



Review: The Evolution of Sex

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result in a set of completely concordant characters. That, however, would be the compatibility method. Elsewhere, in his Fig. 5.12b, Wiley makes use, in one part of the phylogeny, of a character state that is not uniquely derived, a parsimony approach. The suspicion that there is a muddle here is not helped by Wiley's cavalier dismissal of compatibility methods in one paragraph, partly on the grounds that George Estabrook, one of their developers, has advocated the use of paraphyletic groups in classification and thus is not a good Hennigian.

At another point, Wiley gives mistaken definitions for Type I and Type II statistical errors. At another he falls into the trap of giving a detailed blow-by-blow description of one particular, and very approximate, parsimony algorithm, without ever clearly explaining to the reader what it is that the algorithm is trying to do, namely, to find the tree that minimizes the number of character state changes that need have occurred.

I think that these problems have a source that goes beyond individual shortcomings of the book or of its author. The Hennigian arguments are usually stated in a terminology of deduction rather than of inference, with terms such as "refutation," "rejection," and "falsification." Much of the appeal of the Hennigian position seems associated with the aura of certainty that these terms convey, and with the appeal to working biologists of a method that can be used without the need for numbers or algorithms.

This deterministic framework is, however, imposed on a highly stochastic world. Actual data cannot be analyzed effectively without appealing

to criteria external to the Hennigian system, of which parsimony is one. To avoid disrupting the original Hennigian (and Popperian) logical structure, these numerical methods must be grafted onto it in rather strange ways. The pathway from William of Ockham to the "parsimony" method is far more tortuous than first appears.

The conflict between a qualitative framework and quantitative methods is the source of much of the trouble. It can be seen in this book, as elsewhere in Hennigian practice, in the failure to make the statistical notions of hypothesis testing and of Type I and Type II errors concrete and practical. Elsewhere in Hennigian practice it takes the form of a strong emphasis on finding the most parsimonious tree, while no emphasis at all is laid on finding out how large are the confidence limits around that estimate.

The clarity of this book arises from the strengths of the Hennigian school—an intention to convey phylogenetic information clearly, and an insistence on precision and explicitness. Its limitations may to some extent be particular to the author, but must also be those of the Hennigian school—scholasticism and an attempt to impose a rigid, inflexible, and deterministic scheme on a nature in flux, a nature in which pattern cannot be properly inferred without taking process into account. Wiley's book, together with Eldredge and Cracraft's, are beacons, lighting the way out of the fog of inexplicit and intuitive methods, but revealing all too clearly that the path does not lead much farther, and that a different way must be taken.

THE EVOLUTION OF SEX

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A REVIEW OF

THE MASTERPIECE OF NATURE: THE EVOLUTION AND GENETICS OF SEXUALITY.

By Graham Bell. University of California Press, Berkeley. \$45.00. 635 p.; ill.; taxonomic, author, and subject indexes. 1982.

Since 1970 we have witnessed an explosion of work on the problem that many evolutionary biol-

ogists believe lies at the heart of our discipline. Why is sexual reproduction everywhere so common? Why is meiosis and recombination so important? Clearly there is some positive value associated with the production of genetically variable offspring, but what exactly is it?

The critical step came in 1971 when John Maynard Smith appreciated the enormity of the problem. Sex is economically a very inefficient ar-

rangement. In the great majority of species, the female invests resources in each offspring while the male contributes nothing beyond his genes. This lack of male parental investment has had a profound effect on the evolution of male traits, since males are not limited in reproductive success by their parental investment, but by their ability to outcompete each other for access to females. What we failed to appreciate was that from a female's standpoint the absence of male parental investment means that sex is a very wasteful form of reproduction. If the female could switch to asexual reproduction she would enjoy an immediate doubling in her reproductive success.

Consider an asexual mutant in a sexual species lacking male parental investment. She will produce only daughters, the survivors of which will all invest in the production of additional daughters. By contrast, each sexual female will place only half her genes in any offspring, while receiving no complementary help from the male who supplies the other half of the genes. If the species is outbred, as usually seems to be the case in nature, then the female produces males and females in a 50/50 ratio. Yet one generation later her sons will not invest in their offspring, so that reproductive output is halved in every generation compared to the output of asexual females. In short, other things being equal, an asexual mutant appearing for the first time in a sexual species should roughly double in frequency every generation. This is a very powerful selective force.

George Williams was quick to draw some important implications. In a book entitled *Sex and Evolution* (1975) he sought to solve the problem that Maynard Smith had uncovered. First, he pointed out that the 50% cost of sex swept aside group selection interpretations of sexuality. These were perhaps plausible when one imagined that sexual reproduction merely had to prove superior to asexual in order to be selected. One could imagine that sexual reproduction had no immediate beneficial effect on the survival of the resulting young, but over longer periods of time produced the genetic variability that permitted the larger sexual population to survive. This was imagined to occur in two different ways. On one hand, in large populations sexual reproduction permitted favorable genes to be knitted together more quickly. On the other hand, the continual process of segregation produced greater variability, which should permit group survival to more varied contingencies. But a 50% cost means that if there is no offsetting benefit, sexual reproduction would be rapidly eliminated from the population before its long-term benefits could be realized.

Williams quickly established that individual reproductive advantage must somehow explain the

puzzle. He drew attention to the fact that asexual reproduction is so rare in animals that when it does occur, it often alternates with sexual reproduction. In these species there can be no doubt that sexual reproduction must be paying its way, because the alternative is readily available. Indeed, Williams went further and argued that a function for sex was at once suggested by the correlation between changed and locally unfavorable conditions, and the onset of sexual reproduction in those species that alternate between the two modes of reproduction.

In Williams's best known model, sexual reproduction was compared to a lottery, in which each offspring amounted to a separate ticket (since they are genetically unique), while asexual reproduction produced so many xerox copies of the same ticket. If siblings often settle in the same habitats and only one individual is destined to predominate, then sexual reproduction can give a more than two-fold gain. More generally, Williams showed that fecundity and degree of dispersal ought to be correlated with the advantages of sexual reproduction. Since sexual selection also affects genetic variability (for example, through male dispersal and female choice), it may be controlled by deeper factors than merely the imbalance of parental investment. Indeed, if female choice in nature benefits daughters, it may retard the evolution of male investment while partly offsetting the cost of sex.

There was another reason why Williams's book generated so much excitement. Somehow the models he introduced failed to solve the problem. At least these models failed for the great majority of animal species, namely those with low fecundity, chiefly the insects and the vertebrates. For these species Williams could only argue that sexual reproduction was, in fact, selected against but was so deeply mired in the biology of these species that mutations to an asexual mode of reproduction appeared only very infrequently. In fact, he argued, asexual reproduction appeared so infrequently that a greater extinction rate of asexual populations managed to keep asexual reproduction a very rare form of reproduction in these groups. This solution seemed on its face to be unsatisfactory, and suggested that Williams had missed some essential advantage to the production of genetic variability. Few things so excite the imagination in science as the appearance of a major problem, sharply defined but left unsolved. Needed here were new models and much more evidence.

The need for new models was soon satisfied, and Maynard Smith gave us a very thorough review in his 1978 book, *The Evolution of Sex*. The major finding of his book was that uncertain

future conditions were, in themselves, unable to generate high selective values for sex. Future environments must be *capricious* compared to present environments. Capricious means that future conditions are not unpredictable, but negatively related to present conditions. The environment must oscillate so as to select cyclically in opposite directions. This seemed like an unlikely contingency and suggested once again that the problem of finding a workable model for the evolution of sex was more acute than we had imagined.

Now Graham Bell has put this subject on an entirely new footing. He has reviewed and updated the various theories, and has tested these against a greatly expanded range of evidence. His book is organized into five chapters. The first describes the problem to be solved. The second reviews the theories of sex that have been advanced. The third reviews the evidence. The fourth tests the theories against the evidence. And the final chapter considers what Bell calls "epiphenomena of sexuality": automixis, recombination, alternation of generations, and gamete dimorphism. It is a measure of Bell's work that even when treating "epiphenomena" he tests theoretical predictions against a variety of novel evidence.

The key chapter is the third, which is virtually a book within a book. Stretching some 172 pages, it reviews the taxonomic occurrence and distribution in space and time of the various modes of asexual reproduction. It is an immense piece of work, one that only someone schooled in marine invertebrates could attempt. It reviews phyla and classes I did not know existed. Wherever possible it organizes the relevant information into tables, some of which go on for pages. Thus, this chapter is not just a review, but an analytic compilation that opens out the evidence for public inspection and lays a foundation for future empirical work. How good is this foundation? Marine biologists with extensive experience in patterns of reproduction regard the review as very thorough, sometimes masterful, and always useful. Certainly his treatment of creatures I know a little about, such as insects and vertebrates, is very impressive. In my opinion, Graham Bell has earned our gratitude for a monumental piece of difficult, valuable work. His review is instructive and brings to light many correlates of asexual reproduction that have not been seen before, or have only been appreciated by the narrow specialists working on particular groups. As so often before in biology, Bell demonstrates the vitality and power of the comparative method. The Darwinian system draws together all of biology in a single web of evidence. Time and time again Bell shows how mundane work on the life history of living creatures may be

appreciated years later for the light it sheds on fundamental questions.



Having reviewed the evidence, Bell is eager to test the theories against what is known. This he does in Chapter 4, and does very well. The key evidence is organized around three headings: The Distribution of Asexual Species in Nature, The Factors Associated with Sexuality in Species Showing Intermittent Sexuality, and Dormant and Dispersive Stages in Species with Intermittent Sexuality.

The Distribution of Asexual Species in Nature. Asexual reproduction does not occur randomly in nature, but predominates in certain kinds of habitats. For example, asexual reproduction is more frequent in freshwater than in the ocean, at high latitudes instead of the tropics, and among the smallest multicellular creatures rather than the largest. Bell shows that these three facts and many others are aspects of a single, general rule: asexual reproduction tends to predominate in all sorts of novel or disturbed habitats. Consider the contrast between ocean-dwellers and freshwater creatures. Of 18 taxa reviewed by Bell, all but one have their asexual species predominating in the freshwater, and their sexual forms in the ocean. It is well known that physical features of freshwater environments vary more frequently and more drastically than do those of the ocean. If this is a relevant factor, then we expect large bodies of freshwater to be inhabited more often by sexual species than are small bodies. This appears to be true. Ostracods offer an excellent test. Asexual species are very frequent in small, temporary ponds and streams, while sexual species are more frequent in larger, more permanent bodies of water. The most ephemeral habitats are small rock pools and water film found on lichen and moss. These are created suddenly by rainfall and persist for a few days or less. Consistent with the general trend, this habitat is occupied almost exclusively by asexual species. Likewise, marine environments become less stable and more disturbed as we approach the shoreline. For sessile marine invertebrates, such as sponges, position on the substrate can be measured directly, and in such species, asexual forms are found more frequently as one approaches the shoreline more closely. Where other kinds of environments can be classified in a similar way, we find the same pattern. For example, asexual oligochaetes occur in the upper, more disturbed soil layers, while the sexual species of these worms are more often found in the deeper soil.

As we move from the tropics to the poles, the physical features of the environment fluctuate more widely. Asexuality, in turn, is associated with higher latitudes. This is clearest for the insects, but the same pattern is true of many other creatures, such as mites, isopods, and monogonont rotifers. There are a few exceptions, but the general rule is clear. The fact that environmental fluctuations are more extreme in the arctic means that new, unoccupied habitats are frequently springing to life. Small creatures have short generation times and reproduce rapidly. They are therefore able rapidly to recolonize newly available habitats. Consistent with the general pattern, asexual reproduction predominates among very small, multicellular creatures. It is almost entirely absent in the very large.

The evidence is destructive to Williams's theory of sex. For if sex is an adaptation to changed and uncertain future conditions, then we would expect sex to predominate in ephemeral habitats such as small bodies of freshwater, recently glaciated land, the arctic, and so on. To take just one group, asexual reproduction in insects occurs at high latitudes, high elevations, in more exposed, dry habitats, in the disclimax, in recently glaciated areas, and among recently introduced forms that are successful in colonizing new habitats. Under Williams's hypothesis, these are precisely the conditions under which we would expect to find a high frequency of sexual species.

What the evidence suggests, instead, is that the economic efficiency of asexual reproduction is most advantageous in empty, newly colonized habitats. Thus, when new habitats are empty, it hardly matters what genotype you have, mortality is relatively low and the ability to reproduce rapidly is paramount. As numbers increase, it is more difficult to make a living, selection is more intense, and the advantages of genetic variability offset the economic efficiency of producing large numbers. In short, the evidence points instead towards Ghiselin's theory, the so-called "tangled bank" theory. Ghiselin argued that just as human economic firms must diversify when the market becomes saturated, so living creatures must diversify their genotypes as density becomes high. Intraspecific competition favors diversity in order more completely to use the available habitat. The genotypic redundancy of asexual reproduction results in only narrow niche utilization, with resulting decrease in survivorship. Further support for this theory comes from the other evidence Bell reviews.

Factors Associated with Sexuality in Species with Intermittent Sexuality. Although the conventional interpretation put forward by Williams is that

asexual reproduction will occur during the growing season, capped off by the production of sexual, dormant eggs, this fits only the aphids, cladocerans, and monogonont rotifers, and fails as a general rule. Sponges and bryozoans, for example, have a sexual period during the growing season, and are asexual at the end.

Sex may, in fact, occur at any time of the year, and is tied more closely to periods of maximum population size than periods of maximum environmental predictability. The sexual periods of rotifers and cladocerans occur at or shortly after the population maximum. Species with two maxima in the growing season often have a sexual period associated with each. If such a species has only one sexual period, it may be associated with either population maximum, but generally with the larger of the two. Finally, the intensity of the sexual period may vary with the height of the population maximum: larger maxima are associated with higher proportions of males and mictic females.

In the laboratory, the chief factors eliciting sexuality are crowding and starvation. This is true of coelenterates, cladocerans, planktonic rotifers, and the Cecidomyiidae.

Dormant and Dispersive Stages. A dormant stage will almost always be associated with dispersal in space and time, but many organisms also produce dispersive stages that develop directly without a dormant period. Bell finds that although dormant propagules are produced sexually in a variety of organisms, they are produced asexually in as many others. By contrast, in sedentary and colonial animals, purely dispersive propagules are produced by sexual reproduction.



Taken together the evidence argues against Williams's conclusion that sex is an adaptation to novel and unpredictable future contingencies. Instead, the evidence is broadly consistent with the hypothesis that sex is an adaptation to intraspecific competition for resources, permitting greater survivorship at high numbers. Although this is the explanation that Bell favors, he is quick to point out that the evidence is likewise consistent with an alternative view, which to my mind is more attractive theoretically. This is the "Red Queen" hypothesis, which argues that sex is an adaptation to interspecific competition. Competing species are undergoing constant evolution that fits them more exactly to their roles as, for example, parasites and predators. This selection results in a biotic environment that is capricious. If we imagine frequency-dependent selection acting on a

species of predator and prey alike, then as predators are selected to grab prey, only those prey having a defense will survive, which will, in turn, be decimated by new predators specializing on this type. As long as a single predator cannot easily combine both effects, predators will act like a capricious environment, continually reversing the genes that are favored in prey, while prey will have the same effect on the predator.

From this reasoning we are led to expect a correlation between biotic complexity of the environment and frequency of sexuality. Novel and disturbed habitats are low in species diversity. Thus, the major correlate of sexuality is explained. Likewise, the correlation with crowding may secondarily be explained as an increase in effects of parasites and predators. Large, long-lived species will be especially vulnerable to parasite evolution, which may proceed rapidly within an individual host's lifetime. Species diversity is large in the tropics, and asexuality correspondingly rare, and so on.

Bell attempts to test the two hypotheses by reviewing sex in parasites and in extreme environments. Although both give a slight edge to the "Red Queen" theory, neither is very strong nor conclusive, and Bell prefers the "tangled bank" as fitting the other evidence more exactly. But Bell draws attention to two limitations of this explanation. First, it requires complete reproductive isolation between sexual and asexual forms. The association between asexuality and polyploidy is helpful in this regard, but it is not nearly general enough to convince us that this requirement is easily met. Secondly, "the tangled bank seems to be such a weak force that it could not procure the initial evolution of sex in an asexual stock unless this earliest sex were not costly" (p. 390), and it could not prevent asexual mutants from surviving in low numbers in sexual species unless these mutants were very inefficient. Thus, the "tangled bank" theory threatens to take us back to before 1970, in effect declaring that the expensiveness of sex has not really been an important constraint. This may well be true, but if so we must admit that we do not really understand why it is true.

Of course, as Bell admits, there is no reason why the various mechanisms proposed to explain sex may not act in concert. As density increases, selection may develop for genetic diversity to occupy new space in a crowded environment. At the same time, high densities are believed to unleash new attacks from predators and parasites who shift increasingly to the abundant resource. Throwing up a screen of genetic diversity impedes the prog-

ress of these enemies, their very success working against them. They eliminate their easiest targets first, achieving high reproduction which is poorly related to the new targets they will have to face. Large, long-lived species may permit their parasites hundreds or thousands of generations of selection before they reproduce. To be sure, they are slowly being selected themselves via mortality, but this is weak compared to the selective potential following reproduction. In addition, sex permits those who have survived in one space to exchange characters with those selected in a different space. In trying to predict the future, this gives two points from which to work, instead of one. If various factors do operate in concert, our explanation for sex may differ from one setting to another, but Bell wisely chooses not to pursue this possibility now.

In the recent literature it has often been assumed that a theory of sex would predict a theory of recombination. Both factors act so as to affect the degree of genetic variability that will be expressed in offspring, so both might be expected to be influenced in a similar way. In Bell's analogy, the one acts like a switch, the other like a rheostat, the chief difference being that one may be associated with a large economic cost while the other is not. Bell finds that the evidence on rates of recombination fails to establish a connection between high rates of recombination and factors associated with sexual reproduction. This may result from the weakness of our evidence on rates of recombination, where for comparative purposes we must rely on indirect and partial measures of the rate of recombination. Nevertheless, detailed studies of B-chromosome abundance in orthopterans and chromosome number in sedges (*Carex*) fail to show a clear connection between measures of habitat (such as open, northerly, montane, xeric, and novel), and the predicted rates of recombination.

In recommending Bell's book, I should not leave the impression that it is easy reading. The massiveness of his review alone makes this impossible, as does the endless technical terminology that so often differs from group to group. Bell's grasp of the theory appears to be sound, but perhaps not commanding. We are left with the theories ably described but somehow lacking a coherent overview. This limits our sense of how the various theories may be combined and of which possibilities have been overlooked. But Bell's book is essential reading for anyone really interested in the most fundamental problem in evolutionary biology. It should be the starting point for any discussion of the evidence, and it suggests almost

endless avenues for future work, both empirical and theoretical. It probably leaves the major problem unsolved, or only partly solved, and it

certainly leaves many minor problems open. I hope this book achieves a wide readership.

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