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The cost of sex

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Introduction

Between 1870 and 1935, sex presented three major problems for evolutionists to solve. First it was necessary to explain the widespread sexual differentiation of animals that extends beyond the primary requirements of reproduction. Darwin (1871) introduced sexual selection as the solution to this problem. Second, there was a need to explain stability of the sex ratio. This problem was resolved by Fisher (1930), who showed quantitatively how natural selection can stabilize the sex ratio. Third and most significant was the problem of explaining the value of sex in relation to its cost, and of showing by a favorable ratio of benefit to cost why sex should be widely maintained. This problem was dealt with by Fisher (1930) and Muller (1932), who resolved it by reference to group selection. Group selection, if accepted as sufficient to offset the cost of sex to individuals, would also account for the persistence of sexual selection.

Significant additions are still being made to our understanding of sexual selection and of sex ratios (Arnold, 1985; Charnov, 1982; Karlin and Lessard, 1986), but the general form of the original solutions to these problems remains intact. In contrast, the explanation proposed by Fisher and Muller for the maintenance of sex now seems of doubtful validity because of the high cost of sex to individuals and the weakness of the group selection mechanism in maintaining any trait that is accompanied by high cost to individuals (Williams, 1975).

Major costs of sex were evident to Darwin, Fisher, and Muller. Most obvious would have been loss of fitness associated with conflict or risk that occurs as a result of sex. Within a population that is exclusively sexual, this cost can be offset by sexual selection, as shown by Darwin. However, given that asexual reproduction may arise at some low but finite frequency in any group of organisms, sexual selection cannot explain why asexual forms, which would be free of such cost, would not have a great advantage over sexual forms. Also long recognized is the fragmentation of gene combinations of high fitness by sexual recombination, which would seem very costly to the individual, especially among organisms of low fecundity.

Interest in the cost-benefit analysis of sex was essentially dormant from 1935 until after 1960. Three factors seem to have caused a revival of interest

in the subject. First, Crow and Kimura (1965) reopened Muller's work and, while not controverting it, introduced a basis for skepticism, as explained by Williams (1975). Next, widespread uncritical use of group-selectionist arguments by biologists stimulated Williams (1966) to stress the inadmissibility of group-selectionist explanations for most evolutionary phenomena. Shortly thereafter, Maynard Smith (1971 a) identified a broadly applicable twofold cost of sex caused by the contribution of male genetic material to a zygote whose material existence is primarily an investment of the female organism. Given the increasingly critical atmosphere surrounding group-selectionist arguments and the stimulus of Maynard Smith's discovery of a major individual cost of sex that had not previously been identified, the costs and benefits of sex were examined rigorously for the first time, as summarized in reviews by Williams (1975), Maynard Smith (1978), and Bell (1982). As yet, there is no consensus of opinion on the manner in which sex has been widely maintained in the face of its high apparent cost.

Problems posed by the cost of sex can only be resolved by the discovery of major advantages of sex. For this reason, possible costs of sex have received less attention than possible advantages of sex. It is still useful, however, to consider the costs of sex. The costs of sex define the minimum opposing benefit that sex must offer individuals in order to be sustained by individual selection. Because the costs of sex vary among groups of organisms, it is also possible that the costs of sex will help define the advantages of sex.

My aim here is to present an overview of factors that are now known to contribute to the cost of sex, and to show how these may apply differentially across groups of organism. Most of these factors have been well explained elsewhere. However, the cost of sex has not been treated as a unified subject, and it may for this reason be useful to consider all potential costs together.

Mode of selection for sex

The advantages of sex are only peripheral here, but they cannot be completely ignored because they provide context for evaluating the costs of sex. It is impossible here to recapitulate the complex arguments that surround the advantages of sex, but a brief overview of the advantages is possible. A distinction between the group selection mode and the individual selection mode for sex is particularly important.

Williams (1975) searched for advantages of sex that would operate over the short term, and that would for this reason not require logic based on group selection. For organisms that have high fecundity, he showed that sex may offer a sustained advantage to individuals by maximizing the genotypic variety of offspring, and thus maximizing the probability that a parent will produce genotypes that are exceedingly fit for a specific but temporary suite of environmental conditions. According to this model, continual change in

the environmental conditions (low heritability of fitness) prevents an organism from achieving an advantage from a reduced rate of recombination.

In analyzing William's arguments, Maynard Smith (1978) concluded that strong selection, when combined with sib competition, could support a sustained advantage for sex among individual organisms by reducing sib competition. At the same time, he expressed doubts about the magnitude of this benefit in relation to the cost of sex. Furthermore, in exploring the advantages of sex in a complex environment, Maynard Smith (1978) (cf. Felsenstein and Yokoyama, 1976) found that sex (recombination) offers clear advantages for individuals only if there is a continual reversal in the correlation of critical environmental variables, which he considered unlikely. Bell (1982) has called such an environment 'capricious'.

Maynard Smith may have taken an overly dim view of the likelihood that environments are capricious. Bell (1982) noted that the biotic component of the environment is likely to be capricious because of the homeostatic nature of selection among competitors or among predator and prey species. The genetic tracking of hosts by diseases may be an especially important example of this 'Red Queen' phenomenon (Bremermann, 1985).

While Williams and Maynard Smith agreed that individuals may derive advantages from sexuality, both concluded that the individual advantages for sustained sexuality, especially in organisms of low fecundity, are unconvincing as generalities. However, the possibility remains that a satisfactory explanation will yet be developed and widely accepted, and that sexuality will ultimately be understood as an adaptation that is maintained by individual selection.

Bell (1982) applied an hypothesis-testing technique to the entire suite of observations on the occurrence and distribution of sexuality among multicellular heterotrophs as a means of identifying the explanations of sexuality that are most consistent with the occurrence of sexuality. This approach is clearly preferable to the selection of examples that come to mind readily or that most clearly illustrate a theoretical principle. Bell, following principles suggested by Ghiselin (1974), Williams (1975), and others, concluded that environmental heterogeneity, and especially spatial heterogeneity, provides the most likely explanation for the maintenance of sex. Bell found the phylogenetic and ecological evidence in animals to be generally consistent with this interpretation, given two assumptions that seem correct on the basis of present knowledge: 1) The origin of parthenogenesis is assumed to be relatively rare, and 2) Parthenogens are assumed to be immediately reproductively isolated from the sexual forms that give rise to them. If environmental heterogeneity does indeed provide the principal individual advantage of sex, it still remains to be seen whether this advantage is large enough to offset the cost of sex to individuals.

Group advantages, the most extreme of which might be a lower extinction rate for sexual species, are the obvious alternative to individual advantages as an explanation for the maintenance of sex. An important role for

group advantages has not been demonstrated, and any such demonstration would be difficult because it would have to be historical. In contrast, some empirical evidence suggests a sustained individual advantage for sex, even among organisms of relatively low fecundity. Most persuasive is the persistence of sources of genetic variation that are known to be responsive to individual selection. Both crossing-over and the division of the genome into multiple chromosomes contribute to genetic variation among progeny, and both are responsive to selection. Rates of crossing-over can be reduced by selection from their observed levels in natural populations (Bell, 1982; Williams, 1975). Multiple chromosomes are the rule rather than the exception, but the existence of a few species with very low chromosome numbers (*Haplopappus gracilis:* 2N = 2) illustrates the physiological and biochemical feasibility of low chromosome numbers; some species even show polymorphisms for chromosome number (Staiger, 1956). Consequently, it seems that individual selection maintains over the short term recombination rates significantly exceeding the minimum that would be expected to result from individual selection against recombination. This implies a continuing advantage for recombination. If this advantage exists, and yet is not understood in terms of population genetics, then our failure to understand the individual advantage of sex itself is not surprising.

A second line of empirical evidence for sustained individual advantage of sex is the persistence of sexuality in taxa that are also capable of asexual reproduction (Williams, 1975). Because individual advantage of sex in such species is difficult to illustrate in terms of quantitative population genetics, even though such an advantage must exist to prevent the asexual mode from taking over the sexual one, it seems reasonable to conclude that sex in species lacking asexual reproduction may yet be understood in terms of individual advantage.

The cost of sex is a more interesting subject if sex is maintained by individual advantage rather than group advantage. If the advantage is individual, then there must be constant interplay between cost and benefit that will determine the establishment and persistence of sexual life-history features. If sex is carried as a mortgage on phyletic persistence, the interplay will be duller and will have less explanatory power.

Inventory of costs

The overall cost of sex can be divided into two groups of subsidiary costs: 1) costs not derived from anisogamy (broadly defined here as physical gametic differentiation of any kind, and thus including oogamy), and 2) costs derived from anisogamy. These two sets of costs are shown in outline form in Table 1. Beginning with the costs not derived from anisogamy, we have first the cost of recombination, which can be defined as the cost assignable to loss of fitness caused by recombination. As an extreme example, if

heterozygotes for a particular locus have high fitness and homozygotes have low fitness, an asexual line can preserve heterozygosity at the locus with virtually 100 % fidelity, while a sexual line moves constantly toward a 50 % loss of heterozygosity.

Table 1. Inventory of the costs of sex

I. Costs not derived from anisogamy
1) Recombination
2) Cellular-Mechanical costs
a. Meiosis
b. Syngamy
c. Karyogamy
3) Fertilization
a. Exposure to risk
b. Minimal density for reproduction
II. Costs derived from anisogamy
1) Genome dilution (cost of males)
2) Sexual selection
a. Sexual competition (conflict, exposure)
b. Dual phenotypic specialization

A second type of cost not derived from anisogamy has been called the cellular-mechanical cost of sex (Lewis, 1983). This includes any loss of synthetic potential in cells as a result of delays caused by the movement of supramolecular bodies such as chromosomes or gametic nuclei. Under this heading are three subsidiary costs for eukaryotic organisms: meiosis, syngamy, and karyogamy. The cellular-mechanical cost of meiosis should not to be confused with the 'cost of meiosis' identified by Maynard Smith (1971a), which is shown in Table 1 as the 'cost of genome dilution'. For reasons that are not entirely clear, meiosis requires much more time than double mitosis, to which it is superficially similar. The resultant delay in synthetic processes is the cause of the meiotic component of the cellular-mechanical cost. A time delay can also result from the union of gametes; this would be the syngamy component of the cellular-mechanical cost. Finally, a time delay can be associated with the union of the two gametic nuclei that make up a diploid cell; this would be the karyogamy component of the cellular-mechanical cost.

The third and final kind of cost not derived from anisogamy is shown in Table 1 as the cost of fertilization. This cost is caused by any loss of fitness derived from the peculiar necessity in outcrossing sexual organisms of arranging contact between gametes from two different individuals. The cost is broken into two large categories. The first of these is classified as exposure to risk, which refers to increased vulnerability to predation or disease transmission caused by contact between individuals or gametes from two different sources, or from waste of gametes or of effort expended in gamete

transmission. The second is classified as the cost of minimum density for reproduction, and is associated with any delay or prevention of reproduction that may occur as a result of the unavailability of mates.

Anisogamy gives rise to a number of additional costs of sex. The first of these listed in Table 1 is the cost of genome dilution. This is new terminology, which I hope will lead to less confusion and point the way more specifically to the actual nature of the cost. This cost, which was first identified by Maynard Smith (1971a), has been given a number of names: cost of meiosis, cost of males, twofold cost, and cost of sex. The cost can be understood as the comparative success of amictic and mictic females in propagating their genomes. If the two produce eggs of the same size at the same rate, the sexual female contributes only half of the genetic material to each egg, and thus suffers a severe disadvantage. For reasons to be explained below, this cost applies only to anisogamous species, and is therefore derivative of anisogamy. It is misleading to call this the cost of meiosis, because meiosis imposes at least one other cost, as already mentioned above. It is also misleading to call this the twofold cost, because the cost may be less than twofold in some instances, and because other costs may be twofold under some circumstances. It is not so far wrong to call this the cost of males, but this term does not accurately represent the nature of the cost. Having synthesized the protoplasm and reserves essential for a zygote, and thus ensuring the propagation of the genome, an anisogamous female suffers a large loss in propagation efficiency as a result of the male genetic contribution, which effectively dilutes her genes in relation to the cytoplasm and reserve materials that she has synthesized. Because genome dilution is the nature of the cost, it seems best to call this the cost of genome dilution.

In the last category, a variety of other factors are united as the cost of sexual selection. The common feature of these factors is that the environment extracts a penalty as a result of phenotypic manifestations of sex that are established and maintained by sexual selection. In one subcategory, we include increased vulnerability and loss of time associated with sexual competition. In another subcategory costs are associated with dual phenotypic specialization of a single species as a result of sexual dimorphism maintained by sexual selection.

Context for evaluating costs

All of the individual costs listed in Table 1 vary widely according to the circumstances, and all can be negligible or inapplicable under at least some circumstances. The composite cost of sex for a given organism is thus likely to be a complex mixture of individual costs. A change in circumstances can alter the composite cost of sex, even within a single population.

The cost of sex can only be evaluated with reference to a specific alternative system. For present purposes, I follow the example of Maynard Smith

(1971a) and use a hypothetical amictic organism as a reference point for evaluating the cost of sex in its mictic counterpart. This method fails to take into account historical factors related to the rate of origin of amixis from mixis, or of mixis from amixis, but these considerations can be added as needed.

It is useful to distinguish between two kinds of cost associated with each of the factors shown in Table 1. Potential cost is the maximum suppression of fitness that may arise from a given cost factor. Realized cost takes into account simultaneous advantages or modifying factors that reduce the potential cost. The benefit of sex need only balance the realized cost; sex may be made feasible by adaptations that minimize the realized cost.

Categorizing organisms by frequency of sex

In analyzing the cost of sex, a central consideration is the frequency of sex. From this viewpoint, it is possible to identify four categories of organisms. Category 1 can be called continuously asexual. Such organisms lack the capability for sex. Major groups of eukaryotic organisms that fall into this category are few. Examples include the Euglenophyta, numerous species of Chlorophyta and other algal taxa (Fritsch, 1965), and the bdelloid rotifers. Among multicellular organisms, continuous asexuality is principally limited to isolated species or to marginally distributed population of otherwise sexual species (Bell, 1982).

The second category of organisms can be called discontinuously sexual. Species of this category are composed of individuals that have sexual potential, but in which this potential is not expressed in all individuals. Examples include most species of Protozoa or unicellular algae, which grow extensively by vegetative or clonal reproduction, but that become sexual occasionally in response to environmental cues. Some multi-cellular organisms, such as monogonont rotifers and some species of Cladocera also belong to this category.

The third category consists of organisms that are continuously sexual. Among such species, each organism typically becomes sexual at some point in its life cycle, but each organism is also capable of reproducing vegetatively or by budding or fragmentation. Many invertebrates such as coelenterates and polychaetes belong to this group, as do many vascular plants.

The fourth and last category consists of organisms that are continuously and obligately sexual. Such organisms are individually committed to sexuality and lack the capability for reproduction by non-sexual means. In this category are the vertebrates, some of the more complex invertebrates, and some vascular plants.

This classification of sexuality glosses over many significant distinctions among sexual organisms, but in doing so allows us to focus on the frequency of sexuality, which is a key issue for evaluating the cost of sex. At one

extreme of the classification organisms are exclusively committed to asexual reproduction. At the other extreme, organisms are exclusively committed to sexual reproduction. These can be regarded as evolutionary absorption states, within which the inertia favoring continuation of that state is likely to be high. Outside of these evolutionary absorption states, the frequency of sexuality is subject to adjustment in response to natural selection, and this is an important determinant of the realized cost of sex.

Cost of recombination

Recombination has been explored quantitatively by simulation and by deterministic models (Maynard Smith, 1978). These approaches are useful because they yield tangible results. On the other hand, a hypothetical system that approaches intractability for quantitative study is often ridiculously simple by comparison with natural systems. Consequently, there are advantages to approaches that yield only qualitative results but that are capable of representing environmental complexities that are known to be important in relation to the costs and benefits of recombination. I use here one such approach in an attempt to illustrate the range of potential and realized costs that can be expected to result from recombination.

Figure 1 shows a generalized graphical model of a natural environment. The environment is represented as a gradient rather than as a series of alternate compartments, as must often be the case with quantitative models. Although the gradient is shown in only one dimension, it is actually multivariate. The gradient is divided into units, each of which represents the breadth of conditions corresponding to maximal fitness for the genotype that is best adapted to this position on the gradient. The fitness of a specific genotype decays from its optimum in either direction on the gradient. For convenience, I represent this decay function as a smooth curve with a well-defined peak. Although a specific example is shown in the figure, the breadth of the fitness decay curve in relation to the length of the gradient obviously varies according to the specific combinations of organism and environment. As shown in the literature review by Bell (1985b), there is little doubt that such fitness curves exist, even though their shapes and dimensions are seldom known.

Another feature of the generalized environment shown in Figure 1 is carrying capacity, which varies along the gradient. Carrying capacity is given graphically as distance above the line representing the environmental gradient. The irregular variation in carrying capacity along the gradient is explained by two factors. First, the environment is less favorable at some points than others, even for the best-adapted genotype, and the carrying capacity per unit area varies accordingly. Second, the area that is available for occupancy varies along the gradient.

The carrying capacity along the gradient is not stable through time. For

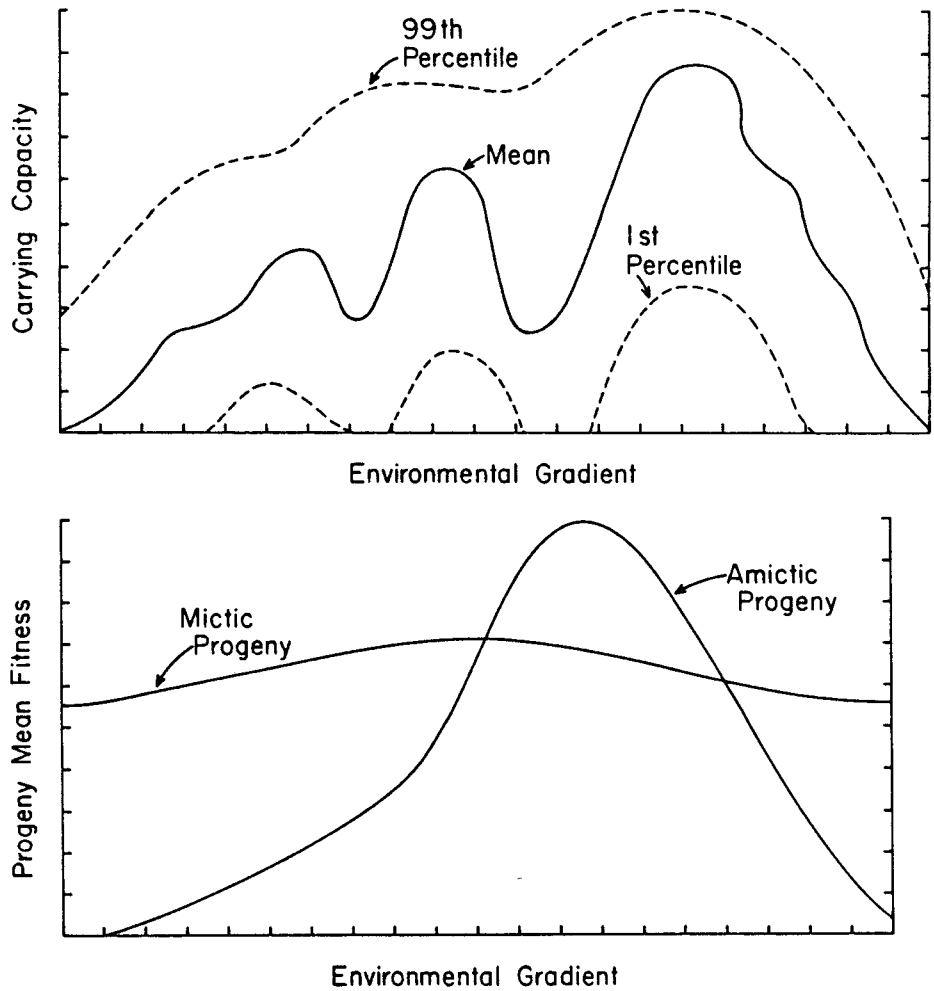

Figure 1. Schematic representation of a natural environment expressed as a linear gradient. The top panel shows the mean carrying capacity across the gradient and the 95 % confidence intervals for variations around the mean carrying capacity. The bottom panel shows mean progeny fitness for asexual organisms of a single genotype and for sexual organisms of similar genotype.

this reason, the graph indicates percentile bands around the mean carrying capacity. These bands correspond to some unspecified frequency distribution of carrying capacities through time for any given point on the gradient.

In considering the cost of recombination, the simplest way to use the gradient model of Figure 1 is by assuming the environment to be occupied by a single amictic genotype and a few mictic organisms of similiar genotype. The amictic population is fixed at a specific point on the gradient, where it consistently has maximum competitive ability. It is also an effective competitor at nearby points on the gradient. In contrast, the mictic population does not occupy a fixed position on the gradient. All offspring are genetically unique, and their fitnesses span the range of conditions on the gradient.

Three categories of potential cost for recombination can be recognized from this example. The first cost arises from the tendency of the mictic

population to produce some genotypes that have negligible fitness under any of the conditions along the gradient. These may be regarded as lethal or sublethal genotypes. The second potential cost arises from the deviation of actual fitness from maximum fitness for any random pairing of a position on the gradient and a genotype produced by sexual processes. This potential cost is lowest if each of the offspring produced by sexual processes has the ability to seek out a position anywhere on the gradient, and is highest if each of the offspring finds a position on the gradient by random processes or by processes controlled mostly by the parent. The third potential cost is derived from the inability of the sexual population to avoid competition with the asexual population over that portion of the gradient where the asexual population is consistently superior.

Because the cost of sex is being measured in terms of the ability of an amictic population to replace a sexual one, most of the potential costs of recombination are realized in this example only as long as it takes for the amictic types to occupy that portion of the gradient where they are optimally fit. The disadvantages of recombination are not likely to lead to extinction of the sexual population because the amictic individuals are fit over only a portion of the gradient. After establishment of equilibrium, the mictic individuals suffer only a small disadvantage from production of some progeny whose genotypes are lethal, sublethal, or merely suboptimal on other parts of the gradient. The production of such genotypes, if accompanied by the production of at least some genotypes of high fitness, has much the same effect as a reduction in fecundity. Reduced fecundity of the mictic population would be important in determining the relative dominance of mictic and amictic types only over a narrow zone where the two types of progeny have nearly equal mean fitnesses; differences in fecundity would not be important over those portions of the environmental gradient where the amictic progeny are substantially superior or substantially inferior in mean fitness.

The realized cost of combination may be reversed by intense sib competition in the amictic population (Price and Wagner, 1982; Williams, 1975). The effect of environmental fluctuations causing changes in carrying capacity over the region of the environmental gradient dominated by the asexual population will be magnified by the phenotypic uniformity of the amictic organisms. If the environment is subject to resource depletion, or if the environment contains biotic challenges capable of focussing on particular phenotypes (e. g., disease organisms or predators), the effective carrying capacity of the environment may be lower for the amictic population than it would be for the mictic population, and this would be reflected in a higher probability of extinction (lower time to extinction (Cooper, 1984)) for the amictic organisms than might be implied by the carrying capacity of the environment for mictic organisms.

Over many generations, well after the establishment of short-term equilibrium, two additional factors come into play. First is a finite probabil-

ity that random fluctuations in the carrying capacity of the environment will reach zero over that portion of the gradient occupied by the amictic population. The realized cost of recombination in this case will return to zero because of the elimination of the amictic population. The realized cost of recombination may also be modified by evolutionary response in the mictic population under certain circumstances. I have assumed that the position on the gradient where the amictic population has peak fitness is determined randomly by the change origin of amictic reproductive features from a mictic progenitor. If the amictic population happens to occupy the center portion of the gradient, it will probably be advantageous for individuals in the mictic population to produce offspring whose environmental optima span the entire range of the gradient, although some disruptive selection is also possible. However, if the amictic population occupies the edge of the gradient, the mictic individuals will experience directional selection leading to narrowing of the variance and shifts in the means of traits in such a way as to minimize overlap with the amictic population. This will reduce competition for both populations. It is a striking fact that amictic populations tend to occupy marginal or extreme environments over the range of conditions covered by their mictic counterparts (Bell, 1982; Bierzychudek, 1985). Numerous hypotheses have been proposed to explain this phenomenon, but none has yet been widely accepted (Bierzychudek, 1985). Directional selection in mictic populations because of the presence of derived amictic populations may be of unsuspected importance in explaining the association of amictic organisms with marginal environments, either directly or by reinforcement of other mechanisms that favor this bias in distribution. From the viewpoint of sexual organisms, the effect of reduced overlap would be to reduce the realized cost of recombination.

The realized cost of recombination is likely to increase in relation to degree of commitment to sexuality. Discontinuous sexuality, and to some degree continuous sexuality that is not obligate, would reduce the realized cost by reducing the frequency of sex and would provide a mechanism by which the realized cost could be adjusted over the short term. A population that has both sexual and asexual capabilities can develop increased emphasis on asexual reproduction in response to competition from a derived asexual line, but this is not possible in organisms that are continuously and obligately sexual.

In summary, the example of a sexual form competing with a corresponding amictic form shows that the realized cost of recombination will depend on the degree of commitment to sexuality and on the portion of an environmental gradient that can be dominanted by amictic individuals. If the breadth of conditions corresponding to high fitness in the amictic type is high in relation to the width of the environmental gradient, then the realized cost resulting from recombination will be high. However, a modification of the realized cost can occur if the amictic population occupies one extreme of the environmental gradient and thus causes directional selection

in the sexual population in such a way as to reduce competitive overlap. In addition, realized costs can be nullified *a posteriori* by extinction of the amictic population, the possibility of which will be enhanced by lack of diversity in the amictic population as a result of (1) focussing by predators, parasites, and diseases on the minimally varying prey or host phenotype, (2) of random fluctuations in the carrying capacity of the environment over the range of high fitness, and (3) of reduction of effective carrying capacity by sib competition for resources.

A second example resembles the first one but is more complicated because it allows for the appearance of new amictic lines at some finite rate. The potential cost of recombination is the same as in the first example, but the realized cost is higher if the rate of origin of asexual lines exceeds the rate of their extinction by a sufficient margin to allow several amictic lines to exist at any one time. If this is the case, the realized cost of recombination could be expressed over the entire gradient, and could thus cause extinction of the mictic population.

The examples show that the potential costs of recombination can be identified in general terms, but that the realized costs are critically dependent on the rate at which amictic lines arise and the rate at which they become extinct. The inefficiency of recombination in preserving genotypes of high fitness has often been taken as evidence of a substantial cost of recombination. Flexibility in reducing this cost to a minimum by adjustments in the frequency of sex is available to all but the continuously obligate sexual organisms, which account for a very low percentage of all taxa. Even among continuously obligate sexual organisms, the cost of recombination is realized only in the presence of an alternate reproductive mode. Among such organisms, the factors that govern the frequency with which amictic strains arise and the probability that they will, once established, become extinct may be more important than short-term disadvantages of recombination. Among multicellular organisms, continuously asexual taxa are unusual (Bell, 1982). This suggests that amictic straits have low frequency of origin, low persistence, or both.

As long as other costs are not involved, it would appear that recombination can be preserved, even in the presence of amictic organisms, by individual advantage, so long as the entire environmental gradient is not occupied by amictic forms. If a variety of amictic forms were to accumulate in such a way as to occupy virtually the entire environmental gradient, it would seem possible that these amictic types could cause extinction of the sexual type. This change, which might qualify as group selection, would not be readily reversed because of the complexity of mechanisms that must lead to the evolution of sexual capabilities in organisms that lack these capabilities (Bull and Charnov, 1985). Thus a case can be made that recombination, in the absence of other costs, could be maintained by individual advantage but overcome by group disadvantage. In such a case, sexual individuals would continue to experience positive selection pressure for recom-

bination as a means of exploiting gaps in the environment, even as these gaps were being filled by competitively superior amictic organisms. Conceptually speaking, this phenomenon would be the equivalent of group selection resulting from organisms 'running out of niche', as illustrated by Williams' example of a parasite that is optimally adapted to a host that is going extinct (Williams, 1975).

The possibility that recombination may be maintained by individual advantage but overcome by group disadvantage seems to run counter to a well-accepted line of reasoning that associates special group advantages with recombination (Maynard Smith, 1978). According to this line of reasoning, potential response to selection is directly related to recombination, which is in turn inversely related to expected time to extinction for a group of organisms. However, the two apparently contradictory conclusions really apply to different situations. The reasoning that associates possible group disadvantages with recombination applies to environmental conditions subject to stochastic but not secular change. If secular changes are occurring in the environment, there will be special advantages associated with recombination as a result of the greater adaptability of organisms that show recombination.

Given the general weakness of group selection (Wade, 1978) in relation to individual selection, the apparently slow origin rates of amictic lines in many sexual groups of organisms, and the prevalence of secular changes in the environment, it is not surprising that amictic lines seldom replace mictic ones (Bell, 1982). Where amictic lines have replaced mictic lines, not only the disadvantages of recombination, but also the numerous other disadvantages of sex may have been responsible.

Cellular-mechanical costs

There is a trend toward increasing commitment to sexuality with increasing size among organisms. Although continuous asexuality is rare, it is much more common in small organisms than in large ones. Discontinuous sexuality is typical of small organisms; continuous sexuality and continuous obligate sexuality are much more likely among larger organisms. It would be difficult to make a general argument that sex has drastically different potential benefits among small organisms than among large organisms. Consequently, the most straightforward explanation for the increase in frequency of sexuality with size may lie in a higher potential cost of sex for small organisms than for large ones.

Sexuality in eukaryotes typically requires meiosis, syngamy, and karyogamy. The time taken up by these three processes is surprisingly great, and far exceeds the time required for two mitotic divisions (supporting primary literature for this section is given elsewhere (Lewis, 1983) and will not be cited here). In order to be retained by individual selection, continu-

ous sexuality in small organisms, and especially in unicellular taxa, would have to confer impossibly high advantages in viability components of fitness to compensate for low reproductive rates. This explains why sexuality is not continuous in unicellular eukaryotic organisms, and may also explain the low frequency of sex in many other discontinuously sexual organisms. Because ameiotic sex in prokaryotes is apparently also time-consuming (90 min for genetic exchange vs 20 min for a full asexual cell cycle in *E. coli* (Bremermann, 1985)), some of the same reasoning may apply to prokaryotes.

The minimum mitotic cycle time for cells increases with the size of the cell, which is in turn directly proportional to the size of the nucleus and the amount of DNA (Cavalier-Smith, 1978; 1985). In eukaryotic unicells, or in the individual cells of multicellular organisms, mitosis requires as little as 15 min or as much as 3–4 h, depending on temperature and cell size. In contrast, meiosis seldom takes less than 10 h, and in multicellular organisms commonly takes more than 100 h. The time for meiosis, as for mitosis, increases with the size of the nucleus and amount of DNA. For example, Bennett (1973) found within a group of 15 diploid higher plant species a range for meiosis times of 25–20 h and a very tight linear relationship of meiosis time to the amount of nuclear DNA ($r = 0.96$).

Unicellular eukaryotes often experience high mortality rates and severe competitive pressure from other small organisms for the exploitation of resources. Even brief reductions in growth rate would seriously impair the fitness of these organisms. For most of the duration of meiosis, cells are not able to carry out any synthetic activities, and are, for practical purposes, growth-arrested. In fact, the cytoplasmic reserves of cells undergoing meiosis are subject to depletion by energy demands that are not offset by intake. The resulting growth handicap caused by meiosis can be very severe. In multicellular organisms, the burden caused by cessation of synthetic activity in meiotic tissus can be averaged across the somatic cells, so that the overall synthetic cost to the organism is smaller. Even so, meiosis has the potential to delay reproduction if meiosis takes more time than somatic maturation.

It is not clear why meiosis is so time-consuming, or what the minimum time for meiosis might be in organisms that have experienced steady and strong pressure for the reduction of meiosis times. However, a survey of the literature (Lewis, 1983) indicates that meiosis times cannot be reduced by selection to a range comparable to that of mitosis. The apparent resistance of meiosis to shortening implies mechanical limits, given that biochemical phenomena can typically be speeded up under strong selection pressure. Mechanical features of meiosis, including orientation, movement, and pairing of chromosomes, may set limits on speed. More detailed information on the specific reasons for differences in the duration of mitosis and meiosis would be useful, but apparently does not exist at present.

Syngamy may also consume time, although it is not likely to be so ineffi-

cient in this respect as meiosis. In some taxa, gametes unite in the environmental medium, and the delay associated with syngamy is limited to the time for gametes to find compatible mating types. Conjugation is an alternative in which the mother cells of sexually compatible strains unite and form a cytoplasmic bridge for nuclei or gametes (e. g., pennate diatoms, desmids (Brook, 1981; Geitler, 1932)). Conjugation might allow the overlap of syngamy with meiosis, which would reduce the overall time expenditure for the two processes. It seems likely, however, that the main advantage of conjugation is to raise the probability of contact between sexually compatible gametes. For multicellular organisms that make direct contact for gamete transmission, delay associated with syngamy would arise over mate location and gamete transmission.

Syngamy is not complete until gametes have actually joined. For oogamous taxa, the incorporation of the male gamete nucleus into the recipient cytoplasm seems to occur quickly. However, in isogamous species, delay is caused by the physical difficulties involved in the merger of two more or less equal cytoplasmic masses. This may be a significant evolutionary force favoring oogamy in small organisms.

Karyogamy, which follows syngamy, may also be important in delaying the resumption of significant synthetic processes. The two separate gametic nuclei must join inside the cytoplasm and become chemically integrated before the cell can resume function. More measurements of this time delay in eukaryotic unicells are needed.

Time requirements for syngamy and karyogamy are poorly documented. In small organisms, observations of the time for meiosis in relation to the time required for conjugation may indicate indirectly the magnitude of the delay caused by syngamy and karyogamy. In general, conjugation lasts significantly longer than meiosis proper.

It would be desirable to have a much broader statistical base than is now available, but it seems certain that the potential cellular-mechanical cost of sex is 5-fold to 100-fold for unicellular organisms. However, a number of mechanisms prevent this cost from being fully realized. The first and most important mechanism for minimizing the realized cost is intermittent sexuality. All other factors being equal, the realized cellular-mechanical cost of sex is reduced in direct proportion to the number of asexual generations that intervene between episodes of sexuality. In many unicellular organisms, sexuality is an annual occurrence. Under ideal conditions, a characteristic mitotic division interval for unicells would be of the order of one day. Given that ideal conditions do not persist over an entire annual cycle for most organisms, the relevant order of magnitude for the number of asexual generations separating annual sexuality for a hypothetical species would be approximately 100. The cellular-mechanical cost of sex would be reduced by this mechanism to a trivial level, but there might be a corresponding reduction in benefits derived from sexuality.

A second mechanism by which the realized cellular-mechanical cost of

sex can be minimized is constraint of sexuality to a time during which cell growth is not occurring, or is occurring at minimal rates. If the instantaneous rate of increase for asexual cells is nearly zero, there is little or nothing to be lost by the cessation of synthetic processes over the interval required for meiosis, syngamy, and karyogamy. The cellular-mechanical cost of sex should thus force intermittent sexuality to occur toward the end of the growing season. This is commonly the case for unicellular eukaryotes. Traditionally, the occurrence of sexuality toward the end of growing season in such organisms has been interpreted in terms of genetic variance: low variance is supposedly advantageous during the growing season, and high variance is advantageous at the end of the growing season in anticipation of possibly changed conditions during the following year. Interestingly, this line of reasoning does not mesh very well with observations on the distribution of amictic populations in higher organisms, for which lack of sexuality is typically associated with marginal and uncertain environments (Bell, 1982). Perhaps the cellular-mechanical cost of sex is the key factor determining the timing of sexuality in small organisms (Lewis, 1983), in which case the distribution of amictic multicellular organisms is not inconsistent with factors governing the timing of sex in small organisms.

Still another mechanism by which the realized cost of sex can be reduced in unicellular organisms is incomplete commitment of cell lines to sexuality during the period of sexuality. The principle is best illustrated by diatoms, which appear to have evolved a mechanism specifically for this purpose (Lewis, 1984). In diatoms, sexuality requires a dual trigger: specific environmental conditions plus a specific minimum cell size (Drebes, 1977). Cell size, however, is controlled by an unusual division principle. The cells that are produced sexually have maximum size, as reflected by the size of the frustule (silica skeleton). The frustule consists of one upper and one lower component (valve). At each asexual cell division, the two valves of the mother cell become the upper valves of two new cells. For a given cell, the lower valve always fits inside the upper valve, and is thus smaller than the upper valve. Consequently, as time goes by, the mean valve size, and thus the mean cell size, decreases steadily, and the variance of valve sizes increases steadily. Only cells that have achieved a certain minimum valve size are responsive to the environmental cues that stimulate the occurrence of sexuality. Because of the variance in valve sizes for a given clone, this mechanism ensures that only a small proportion of the cells in a clone will be committed to sexuality in any one year. Thus the clone is able to follow a dual strategy by retaining good representation of the historically successful genotype, and at the same time creating an array of new genotypes that will occupy different portions of the environmental gradient or that may be more suited to novel conditions on the gradient in the future. This reduces not only the cellular-mechanical cost of sex by limiting the commitment to sexual processes, but also reduces the cost of recombination.

Another alternative for reducing the realized cellular-mechanical cost

exists for unicellular organisms that consist of large cells. Such cells can have two nuclei, one of which can undergo sexual processes while the other continues with synthetic activity (Nanney, 1980). This may well be one of the major adaptive features of macronuclei in ciliates.

The potential cellular-mechanical costs of sex are so large that they may affect metazoans as well as unicellular organisms. Among small animals, the monogonont rotifers and the Cladocera are examples of organisms whose life histories might be strongly constrained by the cellular-mechanical cost of sex. In these groups of organisms, there is an extraordinary premium on rapid growth during brief favorable periods when resources are plentiful and before predators have responded to the availability of prey biomass. All monogonont rotifers and many species of cladocerans are discontinuously sexual; they typically experience a sexual phase when population growth has peaked (Bell, 1982). Individuals are reproductively competent shortly after hatching from the egg, and the size of the egg is high in relation to the body size of the reproductive individual. For these reasons, the time delay inherent in meiosis is likely to reduce the reproductive rate significantly because the synthesis of egg materials may be complete well before meiosis is complete. This will not be the case in organisms that require extended pre-reproductive development. For example, in human beings, meiosis requires a great deal of time (7500 h in males (Clermont, 1977)), but cannot delay reproduction because of the even greater time required for pre-reproductive development.

Another example of possible effects of the cellular-mechanical cost of sex in multicellular organisms is evident in the work of Bennett (1972), who showed that the time required for maturation in perennial flowering plants increases as a function of nuclear volume, DNA per cell, and meiosis time. The meiosis times are sufficiently long that they appear to determine the earliest date of fertilization in these plants.

Discontinuous sexuality in small organisms necessitated by the high cellular-mechanical cost of sex may be responsible for a higher probability that sexual capacity will be lost in these organisms than in larger organisms. Sex appears to be entirely lacking in the bdelloid rotifers, the Euglenophyta, and in many individual species of unicellular algae. Because mixis is much less likely to originate by chance than amixis, these lines may simply represent cumulative evolutionary accidents caused by the individual selection pressures minimizing the cellular-mechanical cost of sex.

Fertilization

Physical contact between organisms or their gametes entails risks that are separate from those that are maintained by sexual competition. At least three kinds of such cost can be distinguished. First, increased risk of disease or parasite transmission accompanies contact between organisms, or even

between gametes. This is the complement to a benefit of sex explained by Rice (1983a): asexual lines may be subject to genetic and environmental focussing by diseases and parasites. Second, contact between motile organisms typically entails loss or reduction of motility, and thus increased vulnerability to predation. Neither of these costs is derived from anisogamy, but anisogamy, operating through sexual selection, can increase the costs by modifying behavior or morphology. Risks associated with primary sexual structures or with a minimal component of sexual behavior can be considered a cost of fertilization, and not a product of anisogamy. A third type of cost associated with fertilization is waste of gametes, or waste of effort transmitting gametes. All three types of cost are reduced by intermittent sexuality.

A second cost of fertilization is the introduction, along with obligate continuous sexuality, of a minimum population size for reproduction. The potential cost could be quite high for continuously obligate sexual organisms that colonize empty habitats or that experience strong fluctuations in density. The realized costs are reduced to negligible levels by facultative sexuality, particularly if sexuality occurs in response to population density. The realized cost is also reduced by self-compatibility in hermaphrodites (Ghiselin, 1974), although suboptimal progeny fitness can be counted as a realized cost associated with the strategy.

Colonizing land plants are most frequently cited as examples of organisms in which continuous obligate sexuality would be disadvantageous (Stebbins, 1950). Planktonic environments provide another example that may be informative because it is different. Planktonic algae, microcrustaceans, and rotifers have only limited abilities of aggregation in the moving medium of a plankton environment. Furthermore, the organisms that occupy such environments are often dispersed very thinly through the environmental medium in relation to their body size. For example, a planktonic rotifer or diatom at a density of one organism per cubic centimeter occupies only approximately 10^{-7} of the environmental space and, because of poor aggregation capabilities, is seldom in close contact with other members of the same species at such densities. While planktonic organisms very commonly exceed such a density by several orders of magnitude, there is a continual and substantial possibility that in any given year any given species will not reach such a density, nor can any planktonic species colonize an empty environment without passing through a considerable amount of time at lower densities than this. Consequently, discontinuous sexuality plays a very important role in reducing the realized cost of sex in planktonic organisms, and has probably also influenced the timing of sexuality in planktonic species. Among planktonic metazoans, it is interesting that continuous sexuality appears first along the size spectrum at about 1 mm, among the Copepoda, which have sufficient motility to seek out mates even when the population densities are relatively low. Even so, it seems likely that obligate sexuality requires copepods to sustain higher birth rates than either rotifers

or cladocerans (Lewis, 1979), both of which are typically smaller but are sexual only under a narrow set of circumstances.

For most organisms, significant cost associated with minimum population density for sexual reproduction seems unlikely. Small organisms are often not obligately sexual. Animals of moderate to large size have very high motility, and thus are capable of behaviorally offsetting very low population densities, and would only be handicapped by lack of asexual capabilities under very special circumstances such as colonization of remote islands. Large plants and sedentary invertebrates have limited vulnerability to low population density because of very different but equally effective adaptations. Many of these organisms are capable of producing vast numbers of microgametes, and thus occupy reproductively a very large area, despite their immobility.

In summary, the potential costs of sex associated with minimal density for sexuality are substantial, but the realized costs are probably small because of the large number of ways in which the potential costs can be reduced. Among large organisms, the ability of individuals or their gametes to saturate reproductively a large area offsets the problem of low population density, and in small organisms discontinuous sexuality allows the organism to forego sexuality or to develop through natural selection environmental cues that cause sexuality to occur when population density is highest.

Cost of genome dilution

Success for reproducing organisms has both a qualitative and quantitative component. The qualitative component is related to the fitness of progeny, whereas the quantitative component is related to the number of progeny, which is in turn a function of the synthesis capabilities of the parent and the optimum investment of cytoplasm and food reserve per gamete. In isogamous organisms, the amount of cytoplasm and food reserve per gamete takes into account the availability of an equal amount of cytoplasm and food reserve accompanying the second gamete that will contribute to the zygote. At the other extreme, in oogamous organisms, the amounts of cytoplasm and food reserve in the macrogamete must be adequate for all requirements of the zygote, since the microgamete will not contribute significantly in this respect. Consequently, the individual producing the macrogamete is providing twice the ratio of cytoplasm and food reserve to DNA as its isogamous counterpart, and suffers a 50 % cost in the efficiency of genome propagation as a result.

Numerous species of organisms occupy middle ground between isogamy and oogamy. These include particularly unicellular eukaryotes (Fritsch, 1965). It may seem surprising that the disruptive selection leading to anisogamy does not always carry through to the fullest extent in causing divergence between the sizes of the gametes. However, among unicellular

organisms for which there is no supporting soma to assist in delivery of the gamete, even the microgamete may benefit from the availability of sufficient energy reserves to ensure its survival and activity for an extended interval. In such organisms, the realized cost of genome dilution is above zero, but is less than in oogamous species.

The realized cost of genome dilution need not always be 50 % for oogamous species. If the male parent enhances the fitness of his progeny after fertilization, the realized cost of genome dilution is reduced accordingly (Maynard Smith, 1978). Benefits to the offspring may be diffuse and subtile, as might be expected from certain types of territoriality, or may be definite and direct, as in the case of dual parental care of the offspring. It is easy to imagine examples in which the probability for survival of offspring is more than doubled by parental care from two parents. Sexuality will be reinforced by these advantages, as well as the advantages derived from recombination. Such a reinforcing effect may well account for almost complete absence of asexual reproduction in birds and mammals.

Oogamous organisms that are discontinuously sexual will also experience a reduced cost of genome dilution. Clonal and vegetative reproduction in oogamous organisms reduce the rate at which the disadvantage of genome dilution is expressed. Partial self-fertilization has the same effect. A reduction in rate at which the cost is expressed will in turn allow greater amount of time for the advantages of recombination to accumulate. If the advantages of recombination are not continuous in space or time, reduction in the rate at which the cost of genome dilution is expressed might well be critical to the preservation of sexuality.

Overall, it appears that the cost of genome dilution may not be so severe or widespread as it might at first seem to be. It does not apply to isogamous organisms, and applies only partially to organisms that are anisogamous but not oogamous. Among some large animals, biparental contributions to the probabilities of survival for offspring are sufficiently high to account for extensive reductions in the realized cost of genome dilution. Among organisms that are not obligately sexual, natural selection can reduce the cost of genome dilution per generation by reducing the frequency of sex.

Sexual selection

Sexual selection can create novel risks in sexually reproducing organisms, or can exaggerate risks that are found in asexual organisms. It is convenient to group costs of sexual selection under two headings, as shown in Table 1: adaptations to sexual competition, and dual phenotypic specialization.

Sexual selection may enhance the performance of individual organisms by comparison with other organisms in the population, while at the same time lowering individual fitness with respect to a theoretical asexual organism not burdened with such competition. Thus sexual selection may work

against natural selection of other types (Arnold, 1985; Darwin, 1871; Ghiselin, 1974). Combat and display behaviors as well as secondary sexual characteristics maintained by sexual selection almost inevitably handicap the organism to some degree, and thus constitute a potential cost of sex. Costs of this type are most obvious in vertebrates, but must also occur widely among invertebrates. For example, Saunders and Lewis (manuscript) documented a sudden increase in mortality between the subadult and the adult instar of freshwater diaptomid copepod, and associated this sudden increase with higher activity and changes in swimming behavior that facilitate mate location but that also make the animals more vulnerable to predators. Costs of this type for higher plants are low or negligible, as in unicellular organisms.

A more speculative and less easily quantifiable category of costs is associated with phenotypic differentiation of sexes. In sexually differentiated species, the male and female organisms essentially occupy differing niches. Separation of these niches is a matter of degree, but is often sufficiently pronounced to be measurable as a result of behavioral or physical specialization brought about by sexual selection. In such organisms, individual selection is optimizing the genotype along two separate lines at the same time. Although regulatory switching presumably directs the organism distinctively into one track or another, there would seem to be opportunity for substantial inefficiency as a result of opposing trends for the two sexes, either in dioecious or monoecious organisms. At the very least, the more extensive genetic information required to support distinct male and female phenotypes in dioecious organisms must be a measurable liability that can be classified as a cost of sex. This cost has evidently not been investigated.

Phyletic distribution of costs

Both the potential and realized costs of sex are distributed unevenly across groups of organisms. Irregularities in cost correspond to differences in life histories, fecundities, environmental grain, and other factors that cannot be considered without a detailed inventory of groups of organisms. At the same time, however, there are certain general trends in potential and realized costs that run parallel to phylogeny. These trends, which are summarized in Figure 2, provide an overview of the cost of sex.

At the top of Figure 2 is a phylogenetic diagram that shows in very coarse terms the four eukaryotic kingdoms and the major groups within these kingdoms in relation to each other. The Protista from the broad base of stocks from which the other three kingdoms were derived. Passing from left to right, we find groups of more recent origin, beginning with weakly integrated multicellular or multinucleate organisms and culminating in the most complex and highly differentiated taxa on the right-hand side of the diagram. A non-linear scale of origins is indicated below the phylogenetic

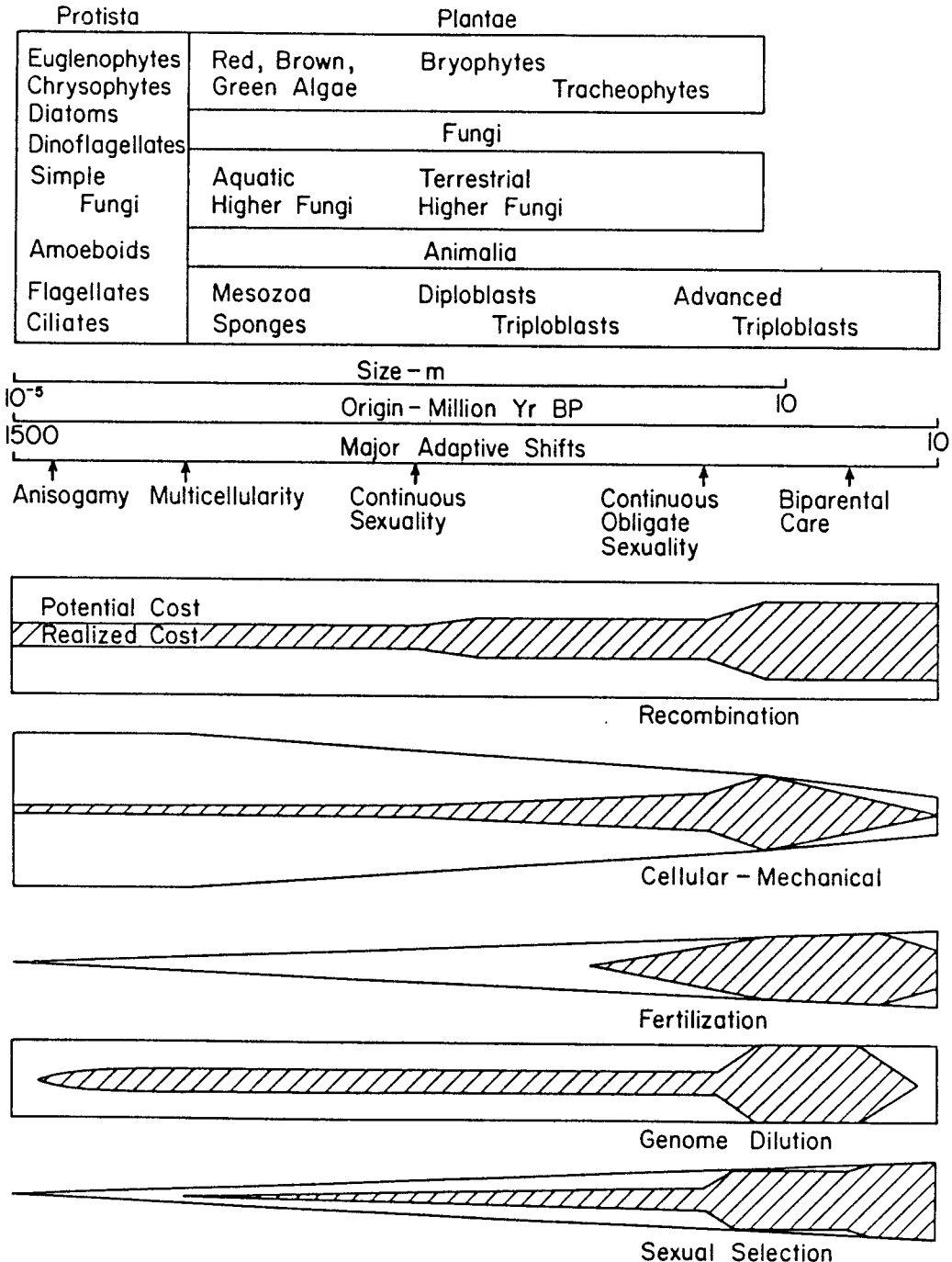

Figure 2. Suspected trends in the potential and realized costs of sex.

diagram. Also paralleling the diagram from left to right is a nonlinear size axis that is important to the phylogenetic trends in cost of sex.

Also shown in Figure 2 is a series of five adaptive shifts that have major significance for the cost of sex. The position of these shifts is indicated according to the approximate phylogenetic position at which they affect a large number of taxa. The shifts include the development of anisogamy from isogamy, the development of multicellularity from unicellularity, the

development of continuous and of continuously obligate sexuality, and the development of biparental post-zygotic investment among animals. Each of these shifts has an identifiable influence on one or more of the costs of sex.

Figure 2 also shows the potential and realized costs of sex in diagrammatic form along the phylogenetic axis. The diagrams are based on suppositions and not measurements. Recombinational costs for sexual organisms are shown first. As the figure indicates, there is no basis for suggesting a phylogenetic trend in the potential cost of recombination. The potential cost of recombination may vary in relation to such factors as fecundity or environmental variability, but these bear no certain relationship to the phylogenetic axis. The realized costs, however, are likely to increase with increasing commitment to sexuality, as shown in the diagram, up to the point at which they are offset by biparental investments in progeny.

The cellular-mechanical cost is shown in the second diagram. The potential cost is high among unicellular organisms, for which the effective delay in synthesis of individual cells would be most costly, but the realized cost is far below the potential cost because of discontinuous sexuality and restriction of sex to periods of minimal growth. Beyond the boundary of multicellularity, the potential costs decrease steadily with the increase in organism size because of the progressively greater time required for the development of somatic tissues and the correspondingly lower potential for delay resulting from the creation of gametes. The realized cost increases, however, because of stronger commitment to sexuality in larger organisms. In some of the smallest organisms that show continuous obligate sexuality, the importance of cellular-mechanical costs is high because of the inability of these organisms to reduce costs by reducing the frequency of sexuality. In the largest organisms, the long pre-reproductive period reduces the cost.

Costs associated with fertilization probably increase with organism size. In animals, potential vulnerability arising from predation is likely to be highest in organisms of intermediate to large size that are adapted to avoid behaviorally complex predators. Vulnerability to parasites and diseases is likely to be an increasing function of size because larger organisms will support a broader diversity of such species. The realized cost is reduced, however, by the intermittent nature of sexuality in most organisms. Minimal population size for sexual reproduction, which is the second kind of cost associated with fertilization, is potentially applicable to all organisms, but is offset in small organisms by intermittent sexuality and in very large organisms by motility and high fecundity.

For genome dilution, the potential costs are essentially uniform, but the realized costs change drastically across the phylogenetic spectrum. For isogamous organisms, the cost is negligible, and for anisogamous organisms that are not oogamous, the cost is small. Beyond the transition to oogamy, there is little reason to suspect a phylogenetic trend until the shift occurs toward organisms that have continuous and continuously obligate sexuality. Up to this point the realized costs are reduced substantially below the

potential costs of discontinuous sexuality. Organisms that are obligately and continuously sexual experience a drastically increased cost, which must approach the maximum potential cost. However, beyond the point at which biparental care becomes a common phenomenon, the realized cost is increasingly offset by increase in the probability of offspring survival through the male parent.

For sexual selection, the potential cost increases with size because of the general increase in complexity and lifespan with size, which allows more scope for sexual dimorphism. Realized costs are reduced by discontinuous sexuality. The realized costs, like the potential costs, increase steadily with increased organizational complexity in larger organisms. There is a shift toward higher costs with the abandonment of asexual reproduction. With the development of large body sizes in motile organisms that are behaviorally complex and sufficiently long-lived to be selected for elaborate strategies that maximize sexual fitness, the cost of sexual selection reaches a maximum.

Conclusions

Several general conclusions are possible from the schematic phylogenetic trend shown in Figure 2. First, there is a tendency for accumulation of larger and more diverse realized costs of sex in complex multicellular organisms, and particularly near the transition from taxa that are discontinuously sexual to taxa that are continuously sexual or continuously and obligately sexual. Asexual capabilities are extremely important in reducing the realized cost of sex, and it is therefore very important to understand what selective forces lead to the abandonment of asexual capabilities.

The phylogenetic trend toward increased commitment to sexuality may well be explained by organism size. As size increases, the time to maturity also increases. For a given level of commitment to sexuality, organisms with shorter times to maturity have the potential to evolve more rapidly than organisms that require longer to mature. Consequently, as organisms increase in size along the phylogenetic spectrum, they are increasingly subject to adaptive exploitation by smaller organisms that would use them as a resource (references in Bremermann, 1985), or to adaptive avoidance by smaller organisms that they would use as a resource. In other words, the Red Queen effect increases as size increases. This trend can be offset be increased recombination, which is manifested as an increased commitment to sexuality as size increases. A corresponding increase in the commitment to sexuality in smaller organisms is not feasible because of higher potential costs of sex that must be held in check by intermittent sexuality. Thus an increase in size allows greater commitment to sexuality in larger organisms, and a greater commitment to sexuality is forced on larger organisms by their slower adaptive responses. Phylogenetic trends in the frequency of sex may

be to a large degree explained by these opposing size-related trends in the potential cost of sex and the rate of adaptive response.

Summary

The potential costs of sex can be divided into two large categories. The first category consists of costs that are not derived from anisogamy, and includes costs associated with recombination, with delay of synthesis at the cellular level (cellular-mechanical cost), and with fertilization. The second large category of costs is derived from anisogamy. Specific costs include the cost of genome dilution (cost of males) and the cost of sexual selection. The cost of genome dilution applies to sexual females in anisogamous organisms because the female provides cytoplasm and reserve materials to support the male genome as well as her own genome. The cost of sexual selection is caused by loss of fitness through selection resulting from sexual competition, or through dual phenotypic specialization of a single species as a result of sexual selection.

All factors contributing to the cost of sex apply potentially to a broad spectrum of organisms. However, numerous mechanisms reduce the realized cost of sex to a level far below the potential cost. The potential cost is likely to be highest in small organisms, but the realized cost among these organisms is reduced greatly by intermittent sexuality. The realized cost of sex tends to increase with size and complexity among organisms because of increasing commitment to sex with increasing size. Increasing commitment to sex is required by the lower reproductive rates and consequently lower rates of adaptation in larger organisms, which would put such organisms at a disadvantage in relation to smaller organisms were it not for increasing commitment to sexual recombination in larger organisms. Comparable commitment to sex is not possible in smaller organisms because such organisms have a higher potential cost of sex, which maintains among them a lower limit on the frequency of sex.

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