J. Genet. Vol. 69, No. 1, April 1990, pp. 1–10. © Printed in India.

The evolutionary maintenance of sexual reproduction: The solutions proposed for a longstanding problem

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Abstract. The evolutionary maintenance of mixis is one of the major unsolved problems in modern biology. This paper reviews the phenomenon of sex, the hypotheses for its maintenance, and recent evidence bearing on the hypotheses. One elegant experiment supports the idea that bacterial transformation, an analogue and possible forerunner of eukaryotic mixis, functions as a repair mechanism. All mechanisms that produce a short-term advantage for sex in eukaryotes and that are supported by experimental results rely on strong genotype by environment interactions for fitness. While many environmental factors are involved, most prominently parasites, disease, and coarse-grained environmental heterogeneity of other sorts, each is effective only insofar as it is involved in a genotype by environment interaction for fitness.

Keywords. Sexual reproduction; genotype by environment interaction; mixis; evolution of sex.

1. Introduction

The existence of sexual reproduction was no-puzzle for evolutionary biologists until 1962, when the publication of Wynne-Edwards' book signalled one of the most productive mistakes in the history of biology. Wynne-Edwards made explicit and clear a kind of group-selectionist thinking that had previously been too implicit and diffuse to stimulate objections. Prior to that, one could explain sexual reproduction as an adaptation that endowed a population or species with the ability to evolve more rapidly than would asexual reproduction. After that, as part of the reaction to the criticisms of group selection (e.g. Williams 1966, Ghiselin 1974), one had to find explanations based on individual selection for all sorts of adaptations, among them sexual reproduction.

Recent progress towards that goal has been summarized in two books, Stearns (1987) and Michod and Levin (1988). This paper aims, first, to summarize the main lines of argument, then to review ideas and evidence published after those two books appeared. Its main conclusion is that all mechanisms proposed to explain the short-term maintenance of sex through individual selection rely on strong genotype by environment interactions in fitness. The problem of sex reduces to the problem of genotype by environment interactions for fitness (Bell 1982)–where do they originate, how are they maintained?

2. Outline of the argument

2.1 *The phenomenon of sex*

The essence of the phenomenon is the mixing of two or more genomes. In the sexual reproduction of eukaryotes, mixis is produced through both segregation and recombination. It is equivalent neither to reproduction nor to gender (Weismann

1913). Mixis can occur without reproduction (bacterial transformation, phage transduction, protozoan conjugation), and reproduction can occur without mixis (clonal reproduction).

However, in sexually reproducing multicellular eukaryotes, mixis is normally tightly bound to reproduction. Here the requirement for nuclear fusion forces a return at some point in the life cycle to the single-cell stage. This "bottlenecking" aspect of life cycles preserves the interests of the germ line and the nuclear genome. It is also deeply imbedded, hard to change, and thoroughly confounded with sexual reproduction (Weismann 1913). As a consequence, tests of hypotheses about the evolutionary maintenance of sexual reproduction will yield results that can be straightforwardly interpreted only in cases where "bottlenecking" can be properly controlled, for example in unicellular organisms. Furthermore, we should not always expect to find short-term benefits from sex because it is such an old, deeply-embedded, and fixed feature of many organisms that asexuality may not be an option open to selection.

2.2 *Why is mixis a problem? The costs of sex*

If mixis were not costly, one would only have to find a very small positive selection pressure to explain its maintenance. However, because it can cost a lot, very strong advantages must exist that explain its existence (Williams and Mitton 1973). (Here, cost is taken to mean a reduction and advantage to mean an increase in individual fitness.)

The costs of mixis can be divided into general costs that do not derive from anisogamy, that hold in unicellular organisms and in organisms that produce gametes of equal size, and costs that derive specifically from anisogamy (Lewis 1987). Recombination is a general cost because it breaks up combinations of genes that are superior in that they have survived to reproduce in the local environment. In organisms with high fecundity, this cost can be large, but it can be countered by selective investment in only those zygotes that have high survival chances (Kozlowski and Stearns 1989). There are a number of general cellular-mechanical costs associated with meiosis, gametic fusion (syngamy), and nuclear fusion (karyogamy). These require little energy but much time. Mitosis takes 15 min to 3–4 h, depending on cell size and temperature; meiosis takes from 10 to 100 h and increases with amount of nuclear DNA (Lewis 1987). Syngamy and karyogamy add to that contrast. The main factor reducing this cost, especially large for the kind of small organism with a short generation time in which sex probably first evolved, is intermittent sexuality. Lewis (1987) describes a number of other factors exploited in particular groups. A final class of general costs are associated with the time required to find a partner and the increased risk of mortality during copulation.

Costs derived specifically from anisogamy are the classical costs of sex whose existence convinced Williams (1975) and Maynard Smith (1971, 1978) that mixis poses an important problem for evolutionary theory. The first such cost is that of genome dilution: every fertilized egg of a sexually reproducing female contains only half her genes. The second is the cost of males, for if she were producing asexually she could make only daughters. This cost can be reduced, in cases of local mate competition, by producing many daughters and few sons, and in cases of sequential hermaphorditism by investing more in female than in male function, but neither

remedy is general. The final cost of anisogamy is indirect and not directly involved in the calculus of advantages and disadvantages to sex for it occurs mostly as a highly derived condition in organisms in which a switch to asexuality is probably not an option. It is the cost of sexual selection, imposed by conflict for mates and increased exposure to risk during mating and by any potential reduction in overall fitness caused by Fisherian runaway processes (Lewis 1987).

In small isogametic organisms, the extra time required for meiosis, syngamy, and karyogamy constitutes a cost at least as great as that of genome dilution. The prominent discussion of the cost of genome dilution has led many experimentalists to search for an advantage of sex that would balance a 50% cost, but in fact we should be looking for advantages that balance the costs that are actually incurred by the organisms in question. In unicellular organisms and small multicellular organisms with short generation times, these costs may be several times greater than those of genome dilution. In multicellular organisms with long generation times, they may actually be less than 50% (Lewis 1987).

2.3 *Questions about sex*

The questions one can pose about the evolution of sex cover a much broader spectrum than the question that dominates the literature – how selection on individuals maintains mixis.

How did sex originate? The problem is to envision the series of intermediate steps required, first, to transform a bacterial cell into a eukaryotic cell with a nucleus, chromosomes, a spindle apparatus, and mitosis, then to transform mitosis into meiosis. No good overview is known to me. Margulis (1981) suggested that the spindle apparatus originated by the incorporation of an endosymbiotic bacterium into the cellular machinery. If true, one must then explain how the spindle genome was incorporated into the nuclear genome.

How did mating types originate? Why should isogamous organisms not mate at random but only with specific classes of partners? And how many mating types ("sexes") should there be? Hoekstra (1987) recognized two processes favoring the evolution of mating types: (1) more efficient molecular gamete recognition, and (2) intragenomic conflict between nuclear and cytoplasmic DNA. Some of his models suggest that only two types can coexist stably, a necessary precondition for the evolution of anisogamy. Iwasa and Sasaki (1987) found that the number of sexes depends on the mating dynamics. If a partner must be found in a limited amount of time, they expect the number of sexes to increase without bound; otherwise, they expect two sexes.

How did anisogamy originate? The traditional hypothesis is that there is disruptive selection on gamete size, in one direction for more gametes and in the other for bigger gametes. Hoekstra (1987) confirms that this process will work, but he also points out that anisogamy could have originated as a side-effect of selection for efficient use of pheromones in finding the partner gamete.

How did gender evolve out of anisogamy? As soon as eggs and sperm come into existence as different sized gametes, females become a limiting resource, for one male can fertilize more partners than can one female. In consequence males compete for access to females and females can select among males: in brief, sexual selection. Gender then evolves as the set of characters under sexual selection and as

adaptations for sex-specific parental roles (for a recent review see Bradbury and Andersson 1987).

Given that differences in gender exist, how are they determined by genetics and development? Gender may be determined genetically either through heterogamy (sex chromosomes) or haplodiploidy; it can also be determined environmentally through a wide variety of mechanisms and for a diversity of reasons (Bull 1983, 1987).

2.4 *The consequences of sex*

These are so far-reaching that one is tempted to answer, "everything interesting in biology" but that is not strictly true. However, if there were no mixis there would be no species (Weismann 1913), and sexual reproduction has produced microevolution as we know it, including virtually all phenomena covered by population and quantitative genetics. Kin selection does work within clones, but the wealth of degrees of relationship provided by sexual reproduction certainly makes the testing of hypotheses of kin selection much easier. Sexual selection has produced the differences between the sexes that constitute most of the subject matter of sociobiology and behavioral ecology, and allocation of reproductive investment to male and female offspring or function has provided the phenotypic diversity for some of the best-confirmed predictions in evolutionary biology (Charnov 1982). [The question of the evolution of sex-ratios and sex allocation was of long-standing interest to Suresh Jayakar (from Jayakar and Spurway 1966 to Jayakar 1987).] In brief, sex is either at the center of or else strongly influences most of the research program of evolutionary biology.

3. Given its costs, how is mixis maintained by selection?

3.1 *The classical hypothesis: faster adaptation, slower maladaptation*

The traditional hypotheses for the evolutionary advantage of mixis are based on the properties of gene pools. Weismann (1913) and Fisher (1930) pointed out that sexually reproducing populations can adapt more rapidly to a changing environment because sexual reproduction can bring together in a single individual advantageous mutations with independent origins in different individuals, a process that can only occur sequentially rather than in parallel in asexual populations. Crow and Kimura (1965) give a particularly clear explanation of this contrast. Just as mixis brings together combinations, so does segregation separate them. This makes it possible to cast off deleterious mutations in sexual populations rather than being forced to let them accumulate, as in asexual populations, a mechanism known as Muller's Ratchet (Muller 1932; Kondrashov 1988).

As envisaged by Fisher and Muller, the advantage of sex arises because genes at different loci can be brought together, or thrown away, in different combinations. Recently, Kirkpatrick and Jenkins (1989a) have shown that these advantages also exist for segregation at a single locus. The advantage exists even for populations in which only a few individuals reproduce sexually (Hedrick and Whittam 1989) or in which sexual reproduction occurs only intermittently (Kirkpatrick and Jenkins

1989b). Such populations enjoy both the advantages of sex and most of the advantages of asexuality.

The problem with the classical hypotheses is group selection. The advantages of sexual reproduction are population-level properties, and the models that investigate them contrast the performance of sexual and asexual populations rather than sexual and asexual individuals. Group selection has regained a certain respectability in recent years (Wilson 1983; Futuyma 1986; Pollock 1989), but for this kind of problem it would require a major suspension of disbelief to suppose that processes driven by differential advantage to populations could explain the evolutionary maintenance of mixis within those populations where asexuality was clearly an alternative. Where a mixture of sexual and asexual individuals within the same population are ruled out by constraints of some sort, these mechanisms might still apply. And it is certainly the case that the phylogenetic distribution of asexuality strongly suggests that a sort of species selection has favored sexuality over asexuality (Maynard Smith 1978; Bell 1982). The question is, should we regard that sort of effect as a direct product of species selection or as an unavoidable byproduct of reproductive modes that evolved within populations for reasons of individual advantage? Most recent work has concentrated on the latter possibility.

3.2 *Hypotheses based on short-term advantage: 1. Saturation of the environment*

Here I use the term "saturation of the environment" to cover all those hypotheses that invoke density-dependence, frequency-dependence, and other sorts of competitive interactions, whether intra- or inter-specific. Ghiselin (1974) proposed that sexual reproduction would be advantageous in saturated environments because it would allow more complete and efficient distribution of resources among a set of progeny. He based his argument on an economic analogy to the advantages of diversification for firms experiencing market saturation.

Bell (1982) called this model the Tangled Bank, making reference to the last paragraph of Darwin's *Origin of species*, and reviewed comparative evidence that broadly supported the hypothesis. In diverse comparisons and experiments, he found that sexual reproduction was more frequent at high population density and in areas of high species diversity than it was at low population density or in areas of less intense biotic interaction. This general trend was confirmed for plants by Bierzychudek (1987) and for cladocerans by Hebert (1987), both of whom found asexuality more frequent at high altitudes and latitudes. In both cases, parthenogenesis is confounded with polyploidy, and it is not clear which factor is the cause and which the effect (Bierzychudek 1987; Innes and Hebert 1988). The important conclusion from this set of observations is that sexuality is not strongly associated with environments thought to be harsh or unpredictable; it does occur regularly under conditions of strong intraspecific competition, a trend consistent with patterns in animals with alternating asexual and sexual generations. In both aphids and cladocera, the sexual generations are just as closely associated with high population density as they are with environmental cues like temperature or daylength.

Comparisons can rule out certain hypotheses, but they are not very enlightening when it comes to mechanisms and causes. To address those issues, models have been built to refine the Tangled Bank hypothesis and check its logic, and

experiments have been done to try to detect density- and frequency-dependent effects on sexual advantage. In the process, the Tangled Bank has disappeared as a general hypothesis, for as originally formulated it was too vague to test, and has been replaced by much more specific models, hypotheses, and experimental designs that nevertheless all had their origin in Ghiselin's insight.

Prominent among the competition-based models are those of Case and Taper (1986) and Koella (1988). Case and Taper investigated a nongenetic ecological model, a single-locus model, and a quantitative genetic model. All three supported similar conclusions: sexual types can coexist or even supplant asexual types when genotypes differ strikingly in their resource usage, the environment is constant, and resource exploitation is severe. Under these conditions, sexuality is favored by frequency-dependent selection on rare genotypes. Koella confirmed these results for equilibrium conditions, and when he examined the dynamics of the system, he found that the introduction of asexual types is destabilizing. Asexual types have more chaotic population dynamics and have a higher probability of extinction than sexual types, whose population dynamics are more stable because their diverse offspring occupy a broader range of the resource spectrum at lower densities. Koella established that the ecological conditions that favor sexual reproduction are somewhat more general and easily attained than had previously been thought. Intraspecific competition, working through density-dependence and/or frequency dependence, can in principle maintain sexual reproduction.

To establish that a mechanism can work is one thing; to show that it does work in a particular case is another. Experiments testing competition-based hypotheses for the maintenance of sex have concentrated either on frequency-dependent (Antonovics and Ellstrand 1984) or on density-dependent (Ellstrand and Antonovics 1985; Browne 1980) advantages of sex. The results can be summarized as tantalizing but inconclusive. For example, in one experiment (Kelly *et al.* 1988) the average reproductive rate of sexuals, summed across 30 parents, was 1·43 times that of asexuals, with a range of 0·96 to 4·52. Under both frequency- and density-dependence, sexual types of sometimes have higher individual reproductive success than asexual types, but the advantages demonstrated so far have not been consistently large enough to outweigh the 50% cost of genome dilution.

3.3 *Hypotheses based on short-term advantage: II. Parasites and disease*

A second major class of hypotheses for the maintenance of sex is based on models of coevolutionary arms races. The central notion is that the environment constantly deteriorates for existing genotypes, that novel genetic combinations have higher fitness. Because of the evolutionary advantage of their short generation times, parasites and diseases have most often been invoked as the agents responsible (Levin 1975; Jaenike 1978; Hamilton 1980; Bremermann 1980; Bell and Maynard Smith 1987; Cohen and Newman 1989).

Some evidence supports this hypothesis. In New Zealand, Lively (1987) studied a series of populations of snails that varied in the proportion of individuals reproducing sexually or asexually. The proportion reproducing sexually correlated positively with the incidence of trematode infections. This is the most direct evidence available implicating parasites in the maintenance of sex. Alexander (1989) has demonstrated that some plant genotypes (of the species *Silene alba*) vary

tremendously (0–100%) in their resistance to a disease organism, a smut (*Ustilago violacea*), but she did not demonstrate a direct advantage for sexual over asexual reproduction by measuring reproductive success. Several groups are currently doing experiments on the interactions between reproductive mode and parasites and disease, and some significant effects have been found, but the work is not yet published.

In contrast, Parker (1988) found little effect of fungal diseases on clonally reproducing mayapples and noted that the plants were protected from serious infection by their morphology. This raises an important problem with the disease hypothesis. Diseases and parasites are only important agents of selection when they have significant consequences for the fitness of the host. However, virulence and resistence do evolve, not always but quite often in the direction of less combined impact on the host. The evolution of increased resistance is certainly common. If the evolution of reduced virulence is also common, then defenders of the idea that sex is maintained by parasites and disease will have to develop a more refined version of the hypothesis. Perhaps it takes entire communities of disease organisms with small individual but major combined impact to maintain sex in hosts. Or, if the rate of origin of new diseases is high enough, even though the virulence of each disease tends to decline, there will usually be some new disease with high virulence spreading into the host population, and that could generate the desired effect.

Some of the models currently being developed that use parasite–host interactions to explain the evolutionary maintenance of sex in the hosts encounter an ironic problem (e.g. Hamilton *et al.* 1990). They appear to generate such strong selection pressures favoring sexual reproduction that it becomes difficult to explain how any asexual organisms have survived at all.

3.4 *Hypotheses based on short-term advantage: DNA repair*

The DNA-repair hypothesis for the maintenance of sex has been most prominently applied to bacterial transformation. Bacterial transformation is at least a prokaryotic analogue and perhaps a genuine precursor of eukaryotic sex; "it is not simply a passive entry of DNA into the cell genome, but instead involves a complex, energy requiring process. In other words, natural transformation is a highly evolved trait" (Elgar and Crozier 1988).

Michod *et al.* (1988) have demonstrated that transformation indeed appears to function as a repair mechanism. They gave bacteria two treatments. In one, the bacteria were offered DNA in the medium and then treated with ultraviolet light to cause damage to their DNA (DNA-UV treatment). In the other, they were first exposed to ultraviolet light and then offered DNA (UV-DNA treatment). In both cases, the UV treatment was varied from 0 to 100 joules per minute. In other words, in one case the bacteria had the opportunity to use available DNA to repair themselves (UV-DNA treatment); in the other case, they did not. As expected under the repair hypothesis, the transformation rate increased with UV exposure in the UV-DNA treatment but declined in the DNA-UV treatment. This elegant experiment strongly suggests that transformation functions as a repair mechanism in bacteria.

Transformation repairs lesions in double-stranded DNA and is restricted to bacteria. An analogous mechanism that might play a significant role in eukaryotes

is biased conversion (Rossignol 1969; Rossignol *et al.* 1978). Conversion is a "non-reciprocal copying of a stretch of the genetic information in one chromosome into the other chromosome . . . The conversion process is said to be biased if for a pair of alleles the second allele is converted into the first more often than the first is converted into the second. With such a bias the conversion process functions as a repair mechanism if the second allele is a mutant while the first is of wild type" (Bengtsson 1985). Bengtsson has shown that conversion processes can substantially decrease mutational load; they appear to be most effective when directed against frame-shift mutations. He also argues that crossing-over is a derived function of conversion for, while crossovers usually occur at the sites of conversions, many conversions occur without crossovers. Clearly experiments are needed to test directly the repair function of biased conversion.

3.5 *Summary of the situation in late 1989*

Experimental evidence suggests that both frequency- and density-dependent selection give sexual reproduction an advantage over asexual reproduction, but an advantage that is not consistently large enough to explain maintenance against invasion by asexuals. In one case evidence has been produced implicating parasites in the evolutionary maintenance of sex.

It has become traditional in this area to regard frequency- and density-dependent selection as somewhat different from selection imposed by disease and parasites. This can be attributed to the tradition of classifying biotic interactions into competition, predation, parasitism, and mutualism. However, all these interactions share an important feature of the internal structure of organisms and could not work without it: they all rely on the existence of genotype by environment interactions for fitness in the organisms whose sexual reproduction is to be explained. Some genotypes are fitter than others at low frequency than at high frequency, at low density than at high density, at low infestation rates than at high infestation rates, or only in tests against certain parasites and competitors. If such rank reversals in fitness did not occur, there would be no selection for sex and recombination, for a single asexual genotype could be fittest under all conditions.

This suggests that the necessary conditions for the maintenance of sexual reproduction are two. The first condition applies to the internal structure of organisms. The epigenetic system must be so constructed that genotype by environment interactions are strong and pervasive. This condition appears to be generally satisfied. The second condition requires that the environment be heterogeneous in such a way that the G × E interactions are evoked. The type of environmental heterogeneity that has most often been invoked is biotic heterogeneity, which is coupled through coevolution and therefore self-reinforcing.

However, we should not forget an important null hypothesis, that the physico-chemical heterogeneity of the environment might be sufficient in itself to maintain sex. Bell (personal communication) has observed that the spatial heterogeneity of the environment remains high no matter whether it is measured on a scale of kilometres, tens of metres, metres, or centimetres. It appears that the geometry of nature may indeed be fractal on the scale relevant to reproduction and survival in many eukaryotes. If so, physico-chemical heterogeneity may evoke strong enough G × E interactions to maintain sex.

4. Conclusion

The study of the evolutionary maintenance of sex is currently a very active field. There are more hypotheses and models than evidence that is strong enough to exclude alternatives. We do not yet know what in general maintains mixis. However, if one had to hazard a guess at this stage, one would say that *mixis originated as a repair mechanism and is maintained by pervasive genotype by environment interactions for fitness.* I let that statement stand as a challenge for further experimentation.

Acknowledgements

I would like to thank Laura Zonta, Franco Scudo, and their colleagues at Pavia for their hospitality at the memorial symposium for Suresh where I gave the talk on which this paper is based.

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