inbreeding should be associated with low fecundity, and the three associated with increased outbreeding should occur in high fecundity species (Table 3).

Because of the absence of data collected or presented in a manner suitable for testing these predictions directly, only weaker indirect tests are possible. Over the years, plant biologists have developed a number of empirical generalizations about relationships among growth habits (annual vs. perennial), environmental stability, and mating systems (selfing vs. crossing). Perhaps the best confirmed and most widely cited of these rules is the association of selfing and the annual habit and crossing and the perennial habit (Table 4; and for reviews, Stebbins, 1950; Grant, 1958; Baker, 1959; 1963; Harper, 1977). One factor con-

Table 4. The relation between inbreeding intensity and growth habit in selected grass species (Gramineae, after Stebbins, 1950).¹

Mating System	Perennials	Annuals
Self-incompatible obligate crossing	26	0
Self-compatible frequent crossing	40	3
Self-compatible cleistogamous obligate selfing	5	27

¹ Similar correlations have been demonstrated in a wide variety of angiosperm families (Grant, 1975).

sidered partially responsible for this association is the joint correlation of the annual habit and selfing with unstable habitats that place a premium on colonizing ability (Table 5, Stebbins, 1958; Baker, 1963; Grant, 1975; but, see Jain, 1976).

Table 5. The associations between mating systems, chromosome numbers (increased number = increased recombination = greater effective outbreeding), and habitat type in plants of the composite tribe Cichoreae (after Stebbins, 1958).¹

Mating System	Chromosome #	Habitat Types		
		Stable	Intermediate	Unstable
Crossing	9-8	47	44	7
Crossing	7-6	2	26	0
Crossing	5-3	4	13	1
Selfing	-	6	28	23

¹ Tabled values are the number of species observed.

The rationale is that a self-fertile organism is more efficient, both ecologically (e.g., pollen always available, a single propagule is enough to start a population,

high intrinsic rate of increase), and genetically (owing to selfing's capacity to preserve a well-adapted genome, e.g., Grant, 1975) at colonizing suitable empty habitat. Grant (1975) explicitly suggests that the entire association may be viewed within the theoretical frame of *r*- and *K*-selection. He concludes that unstable, i.e., ephemeral habitats, and the resulting needs of colonizing, generate *r*-selection favoring rapid development, "high" fecundity, and the annual habit. In contrast, stable and saturated environments select for the perennial habit and the other correlates of a more competitive *K*-strategy.

There are difficulties with this interpretation of the factors likely to be important in controlling the occurrence of self-fertilization. For example, the interpretation is inconsistent with the associations observed in superficially similar marine invertebrates. In the animals, the colonizing, high fecundity, *r*-strategist species disperse passive propagules that travel great distances before settling, in much the manner of a weedy annual. Like the plants many are hermaphrodites. Unlike the plants, all are almost exclusively cross-fertilizing and therefore outbreeders. In the marine invertebrates, selfing and other traits promoting inbreeding appear in species living in stable and saturated environments (Shields, 1982). In contrast, equivalent *K*-selected plant species living in stable habitats appear to cross-fertilize and outbreed (Table 5).

The same plant-animal comparison illustrates some of the difficulties the fluctuating environment hypotheses have in explaining the advantage of sexual reproduction. These predict that species living in relatively unstable environments that produce progeny likely to face changed conditions should reproduce sexually. On the other hand, species living in relatively stable environments would be expected to reproduce more conservatively via increased inbreeding or even asexuality. The associations observed in the marine invertebrates appear to be consistent with this hypothesis. Yet the hypothesis is flatly contradicted by the reversed pattern observed in plants (Table 5). Must we conclude that the plant and animal kingdom have evolved in opposite directions in response to the same selective pressures. Or is there a simpler, and perhaps more nearly universal explanation for the patterns characterizing both kingdoms?

I believe that the problem stems from concentrating on annual (clutch size) rather than lifetime fecundity (e.g., Grant's description of the higher fecundity in annuals relative to perennials, Fig. 4). Of course it is lifetime fecundity that is important in evolutionary arguments. The association of low lifetime fecundity and the annual habit, which is correlated with selfing, supports the predicted association of low fecundity and increased inbreeding. Selfing may be adaptive in many colonizing plant species, but for different reasons than are usually offered. Given an ephemeral environment selecting for vagrant seed dispersal, the only mating system permitting inbreeding is self-fertilization (Table 3). If the annual habit and the specific environmental conditions limit lifetime fecundity below the critical level necessary to favor outbreeding ($< 10^4$ OFL), then an annual should inbreed (unless mutation rates are low enough to favor asexuality). If it is to inbreed at all, the low fecundity, colonizing annual must self-fertilize. Truly high fecundity plants with vagrant seeds including both annual and perennial epiphytes or parasites (e.g., orchids, reviewed in Salisbury, 1942) normally cross-fertilize and thus outbreed. Since they are also colonizers, if the more traditional arguments (e.g., Baker, 1959) were correct, they might be expected to inbreed (i.e., self). That they, like their high fecundity marine invertebrate counterparts, are actually outbreeding is more consistent with the hypothesis predicting an association between fecundity and mating system. From the perspective of genetic consequences, the non-optimal selfing observed in annual plants may be the only option available if inbreeding is a necessity (Shields, 1982).

The large overlap in fecundities between annual and perennial species of plants (Fig. 4) permits a more detailed analysis of my predictions. Since the primary determinants of seed dispersal distance by wind are seed weight, height of release, and the efficiency of auxiliary structures affecting air-worthiness (Harper, 1977),

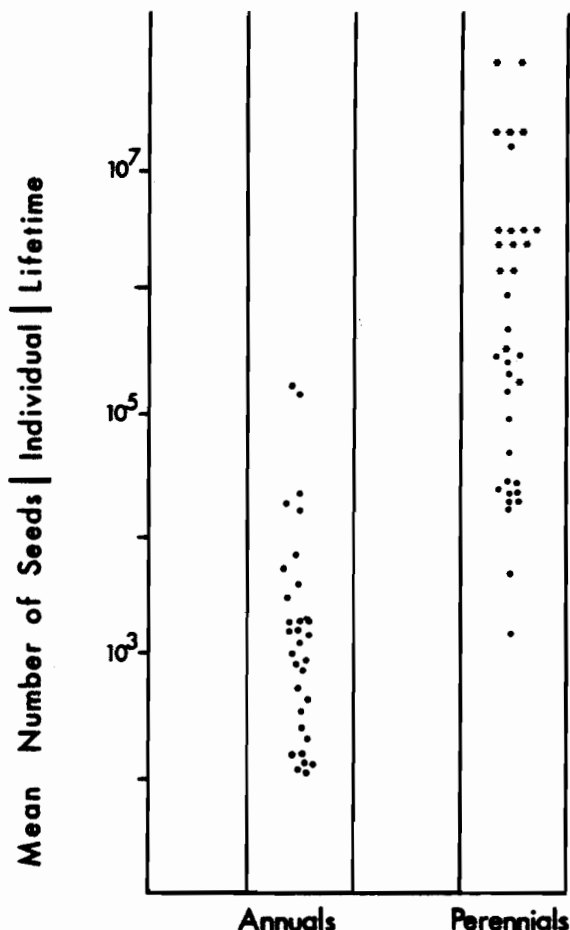


Fig. 4. The association between lifetime fecundity and an annual or perennial habit for selected plant species: herbs or shrubs (•), trees (*). Unless they were given, lifetime fecundities are the products of annual seed production (average clutch size) and minimum estimates of reproductive lifespan, i.e., 5 yrs. for herbs and shrubs, 100 yrs. for trees (taken or calculated from data in Salisbury, 1942; Harper et al., 1970; Harper and White, 1974).

increasing the number of seeds produced will usually increase vagrancy by reducing each seed's weight. If we assume that tiny "dust" seeds will disperse more vagrantly than larger seeds, then low lifetime fecundity species with large clutches of small seeds (colonizing annuals) should self-fertilize (Table 3). High fecundity species with similarly vagrant dust seeds must cross-fertilize to insure the predicted outbreeding, which they appear to do (e.g., perennial orchids like *Goodyera repens*, some trees, *Betula* spp. and *Pinus* spp., and some annuals *Sonchus asper* and *Linaria minor*, see Salisbury, 1942; Harper and White, 1974).

When environmental pressures (e.g., the requirements of successful germination) select for larger, less motile seeds, there are three possible strategies (Table 3). In high fecundity, and therefore usually perennial, species, increased pollen vagrancy could increase outbreeding. Species such as Oaks (*Quercus* spp.) should, and apparently do, disperse pollen fairly widely (Grant, 1975). Finally, in non-colonizing, low and medium fecundity species, philopatric seed dispersal should be coupled with philopatric pollen dispersal or selfing, regardless of individual longevity (Table 3). The optimal inbreeding arguments (see above), however, suggest that under such conditions selfing should be rare. The expected seed and pollen philopatry resulting in random mating in small demes is extremely common in plants (e.g., Ehrlich and Raven, 1969; Levin and Kerster, 1974), and is often discussed under the apt de-

scriptive term "vicinism" (e.g., Grant, 1971; 1975; Bradshaw, 1972; Antonovics, 1976).

Although the evidence is less direct, it appears that plants like their marine invertebrate counterparts show the predicted association between fecundity and inbreeding intensity. That both groups show this association, while showing contradictory associations in light of common alternative explanations based on colonizing ability, or r- and K-selection, is perhaps the strongest evidence for a causal relation between fecundity and mating strategy. The actual selective pressures which help shape the associations remain unknown, but the observed correlation fails to falsify the general model (Table 2).

CONCLUSIONS

Williams (1975, p. 7) maintains that, "For answering questions on function in biology, comparative evidence is more reliable than mathematical reasoning". While there are problems (e.g., non-philopatric wildfowl and perhaps the rare male phenomenon reviewed in Shields, 1979; in press), the bulk of the comparative evidence reviewed here is consistent with the hypothesis that inbreeding may be adaptive. The paradox that sex appears to benefit species, while harming individuals, rests on an assumption that sex is equivalent to wide outbreeding. Inbreeding can reduce the expected costs of sex, while maintaining an advantage over asexuality. Relative to outbreeding, inbreeding will reduce the costs of meiosis and syngamy owing to the increased relatedness of mates and the resulting possibility of reducing investment in males or male function. Inbreeding can also reduce recombinational load by facilitating the faithful transmission of coadapted combinations of alleles at interacting loci. Relative to asexuality, inbreeding will not suffer a mutation accumulating "ratchet", and thus inbreeders are likely to gain the immediate benefit of a reduced mutational load in at least some of their progeny. Owing to its flexibility and capacity to transmit successful parental genomes with maximum fidelity, inbreeding is expected to be common in organisms produced by stable lineage-environment associations. The occurrence of predicted associations between (i) mutation rates and the occurrence and relative frequency of sex and asexuality, and (ii) fecundity and inbreeding intensity are consistent with a view that inbreeding functions to conserve adaptation by preserving parental genomes. While the argument is far from proven, the consistency of its theoretical predictions with the empirical evidence makes further consideration appropriate. If the argument is true, it may resolve the paradox of sex. Inbreeding can have immediate positive effects on individual reproductive success relative to alternative strategies. If conditions are such that inbreeding's notorious segregational load (borne by a portion of an individual's progeny) is less than outbreeding's recombinational load (borne by a larger portion of progeny), and asexuality's ratchet-induced mutational load (borne by all progeny, given sufficient mutation rates), then inbreeding sex can be maintained by individual selection. It may no longer be necessary to invoke future needs, species benefit, or an inability to evolve adaptively in order to explain the ubiquity of sex.

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