

## **The Evolution of Sexual Reproduction: A Model Which Assumes Individual Selection**

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It is commonly thought that sexual reproduction evolved and is maintained because the more rapid production of recombinant genotypes is of advantage to the species, but this advantage is long-term and is maintained by group selection while the individual committed to sexual reproduction is at an immediate disadvantage. However, Williams & Mitton (1973) and Williams (1975) have recently put forward models for the evolution of sexuality which derive it from individual and not group selection. These are reviewed below and certain limitations pointed out. An alternative, more general model is described. This accounts for the evolution and maintenance of sexual reproduction by processes of individual selection, but does not require to assume enormous fecundity, hyperintense selection, or special life-history features. It is suggested that the present model is sufficiently general to apply to most or all cases of the evolution of sexual reproduction.

### **1. Introduction**

In 1971 Williams considered that "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", since the genome of a parthenogenetic female would be twice as well represented in the next generation as that of a female producing an equal number of monoploid fertilizable eggs. Further, "the existence of such adaptations is formally incompatible with the accepted picture of evolution. . . . Sexual reproduction must stand as a powerful argument in favour of group selection, unless someone can come up with a plausible theory as to how it could be favoured in individual selection." Similar points have been made by others (e.g. Crow & Kimura, 1965; Emlen, 1973; Kalmus & Smith, 1960) and Maynard Smith (1971*a*) has stressed two problems in particular: "if the advantages conferred by sex are long-term ones, conferred on a group as a whole, how could the complex genetic basis for sexual

reproduction arise in the first place? And if the disadvantages of sexual reproduction . . . are as great as they appear to be at first sight, why is not sexual reproduction more frequently lost?"

Recently Williams & Mitton (1973) and Williams (1975) have taken issue with the view that the evolution of sexual reproduction necessarily required group selection and have argued that it is an adaptation for individual advantage. Unfortunately, their models have serious limitations. The object of the present note is to strengthen their position by putting forward a somewhat more general model. But first their proposals will be briefly reviewed.

## **2. Williams' Models of Advantageous Sexual Reproduction**

Maynard Smith's first question, "how could the complex genetic basis for sexual reproduction arise in the first place?" has been discussed by a number of authors (Bodmer, 1970; Dougherty, 1955; Maynard Smith, 1971a; Williams, 1966). It seems possible that sexual reproduction may have derived from fusion processes and cellular repair mechanisms in primitive organisms (Bodmer, 1970; Maynard Smith, 1971a), but this will not be discussed further here. However, given the emergence of a potentiality for sexual reproduction, we require to account for its maintenance and development at further stages in the evolutionary sequence. Williams & Mitton (1973) and Williams (1975) have attempted to advance the problem by providing models for certain special cases in which they consider that sexual reproduction is of benefit to the individual, in the hope that their approach may prove capable of extension.

Williams' arguments rest on two main propositions. The first is that an evolutionary explanation for sexual reproduction must identify an immediate, individual advantage to the sexual parent; group selection explanations are to be scouted. The second is that the sexual process is genetically inefficient since half the genotype is lost in the process of meiotic oogenesis whereas asexual reproduction preserves the whole. Thus he believes that a superiority of at least two-to-one in the fitness of sexually produced offspring, as compared with asexual propagules, is necessary before sex can present an advantage for natural selection to operate on.

Williams' (1975) arguments are of wide-ranging interest. However, only his three main models will be discussed here. In the first, the "aphid-rotifer model", a diploid species propagates asexually throughout a growing season in small, separated habitats. At the end of the season propagules are produced, sexually or asexually, which disperse to colonize new habitats, and

the cycle recommences. Consider a habitat colonized by  $m$  descendents of an asexual parent, all with the same genotype, and  $n$  sexually-produced propagules with varying genotypes (where  $m$  and  $n$  have the same mean,  $\lambda$ , over habitats). The colonists now propagate asexually until the habitat is saturated. The fittest clone then displaces the others, becoming exclusively dominant. Its victory depends not on the original abundance of this genotype but only on its greater fitness relative to the others. "The presence of  $n$  genotypes gives the sexual progeny  $n$  chances of including the winning genotype, while the asexual progeny has only the single chance for its single genotype (Williams & Mitton, 1973)." The authors show that as the number of asexual generations in the new habitat, and as  $\lambda$  (determining  $n$ ) increase, the proportion of surviving animals with genotypes of sexual origin rises. When this proportion exceeds two-thirds the cost of meiosis is more than compensated for and sexual reproduction has proved more advantageous.

This situation is conceivable and is of interest. But the model depends rather critically on the precise assumptions made. Normally we might expect that as the initial number of colonists in a new habitat increases their sources of origin will become correspondingly diverse, but Williams & Mitton (1973) avoid this assumption, comparing the progeny of only two parents in all cases. They say "Other individuals from other parents may also be present but are not relevant to the comparison." But this may be questioned. Suppose that we compare sexual and asexual colonists when each derive from a number (the same number) of parental habitats. If these habitats all differ and each is dominated by the locally fittest genotype, then the number of asexually produced genotypes in the colony will increase approximately linearly with the number of habitats of origin. But it is not evident that the range of sexually produced propagules will increase in the same way since the ranges of genotypes produced by different sexual parents may overlap increasingly as the number of such parents increases, even though they occupy different habitats. In the extreme, all possible sexually produced genotypes and all fit (for their parental locations) asexual genotypes will be represented in a new colony, and it is not obvious that in this case the sexual descendents will have the two-to-one advantage over their asexually generated conspecifics which Williams considers necessary.

Maynard Smith (1971*b*) proposed a very similar model and came to a different conclusion: it is the asexually produced propagules which are at an advantage except in the extreme case in which "the correlations between selectively relevant features of the environment commonly change sign between one generation and the next". This is an extreme condition. It does not merely require that the environments are rather different in the two seasons. It requires that if, for example, habitats which are sandy are

drier than average in the first year, then in the second year sandy locations must be more than usually moist.

Williams & Mitton (1973) comment that Maynard Smith reaches his conclusion because his model "deals with the probability of a propagule having a required level of fitness in the colonized habitat", whereas in their model "the fittest genotype . . . is assured of winning, no matter how sub-optimal it may be". But this does not, in fact, seem to be the critical difference between the two proposals: if in Maynard Smith's model one substitutes the locally fittest for the ideal genotype his conclusion is little affected. The difference between the Williams & Mitton and Maynard Smith models which is actually responsible for their opposite implications is that the latter implicitly assumes that every colonist, whether sexually or asexually produced, is randomly and independently chosen from all those available. Thus the Maynard Smith model would apply when colonies are reasonably accessible to a considerable number of the previous years' imperial centres, the Williams & Mitton model when potential colonies are so remote from the parental habitats that it is unlikely that more than one or two ship-loads of colonists will ever find them.

Williams & Mitton (1973) also put forward an "elm-oyster model". This applies to large organisms which reproduce sexually only, producing propagules in such enormous number that many will colonize a location in which only one can survive. The intense competition which results will select the fittest genotype present, independent of its abundance among the original propagules in the habitat. A simulation showed that when their number exceeded about 700 there was sufficient advantage to sexual reproduction to outweigh the cost of meiosis. But again, the analysis rests on the assumption that only a single asexual parent contributes offspring to any habitat. This may be reasonable if we consider two neighbouring elms, one sexual, one asexual, carpeting the subjacent ground with a lawn of seeds. But since a female oyster may produce 100 million young in a lifetime, distributed by water throughout the bay or estuary, it is difficult to believe that a single colonizable location would not receive spat from a large sample of asexual parents, in which case an analysis along the lines of that offered by Maynard Smith (1971*b*) seems more likely to apply. Thus the advantage of sexual reproduction seems better established for the elm than for the oyster.

Williams (1975) also presents a "strawberry-coral model". The argument is that by asexual reproduction a strawberry clone can expand to the limits of the area to which it is adapted or in which its genotype is the fittest present. But if it can also reproduce sexually, seed will be distributed beyond these limits and may reach and colonize new habitats. The model is not worked

out quantitatively and is described as an "intuitive visualization". Unfortunately, since it does not distinguish the advantages due to sexual reproduction *per se* from those arising from the wide dispersion made possible by the production of seed it is difficult to evaluate.

Williams (1975) notes that his models all require specialized assumptions. He considers that "additional models may be valid, but . . . all will require special life-history features" and is convinced "of the unlikelihood of anyone ever finding a sufficiently powerful advantage in sexual reproduction with broadly applicable models". He believes that only in "large trees with small seeds, large fishes and invertebrates with small eggs, macroscopic lower plants with microscopic spores [and organisms with] clonal proliferation of genotypes . . . sexual reproduction can be adaptive and currently in evolutionary equilibrium with asexual". To explain sexuality in organisms which are not of outstanding fecundity and subject to hyperintense selection he appeals to "historical constraints that preserve sexual reproduction when it has ceased to be adaptive".

Although Williams' contribution is important and thought-provoking it is evident that his models are restricted in application. Furthermore, the proposition that in a large range of species such as "mammals, birds, and many insects" sexuality is "a maladaptive feature" derived from a remote high-fecundity ancestor, "piscine or even protochordate", and perpetuated because they lack the preadaptations necessary to revert to asexual reproduction is unconvincing if only because of the sporadic occurrence of asexual reproduction in higher forms (Emlen, 1973).

In the next section I outline a simple general model which appears to avoid some of these difficulties.

### 3. A Model for the Evolution of Universal Sexual Reproduction

A popular explanation for sexual reproduction is that it "confers on a species a greater capacity for rapid evolutionary change, and consequently that when the environment changes, those species which reproduce sexually are more likely to survive", an argument which relies on group selection (Maynard Smith, 1971a). I shall attempt to show that such rapid adjustment may be mediated by individual selection. The model below rests on two assumptions. The first is that environmental variation is frequent and not exceptional, it affects individuals and produces its results by selecting between them. The second assumption is that adaptation to a major environmental variable is likely to be polygenic rather than depending on a single locus.

We consider a population of diploid animals consisting of parthenogenetic and sexual females, and males. To avoid the objection that an asexual

clone cannot be considered to be part of a Mendelian population it can be assumed that the genes for parthenogenesis have less than perfect penetrance, so that lineages may alternate irregularly between sexual and asexual reproduction. However, for the several generations covered by the model it will be simplest to let descendants retain their parents' status.

Let there be initially  $n_p$  parthenogenetic females,  $n_s$  sexually reproducing females, and  $n_m$  males, the total population consisting of  $n_t = n_p + 2n_s$  individuals. Following Maynard Smith (1971a) we assume that each parthenogenetic female produces  $k$  female offspring, each sexual female  $k/2$  daughters (and  $k/2$  sons). Thus, other things equal, the proportion of sexually reproducing females should fall in each generation, until eventually only asexual reproduction is shown.

But other things may not be equal. Suppose that the success of these animals depends on adaptation to an environmental variable, such as temperature, which may change. It is not unreasonable that the response to major environmental variables, likely to affect an organism in many ways, should depend on alleles present at a number of loci. We shall assume that adaptation to temperature change depends on a polygenic system consisting of  $N$  loci, at each of which there are two homologous genes. The total effect of the  $2N$  genes may be represented by a genotypical score,  $G$ , for each animal, made up of contributions from the two genes at each locus. For simplicity we assume that the different loci contribute to  $G$  with equal weight and that their effects sum additively, that at each locus two alleles may occur, a "high" allele contributing a value of  $+0.5$  to  $G$  or a "low" allele contributing  $-0.5$ , that there is additive gene action at each locus, a "high" homozygote contributing a score of  $1$ , a "low" homozygote  $-1$ , and a heterozygote  $0$ , that when sexual reproduction occurs segregation at each locus is independent, and that the effect of mutations can be ignored. These assumptions are not essential but they simplify the argument. Thus a polygenic system with  $N = 2$  would allow  $G$  to range from  $-2$  to  $2$ , with  $N = 3$ ,  $G$  would range from  $-3$  to  $3$ . We also assume that as the average environmental temperature rises the value of  $G$  giving optimal adaptation increases correspondingly, that males are fertile at all temperatures, but that any given ambient temperature determines a corresponding range of adaptation for females, i.e. a set of genotypical scores, such as  $-1$  to  $+1$  [which we shall represent by  $(-1, 1)$ ], within which a female's value of  $G$  must lie if she is to be fertile.

Certain implications of this model are immediately apparent. If there are initially  $n_p$  parthenogenetic females and  $n_s$  sexual ones, and environmental conditions are stable, then in each case only those sexual females whose  $G$  scores lie in the range of adaptation, say between  $-1$  and  $+1$  will breed.

If all the parthenogenetic females have the same genotype, with a  $G$  score within the range of adaptation, then they will all breed, and they will each produce twice as many female progeny as those sexual females able to breed at the prevailing temperature. Their advantage will be even greater than this suggests, since their young will all have  $G$  scores within the range of adaptation, while this will be true of only a proportion of the sexual females' daughters. Thus asexual reproduction should eventually become the norm.

Suppose, however, that the average temperature changes with time so that the range of adaptation is different for each generation. Thus it might increase from  $(-1, 1)$  to  $(0, 2)$  for the second generation. If the genotypical score common to the parthenogenetic females is  $G = 0$  they will still be able to breed. But if the range of adaptation rises to  $(1, 3)$  for the subsequent generation, the parthenogenetic strain will no longer be able to breed and will disappear. Each successive range may, however, include some descendants of the original sexual females, and the mean  $G$  scores of their progeny will tend to move in the direction taken by the range of adaptation. Thus, provided the shift in environmental temperature does not proceed so rapidly that reproduction by the sexual individuals falls below the level necessary to sustain a population, the mean  $G$  score will adapt to the shift and may end at a value far removed from its starting point.

Table 1 presents values of  $n_p$  and  $n_s$  calculated for successive generations of a population which suffers a long-term fluctuation in environmental temperature. The original ( $F_0$ ) population consists of 16 parthenogenetic females and 16 sexual females (and 16 males), the parthenogenetic females all having the same genotypical score,  $G_p = 0$ , and the sexual females having the mean score  $\bar{G}_s = 0$ . The "high" and "low" alleles are initially equally

TABLE 1  
*Numbers of females in successive generations*

Generations	$n_s$ ( $k = 4$ )	$n_p$ ( $k = 4$ )	$n_s$ ( $k = 8$ )	$n_p$ ( $k = 8$ )	$n_p/n_s$	$\bar{G}_s$	Range
$F_0$	16	16	16	16	1.00	0	-1, 1
$F_1$	28	64	56	128	2.29	0	0, 2
$F_2$	39	256	156	1024	6.56	0.26	1, 3
$F_3$	31.1	0	249	0	0	0.73	2, 4
$F_4$	11.4	0	183	0	0	1.37	2, 4
$F_5$	10.4	0	332	0	0	1.68	1, 3
$F_6$	20.3	0	1298	0	0	1.53	0, 2
$F_7$	40.5	0	5187	0	0	1.53	-1, 1
$F_8$	33.4	0	8541	0	0	1.19	-1, 1
$F_9$	43.7	0	22350	0	0	0.98	—

frequent at each locus in the sexual organisms and are binomially distributed. Adaptation to the prevailing temperature depends on a polygenic system consisting of two loci. The original population is adapted to the starting temperature and females with  $G$  values in the range  $-1$  to  $+1$  are fertile. Thus all the parthenogenetic females in the initial population reproduce, giving 64  $F_1$  daughters (for  $k = 4$ ), while only 14 of the sexual females do so, giving 28 daughters. Figures for subsequent generations calculated for  $k = 4$  and  $k = 8$  are shown. It is evident that when temperature variation is small the parthenogenetic females outstrip their sexual sisters but the latter are far more resilient in adapting to a major temperature fluctuation. Thus the part of the genome determining that reproduction shall be sexual benefits at the individual level by making it possible to realize the capacity for genetic adaptation to environmental change latent in the polygenic adaptational system.

In Fig. 1, relative frequency polygons for the different values of  $G$  for the successive generations are shown. The generations produced under the highest environmental temperature,  $F_4$  and  $F_5$ , contain no members having  $G$  values of  $-2$  or  $-1$ . These genotypes reappear as the temperature swings down again. Thus the emergence of genotypes far beyond the initial extreme, as has been shown to occur in directional selection experiments (Crow & Kimura, 1965), presents no special difficulty. Since the genotypes in our example were limited to the range  $-2$  to  $+2$ , the sexual females would have ceased breeding and become extinct had the temperature fluctuation proceeded so far that  $G$  values in the range  $(3, 5)$  were required. This illustrates the advantage of having adaptation to fluctuating environmental variables determined by large rather than small polygenic systems, giving wide ranges of potential genotypes. This constitutes one advantage of polyploidy.

#### 4. Discussion

The present model develops suggestions contained in earlier formulations (Maynard Smith, 1971*a,b*; Williams, 1975; Williams & Mitton, 1973). It differs in being far more widely applicable but is similar in avoiding the requirement of group selection: it is not necessary to suppose that selection within a group proceeds in one direction, between groups in another. It rests on assumptions—polygenic genetic adaptation, and a fluctuating environment—sufficiently general to make it plausible that these may have applied in most or all cases of the evolution of sexual reproduction. The example which has been worked through illustrates that when the model is appropriate selection of the individuals which adapt most successfully to environmental variations may result in sexual reproduction prevailing



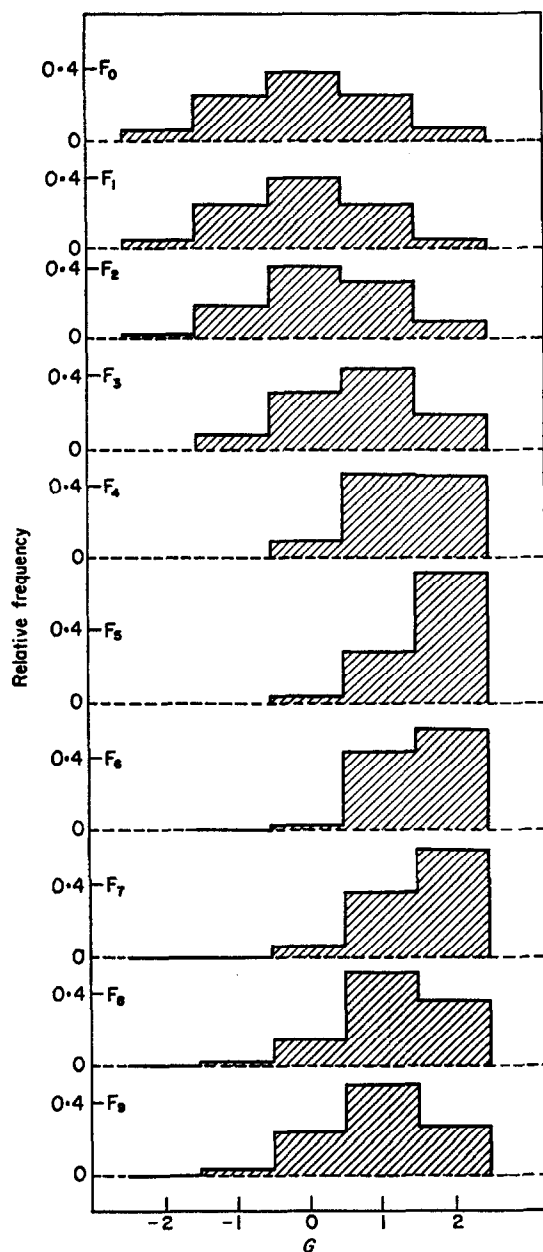


FIG. 1. Relative frequency functions for different genotype values in successive sexually produced generations under selection.

because it allows genetic adaptation to supplement physiological adaptation to an extent or at a rate not possible when animals reproduce asexually. Genetic adaptation by the accumulation of beneficial mutations would be a far slower process. The variation in environmental variables required by the model need not be unidirectional. Oscillations of sufficient amplitude will be effective.

The same conditions which may account for the evolution of sexual reproduction would tend to maintain it. For complex higher organisms it must be rare that every important environmental variable is reliably stable. When this is not the case strains relapsing into asexual reproduction may be weeded out by changing adaptational demands with sufficient frequency for this to constitute a pressure selecting against the pre-adaptations which allow such relapses to occur. Thus obligatory sexual reproduction is likely to be found in species which have lived in continuously unstable environments sufficiently long for the machinery preserving the asexual option to have been largely or completely eliminated. Maintained parthenogenesis or asexual reproduction would be expected in populations living in stable and invariant niches, as with some tropical fish or the symbiotic intestinal flagellates of termites (Vickerman, 1966). If periods of stability and change alternate in a predictable way then it would be useful to employ asexual reproduction during stable periods and revert to sexual fusion when environmental conditions deteriorate, become variable, or otherwise require a change in genetic adaptation (Bodmer, 1970; Maynard Smith, 1974). This characteristic is shown by many micro-organisms and by some higher organisms, such as aphids.

The importance of short-term genetic adaptation has been stressed by Williams (1975) especially in relation to his elm-oyster and triton models. Although it has not usually been given much weight in higher animals, repetitive changes in gene frequencies at two loci have been observed to accompany population cycles in the field vole and this has been interpreted as evidence that "demographic events in *Microtus* are genetically selective and that losses are not distributed equally over all genotypes" (Krebs, Gaines, Keller, Myers & Tamarin, 1973).

Williams (1975) devised his models to overcome the "cost of meiosis". He considers that "parthenogenetic eggs would each contain twice as much of the mother's genotype as is present in a reduced and fertilized egg" (Williams, 1971) and this gives asexual reproduction a two-to-one advantage. Maynard Smith (1974) argues that this does not apply to organisms with isogamy, and that as sex and meiosis almost certainly preceded anisogamy this disadvantage need not be taken into account when considering the origin of sex. Elsewhere he has made the assumption that sexual mothers produce

fewer daughters than asexual (Maynard Smith, 1971*a,b*), and this assumption was included in the model given above. This is a different argument for the disadvantage of sexual reproduction from that based on meiotic cost, and the relation between them deserves further consideration. But at this point it is sufficient to note that on whatever grounds an advantage is assigned to parthenogenesis, and even if its magnitude is two-to-one, the events postulated by the present model appear capable of rapidly outweighing it, especially if we consider that normally the average values of several environmental variables may vary simultaneously.

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