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NATURAL SELECTION AND SEXUALITY

'Introduction'

*meiotic shuffling
(meiotic drive alternative)
crossing-over
(Drosophila Y chromosome example)*

The origins and functions of sexuality had until recently remained as problems that biologists seemed to have no way of even approaching. For decades the only real comment on sex in relation to natural selection was Fisher's (1929) statement, often described as demonstrating that sexuality is the one subject which Fisher could not explain except by group selection (e.g., Maynard Smith, 1968). Williams (1971:p. 12) can be quoted on this general view of the long-term group benefits of sexuality:

"Almost universally, opinion has been that the significance of sexuality, which assures a shuffling of hereditary factors in lines of descent, is that it refines and facilitates the process of evolution. Without sexual recombination, evolution would go more slowly and could probably not have produced the observable diversity and complexity of animals and plants. It aids evolution by providing a way for genes in one line of descent to be combined with those in other lines to produce new combinations to be tested by selection There is near unanimity on the point that sexuality functions to facilitate long-range evolutionary adaptation, and that it is irrelevant and even detrimental to the reproductive interests of an individual."

Williams also says (1971: p. 13, 14):

"In other words, sexuality, a phenomenon of near universality and paramount importance, is exactly the sort of thing for which group selection must be postulated, although the force of this conclusion is only slowly coming to be realized. The reason why group selection is indicated here, or even demanded, is clear when we consider what happens to individual reproductive interests when, in meiosis, the number of chromosomes and constituent genes is reduced by half. Each resulting gamete, and zygote that is formed by fertilization, will have a sampling of half the genes of the individual that provides the gametes. In the usual mitotic divisions, each resulting cell preserves the entire genome intact.

"Suppose there were two kinds of females in a population; one produced monoploid, fertilizable eggs, and the other skipped meiosis and produced diploid eggs, capable of development without fertilization, and each with exactly the mother's genetic makeup. These parthenogenetic eggs would each contain twice as much of the mother's genotype as is present in a reduced and fertilized egg. Other things being equal, the parthenogenetic female would be twice as well represented in the next generation as the normal one. In a few generations, meiosis and sexual recombination should disappear and parthenogenesis become the normal reproductive pattern. Males would no longer occur.

"Meiosis is therefore a way in which an individual actively reduces its genetic representation in its own offspring. Any success that these offspring achieve is shared equally by the mother and the father. The parthenogenetic female shares her reproductive success with no one. Sexual reproduction is analogous to a roulette game in which the player throws away half his chips at each spin. The game is fair as long as everyone behaves in this way, but if some do and some don't, the ones who keep their chips have an overwhelming advantage and will almost certainly win.

"Sex has been recognized as an adaptation for long-term group benefit for perhaps forty years, and the existence of such adaptations is formally incompatible with the accepted picture of evolution. Yet only after group-related adaptation had been recognized in social behavior, and a controversial theory proposed to explain it, did the paradox of sexual reproduction begin to be recognized as relevant to the problem. This sequence of developments will someday be recognized as a curious feature of the history of biological thinking in the twentieth century."

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So the developments against group selection were responsible for turning biologists' attention to explaining the functions of sexuality. The result, after almost 40 years of near-silence on this issue, have been the papers of Maynard-Smith (1968, 1971a, 1971b), Parker et al (1972), Baker and Parker (1973), Williams and Mitton (1973), Ghiselin (1974), and, most recently, Williams (1975) book and Maynard Smith's 1978 bo

The importance of understanding sexuality in analyzing social behavior is obvious. Most organisms are sexual, and expressions of sexuality vary widely, among gonochorism (or dioeciousness), hermaphroditism (or monoeciousness), parthenogenesis (both apomictic and automictic), and inbreeding and outbreeding. All complex social organization depends upon sex ratios, parental investment patterns, varying genetic relationships, and other phenomena which derive from patterns of sexuality and vary with them.

What is Sexuality?

Sexuality in most modern organisms is identifiable as the tendency of some organisms to recombine their genetic materials with those of other individuals in the same species, producing arrays of novel genotypes in their offspring and descendants. Baker and Parker (1973) define it as "the coming together and recombination of the whole or part of the hereditary material of one or more organisms followed by division with or without separation, to the mutual advantage of each of the original parent organisms." They argue that, "present day sexual reproduction is likely to have been of single origin coincident with the origin of life and . . . its subsequent evolution has been a gradual process with no qualitative or chronological break between any one stage and the next." If so, then the above definition, with some modification, may apply more or less throughout the history of life.

Hermaphroditism refers to cases in which both male and female gametes are produced by single individuals. Except for sequential hermaphroditism in some fishes, it is evidently absent in vertebrates and it is rare in insects, but common in many plant groups (where it is termed monoeciousness); in marine invertebrates, and in some others such as earthworms and freshwater annelids (Ghiselin, 1963). Biparental animals are generally termed gonochoristic, biparental plants as dioecious.

Parthenogenesis refers to cases in which, in evidently previously gonochoristic or hermaphroditic species, females have become capable of producing diploid offspring with or without meiosis, without a genetic contribution from a male. Such conditions are derived, hence commonly termed unisexual rather than asexual. Production of male offspring by parthenogenesis, as with all sawflies, bees, wasps, and ants (Hymenoptera), is termed arrhenotoky; production of females is called thelytoky; and production of both sexes is referred to as deuterotoky. If a meiotic process is retained, parthenogenesis is said to be automictic, if meiosis has been lost completely the process is termed apomictic parthenogenesis (White, 1970; Asher, 1970; Quellar, 1974).

As Baker and Parker note, ". . . sexual reproduction can be subdivided into several phases, each of which share a common time of origin but each of which can be modified evolutionarily independently of the other phases. . . . Recombination may be either linear as in crossing over in diploid organisms and by the breakage and recombination of genetic material in haploid or partially diploid organisms or it may be allelic as with the pairing of new sets of alleles in diploid organisms."

The exact manner of recombination, that is, which combinations of genetic alternatives arrive together in the resulting genotypes, is generally regarded as most often random in respect to the fates of genetic alternatives during the meiotic processes yielding the gametes, although there are numerous reports of non-randomness (Levontin, 1970) -- for example, Dobzhansky ; (1970) reports non-randomness in allocation of an inversion to the polar bodies in Drosophila. Meiotic drive,

differential mortality before mating, and differential mating success all represent non-randomness in the combination of gametes to form zygotes, and linkage is a source of one kind of non-randomness in the distribution of genes during meiosis.

The apparent tendency of sexual recombination to be random during meiosis is in striking contrast to its tendencies to be non-random (selective mating) during zygote formation. This randomness has two possible selective backgrounds: (1) allelic and chromosomal competition to avoid being relegated to polar bodies may have resulted in a standoff competition among alternate genetic elements or (2) the maternal phenotype (i.e., the genotype as a whole) may somehow control meiotic distribution of genetic elements, with those genotypes (parents) being favored which cause essentially random distribution. In selective terms these two backgrounds will be exceedingly difficult to distinguish, since they seem to lead to the same result: general randomness, with occasional brief non-randomness. If generally random distribution of genetic elements during meiotic oogenesis cannot compete with either non-random distribution or asexuality, in the first case sexuality may continue to be favored because non-random allocation of genetic elements to polar bodies is favored over sexuality, in the second case sexuality will disappear. . . . Paucity of known cases of markedly non-random allocations of genetic alternatives, assuming that such would have been detected if they exist, would mean that the environments of species are such as not to favor it (but see Alexander and Borgia, ms.).

Sexuality and Developmental Plasticity

As a continuing source of variability among organisms sexuality may be compared to phenotypic or developmental plasticity. Together with extrinsic and intrinsic barriers to gene flow, selection accounting for sexuality and developmental plasticity presumably explains all phenotypic variability in living organisms. The only obvious additional sources are genic mutations, chromosomal aberrations, and breakdowns of canalizations of an accidental or incidental nature in terms of evolutionary history; all of these may be regarded as trivial for purposes of the present discussion.

All organisms, with the possible exception of viruses, may be regarded as having phenotypes, and the vast majority are also sexual, even if only at infrequent or irregular intervals. To the extent that sexuality and phenotypes can be viewed together, or compared as sources of variability, it is apparently of considerable importance to understand their relative contributions to variability in different circumstances. Anyone who has considered this problem at length may also be willing to concede that to extricate the separate influences and natures of sexuality and phenotypes is likely to contribute mightily to the solution of problems of life cycle variations that have long remained outside the reach of evolutionary explanations or generalizations.

Phenotypic plasticity has not been regarded as generally paradoxical to evolutionary biologists, although its most extreme forms, such as learning, have rarely been investigated or generalized in reproductive terms. Nor has the concept of phenotypic plasticity commonly been extended, as it must eventually be extended, to the point of explaining the general absence of "naked" genes (genes that do not produce phenotypes) multiplying in the modern environment. Phenotypes are evidently viewed generally as cushions or buffers against selective forces in the environment. Perhaps in a superficial way the kinds of selective forces to which ontogenetic plasticity represents adaptation are obvious. But biologists seem not to have become very much concerned about the kind of environmental conditions responsible for different kinds and amounts of phenotypic plasticity, and how these might relate to situations accounting for the various forms and expressions of sexuality.

Probable Benefits or Functions of Sexuality

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As Williams (1966, 1975) notes, that sexual reproduction sometimes has short-term advantages to individuals is demonstrated by the existence of populations (e.g., of aphids) that continue to reproduce asexually for one or more generations then return for one or a few generations to sexuality (Williams and Mitton, 1973). One needs only to assume that such species occasionally produce individuals that fail to return to sexual reproduction or begin an increase in the proportion of asexual generations. Although these possibilities may not actually have been demonstrated in a species of this kind, both seem virtually certain to occur now and then. White (1964), for instance, remarks that nearly every insect species studied carefully now and then reproduces parthenogenetically.

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

Conjugating ciliates recombine their genotypes and continue as individuals, presumably modifying their phenotypes and dividing later asexually. But most sexual organisms, like ourselves, use their phenotypes to produce gametes, which are themselves products of a meiotic recombination during gametogenesis, and to place those gametes into a genotype that is additionally novel because the other half of it comes from another organism. Thus, short-term advantages of sexual recombination to individuals are usually represented by effects on their descendants. I suggest, following Williams (1966, 1975), that the usual advantage of sexual recombination may be usefully described as the value to parents of placing their gametes into better genetic environments. Since the nature of the superior genetic environment may be partly or completely unpredictable to the sexual parent (because the ecological environment is unpredictable), we may expect the parent to evolve to produce numerous genetically diverse offspring as a result of a history in which some of the offspring so produced have failed, compared to asexual genotypes, while others have proved superior. The unpredictability of winning combinations and the relative success of collections of winning combinations that represent entire progenies of individual parents (sets of parents), compared to the success of broods produced by asexual genotypes, are the factors determining whether or not sexual recombination will be maintained. Sexual reproduction has been described as the better method of producing a superior genotype, asexual reproduction as the better method of maintaining a superior genotype.

In organisms that are sexual at the end of a period of asexual reproduction, as is true of metazoan organisms as well as heterogonic* species, the recombination to which sexuality exposes a gene cannot be primarily with untried mutants. Instead, what will be recombined are mutants that have been successful in different places. The recombinants will have lived in different environments so long as they are not parts of the same genome -- products of hermaphroditic selfing or apomictic parthenogenesis. How different the environments in which they have demonstrated their success actually are will depend upon two things: (1) in what fashion and to what degree the environment in the species varies and (2) to what extent outbreeding is practiced, or to what extent mating is selective between individuals that have grown up or lived in different places or different kinds of places within the species' range. If sexuality is a response to variation among environments within species' ranges, then to understand the expression of sexuality requires that we understand what the variations within

* Heterogonic species are those which change back and forth between sexuality and asexuality.

If only one
of many
genomes
will win
& you can
tell which
one is
best

species' ranges mean to the individuals and populations of the species.

These are some of the reasons why sexuality has not yielded easily to efforts to explain its selective background. Most often its benefits have been supposed to assist the population by maintenance of evolutionary plasticity. Williams (1966, 1974) recast this problem, as Fisher (1930) did the problem of sex ratio selection, by considering it in terms of the success of the broods of offspring of individual parents. In essence, he argued that sexuality will be maintained whenever the heritability of fitness between generations is sufficiently low that the genetic diversity of sexually produced broods reproduces more of the parents' genes than does the faithful genotypic replication of asexuality. Low heritability of fitness between generations implies environmental change, but the roulette of sexual recombination suggests that unpredictable change is the critical factor.

Consider a hypothetical environment, stable in every regard for an indefinite period. No one would doubt that in such an environment alleles would ultimately come to prevail which reproduced asexually a maximally appropriate and rigid phenotype, ultimately describable as essentially no phenotype at all. The only unpredictable element in this environment would be the inescapable one deriving from the appearance of mutations in some genotypes, leading occasionally to the production of superior genotypes which would displace the old genotypes. Except for changes when such mutant genotypes appear, not even changing densities or openings in the habitat are allowed as sources of change or uncertainty in this unreal model. We may assume that no known organism lives in such an unchanging environment, at least not today.

meaningful
Change in a species' habitat will always have two possible components, temporal and spatial, or some combination of these two. Spatial change, or variation, is only significant if local units of habitat are finite in duration. In fact, all habitats of all species are finite in duration, although those of some tree or grass species may last so long as to affect selection on their dominant species in the same fashion as a habitat of infinite duration. For a species to persist indefinitely when its habitat, in any certain location, does not, requires dispersal and means that changes in density and empty niches will occur. It is possible to imagine that in such a case enough propagules are produced that each empty bit of habitat will instantly and simultaneously receive propagules from all genotypes. Even if we introduce density-dependent effects in this model the habitat, while now having an element of change, is still as predictable as the habitat of infinite duration. Again, sexuality is unlikely to be evolved or maintained, but phenotypic plasticity will evolve because density-dependent effects are difficult to rule out.

Commonly it is suggested that phenotypic plasticity evolves in response to environmental changes within the lifetimes of individual organisms, while sexuality evolves (or is retained) in response to changes whose cycles are longer than the lifetimes of individuals. This idea seems inadequate for several reasons. First, it emphasizes changes, omitting mention of the predictability of change. But phenotypic plasticity can only evolve in response to changes that are in some fashion predictable: If changes are totally unpredictable there can be no way for ontogenies to be adjusted in the appropriate directions or for the right things to be learned.

maybe not
Furthermore, if cycles of change exceed in length the lifetimes of individuals, their effects can still be compensated by phenotypic plasticity during individual development if their direction and timing of change is signalled by prior changes of less consequence to the organism.

if
the habitat is sufficiently coarse-grained, geographic or spatial variations across the range of a species in which local units of habitat are finite in duration can

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represent cycles of change longer than the lifetimes of individuals. Individuals live out their lives within habitat units but their offspring or later descendants ultimately find themselves in other kinds of habitat units. Something similar happens when local habitat units change slowly, within the range of variability exhibited by suitable habitat across the species' geographic range. In both cases phenotypic plasticity can obviously be adaptive if the changes are sufficiently predictable.

It seems to me, then, that temporal and spatial changes in a species' habitat alone cannot sustain sexuality -- that unpredictability is the critical prerequisite.

Consider a hypothetical environment with two states A and B, but with all other attributes the same as the second environment described above: Units of habitat A and B disappear and reappear, but in such fashion that each niche receives all kinds of propagules upon its appearance. The purpose of this model is to consider what kind of organism will evolve eventually when the only variables are completely predictable and simple change, such as alternation between two states. Since each genotype is able to place offspring in each new habitat the instant the habitat becomes empty, it would seem that genotypes specialized for A and B niches, respectively, will win. But the ultimately favored genotype will not be a single one that produces two different genotypes by the costly roulette of meiosis, but two different asexually reproducing genotypes, one fitted to habitat A the other to habitat B. In this changing but entirely predictable environment asexuality and phenotypic rigidity will both win, and this would apparently be true if a very large number of habitat units were involved. Only the number of genotypes would change.

On the other hand, if changes of state in the environment are such that different parents are unable to place offspring into each niche upon its appearance, there may be some advantage in (1) maximizing the likelihood that each genetic kind of offspring appears in the right niche at the right time and (2) phenotypic plasticity that improves a genotype's likelihood of reproducing itself if it happens to appear in the wrong niche or at a less than optimal time. To the extent that a parent is unable to optimize offsprings' likelihood of appearing in the right habitat at the right time there will be a competition between sexuality and plasticity to compensate the adaptive deficit. Phenotypic plasticity will win whenever change that is unpredictable by parents is sufficiently slight as not to cause genotypic extinction, and sufficiently predictable by more immediately contingent circumstances as to allow selective improvement of plasticity. Sexuality will win whenever the unpredictable change is so great as to lead consistently to extinction of maladapted or misplaced genotypes and so unpredictable by ecological precedents that advantage is gained by utilizing as predictors (ie., mates) the genotypes that have already survived across the species' range.

Sexuality, then, seems unlikely to be maintained except under conditions favoring not only sexuality but outbreeding as well -- either passively by dispersal or actively by failure to mate with nearby individuals or known relatives. Sexuality is favored when environments vary in such fashion that their future states are only predictable, or are best predicted, on the basis of which genotypes have survived in them in the past, and when success in prediction is often enough maximized solely by identifying and using in recombination those genotypes that are unlike one's own genotype.

The maintenance of both phenotypic plasticity and intermittent genetic recombination thus appears to require environments which vary unpredictably within predictable limits and the prevalence of sex and phenotypes implies that this is a significant way to begin the immense problem of generalizing about environments in fashions that are directly relevant to the attributes of organisms -- in other words, in fashions likely to result in actual meaningful descriptions of species' niches.

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The Origin of Sexuality

Baker and Parker (1973) have constructed essentially the only detailed effort to account for the sequence of events during early stages in the evolution of sexuality. They reason that this process, comprising subprocesses of fusion, recombination, and fission of the genetic materials, ". . . is likely to have been of single origin coincident with the origin of life and that its subsequent evolution has been a gradual process with no qualitative or chronological break between any one stage and the next." They note that since no organisms lack all ability to reproduce asexually when it is stated that a line becomes secondarily asexual, what is really meant is that an organism that originally shows both asexual and sexual reproduction comes to show only asexual reproduction. The prevalence and distribution of sexuality indicate as do arguments from parsimony, that restrictions to asexual means of reproduction are derived, and that the presence of sexuality is not.

The fusion aspect of sexuality Baker and Parker identify as those combinations of different living things that result in "mutual advantage to the participating self-replicating molecules." Thus, they intend to exclude predation and parasitism as well as the combining of living with non-living materials. ?

Baker and Parker further note that optimum levels of recombination should evolve as a result of two opposing selective pressures, which are restated here in terms of advantages and disadvantages to hereditary units (genes) within the genome, whose effects would be to alter rates or timing of fusion, recombination, and fission.

1. The advantage of the fusion-recombination-fission process (as measured by the advantage of recombination), involves its likelihood of placing the gene in a more reproductive genotype by reorganizing the genetic materials through fusion with genes successful in another part of the species' habitat. In these terms there is likely to be favored: (a) an increase in fusion between dissimilar organisms (b) an increase in recombination (Recombination has 3 aspects: (1) crossing over, (2) which chromosomes get into the gametes and (3) which gametes combine), and (c) a decrease in the number of fissions per fusion. This trend is likely when the habitat of a population of organisms capable of recombining their genetic materials with one another varies temporarily and spatially in a manner sufficiently changeable that the heritability of fitness of genes depends upon their transfer among genotypes successful in different subunits of the habitat and (in terms of modern sexual organisms, at least) sufficiently unpredictable to give maximal advantage generally to an essentially random reduction and recombining process.

2. The advantage of adaptation to the environment in which the organisms has survived so far is likely to favor: (a) a decrease in fusion between dissimilar organisms, (b) a decrease in recombination and (c) an increase in the number of fissions per fusion.

The problem in explaining sexuality lies in understanding why the second pressure has not taken over entirely, and what have been the consequences of this failure.

We can note, incidentally, that when particular combinations of these forces result in shifts between processes favoring, respectively, fission and fusion, genes may be expected to spread which give to their phenotypes the ability to use environmental predictors of impending changes to alter the degree or timing of sexuality.

The Origin of Anisogamy and Gonochorism

Parker, Baker, and Smith (1972) attribute anisogamy (the evolution of different-sized gametes) to disruptive selection on gamete size owing to differences in

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selective forces operating before and after fusion (zygote formation), and the complementary aspects of the strategies of producing, respectively, (2) large gametes in small numbers but likely to form viable zygotes and (b) small gametes in greater numbers (and eventually locomotory), hence more likely to accomplish fusion with the smaller number of large gametes.

The originally anisogametic organisms could have been either hermaphroditic or gonochoristic. If they were hermaphroditic, they would have been unlikely to evolve anisogamy unless a significant amount of non-selfing (outbreeding) was occurring. If they were gonochoristic, some outbreeding was inevitable. Anisogamy thus implies outbreeding; therefore, all cases of inbreeding are likely to be secondary, appearing only in previously outbreeding populations.

As we shall see later, the selective forces that led originally to anisogamy maybe regarded as responsible for the evolution of the male-female phenomenon, the costs of sexuality, and the different patterns of parental investment, outbreeding, and sex ratios existing today.

With the advent of anisogamy, patterns leading to increasing costs of sexuality were set in motion, because environments were changeable and unpredictable in the fashions described earlier. These trends have been reversed repeatedly in the form of asexuality, parthenogenesis, hermaphroditic selfing, inbreeding accompanied by decreases in proportions of males in broods, and parental investment by males culminating in monogamy with nearly equal male and female parental investment.

The Costs of Sexuality

(This section is a revision of an essay written by Gerald Borgia, who is responsible for the key idea)

Even if the benefits of sexuality have been correctly identified, they are difficult to measure. In contrast, several costs of sexuality have been discussed, and they have been claimed to be quantifiable and severe. One, termed the "cost of meiosis," has been described as representing a 50% loss of genetic materials. The severe costs of sexuality have made it difficult to suppose that its functions have been correctly identified, and have led to arguments that sex remains as a deleterious but so far irreversible specialization in low fecundity organisms, such as all vertebrates (Williams, 1975).

Williams and Mitton (1973) define the cost of meiosis as "the 50% loss in genetic material in meiotic oogenesis." This definition, however, seems inadequate, since genetic material, as such, is relatively inexpensive to produce, as is evidenced by the extensive discarding of eggs and sperm by many organisms in the normal course of reproduction.

Williams (1975, p. 8) also refers to the "50% hazard per generation" suffered by each gene as a result of meiosis, which is contrasted with the 100% expectation of every gene in an asexual species of being represented in every offspring. The hazard to alleles in eggs derives from the 50% likelihood of ending up in a polar body. The hazard to alleles in sperm does not derive directly from meiosis but from the risk of being in a sperm that fails to fertilize an egg. To the degree that the success of sperm is random, the hazard of failing to become part of a successful zygote is evidently 50% for each paternal allele, since each allele is represented in half of the individual sperm.

Under density-independent conditions asexual clones can multiply twice as fast as similar sexual populations because all offspring are females capable of reproduction.

on their own. This "cost of producing males" has also been cited as the principal disadvantage for sexuality. (Crow and Kimura, 1965; Maynard Smith, 1971a, b and others). Evidently, the "cost of meiosis" and the "cost of making males" are either related or even identical, although how this may be true has never been fully explained. (End of Borgia essay)

Various ways of reducing the "cost of meiosis" or the "cost of making males" have been proposed, which may enable us to clarify these concepts further. Thus, Maynard Smith (1971a) suggested that a consistently self-fertilizing hermaphrodite largely escapes the cost of making males because only a small proportion of the reproductive soma need be devoted to producing sperm to fertilize the available ova. Similarly, Williams (1975) states that the cost of meiosis is negligible in monogamous species in which male and female invest equally in the offspring. In both of these cases the brood size can be increased to produce essentially the same potential rate of increase as in a parthenogenetic species. This essential doubling of brood size also appears to counteract the 50% hazard otherwise suffered by each allele, and because male functions are essentially identical to female functions, there is little or no cost of making males. The extreme contrast would be with a gonochoristic species in which the males contributed no parental investment, and in which the cost of meiosis would be 50%.

(The following section is from discussion with Paul Sherman)
Still another way to view the cost of meiosis, of making males, or of diverting parental investment, involves kin selection. The basic postulate of kin selection is that when abilities of potential recipients to translate benefits received into reproduction are equal, genes which cause their bearers to dispense nepotism preferentially to closer relatives will be favored. It must also be true that when other variables are absent, genes will spread which cause their bearers to behave so as to increase the genetic relatedness of relatives available for nepotism. Inbreeding, hermaphroditism, or parthenogenesis would accomplish this. Tendencies in these directions must, then, be counterselected by the benefits of recombination, and it is a cost of sexuality that nepotists, including parents, cannot simultaneously benefit maximally from sexuality and kin selection.

The first case above, that of ordinary kin selection, depends upon already existing variations in the relatedness of potential recipients of nepotism to ego; the second case leads to the creation of such differences. Such newly created differences could feasibly appear either within or between broods.

If some females have wholly sexual broods and others wholly parthenogenetic broods, each female can do no better than to tend her brood to the fullest of her ability. Despite the fact that the sexual female is only half like each of her offspring in genes identical by descent, she has no better strategy available, in regard to her offspring, than to tend her brood with precisely the same intensity as the parthenogenetic mother who is wholly like each of her offspring.

If, however, any female is ever able to introduce into her sexual brood one or more parthenogenetically produced offspring, then in populations in which sexuality is disadvantageous, such females will gain from tending the parthenogenetic offspring with twice the effort that she tends her sexually

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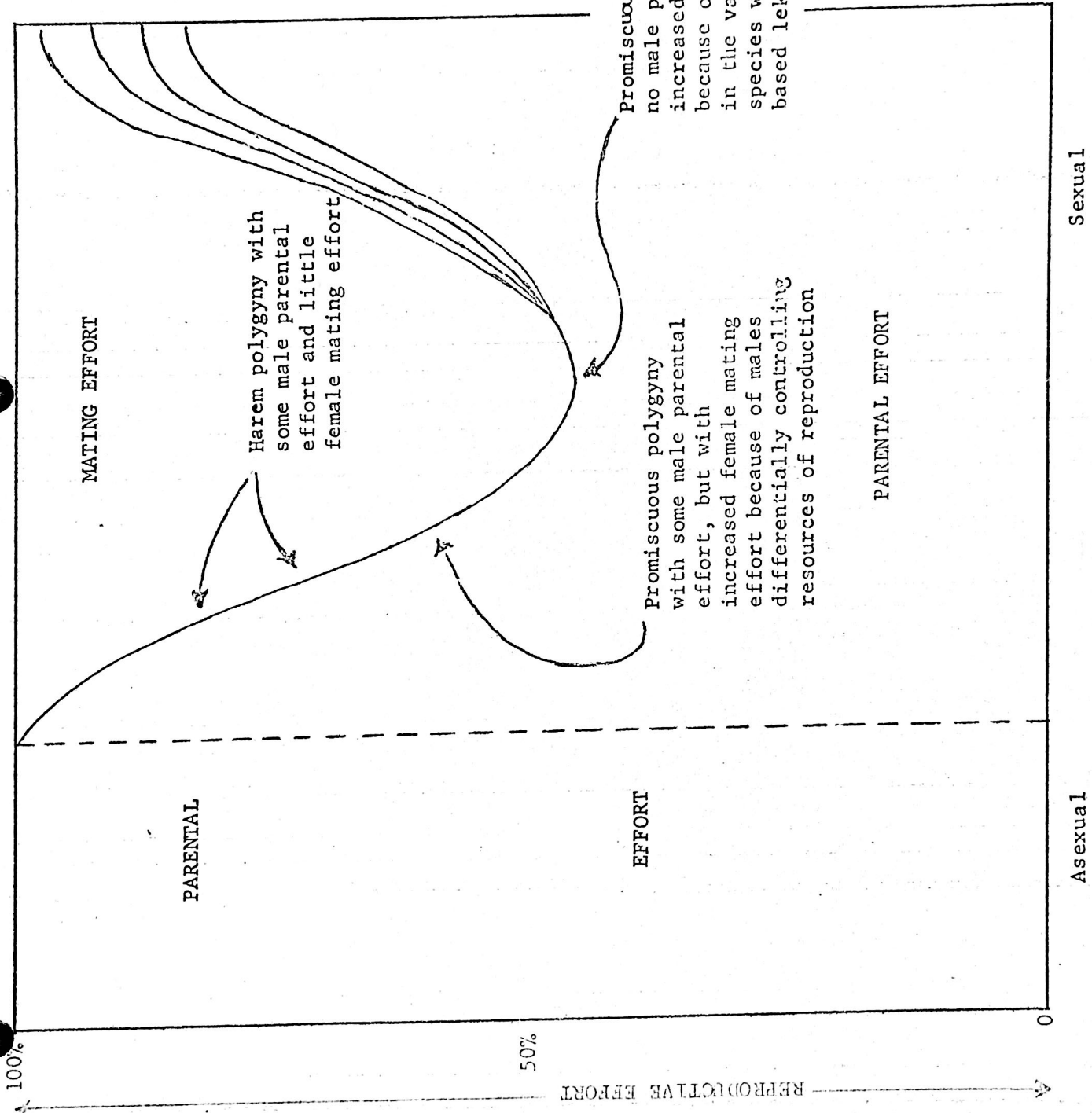
produced offspring. This assumes that each offspring is equally capable of translating parental benefits into reproduction: if asexuality is favored, the female with a mixed brood will gain by concentrating her parental investment to an even greater extent on her more valuable parthenogenetically produced offspring; and vice versa. This model requires that females producing mixed broods are able to distinguish sexually- and parthenogenetically-produced offspring.

In some sense, then, it can be viewed as a cost of sexuality that one is not afforded the opportunity of tending relatives with identical or near-identical genotypes. This consideration, which also involves a cost potentially as high as 50%, must be another way of viewing the same costs Williams and others have discussed as the cost of meiosis. We are returned once again to the notion that this cost of sexuality must somehow be explained in terms of parental investment diverted from the genetic materials of the parent.

At this point it would seem that the 50% cost of sexuality subsumed under "cost of meiosis" and "cost of making males" is actually the cost of omitting genetic material from zygotes destined to receive expensive parental investment, and of having this genetic material replaced by genetic material from a partner who does not invest in the zygote. The 50% cost of sexuality, then, does not refer to the genetic materials as such, but to the genetic materials in which the parent invests. It is the cost of diverting potential parental investment into mating effort or competition. It is a result of competition among members of the sex investing less in each offspring for mating privileges with the sex investing more in each offspring. It represents a diversion of parental effort from contributions that would enhance reproductive competition with other species or nonsexual forms to mating effort which only affects the question of which males within the species will be most successful in mating, but a diversion that helps the individual carrying it out (Borgia, Pers. comm.)

If we have properly identified the cost of meiosis as reflecting parental investment in other than one's own genetic materials, the question arises as to the cost paid by non-investing males. Because such males devote all of their reproductive effort to improving their mating success, they may be viewed as parasitizing the parental effort of their mates. They pay no cost of diverted parental investment (except through their daughters). Yet a female in such a species cannot improve her reproduction by producing only males, if she thereby creates a local surplus of males, reducing the number of matings available to her sons. Nor can she win by producing males which divert reproductive effort, from mating to parental effort, if other females' sons which do not do this achieve sufficiently more matings to secure a greater genetic representation among descendants.

Fig. 6 diagrams the effects of sexual competition upon parental effort in a hypothetical population that is first asexual, becomes sexual with males gradually diverting all of their parental effort into mating effort, and then becomes (1) wholly monogamous, the two sexes reducing their mating effort to an equal minimum and contributing equally in parental effort, (2) hermaphroditic and self-fertilizing, (3) wholly inbreeding, with females all being inseminated by their brothers, and (4) the social insects (which we'll discuss in detail later) (I only speculate that the relative costs of sexuality in the three cases are as shown on the diagram).



Self-fertilizing hermaphrodites
 Sibling matings
 Monogamous species
 Social insects (because workers are diploid and do the parental care)

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FIG. 6

In all four cases the cost of sexuality is greatly reduced, with only minimal costs of mating, or of combining eggs and sperm, remaining. In the case of inbreeding, females will evolve to produce just enough males to inseminate all of the females, and invest in such males less than in the females, since their function will be minimal compared to that of the parentally-investing females. One important thing about this diagram is that all of the changes could occur, in either direction on the diagram through selection at the individual level, even though it would appear that diversions of parental investment into mating effort are always detrimental to the population as a whole. As with genetic load, such expenses are fictitious if the actual rate of increase of those genotypes diverting parental investment into seemingly wasteful within-species sexual competition is increased over those continuing to expend all their reproductive effort parentally.