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The evolutionary significance of sex

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The evolution of sex and the role of sex in evolution

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1. Introduction

Why sex evolved, how it is maintained by natural selection, and what consequences it has for the evolution of other traits are questions of central importance for evolutionary biology, and for at least two reasons. First, sex is a pivotal process with molecular, cellular, organismal, and populational consequences: explaining it gives us a chance to integrate several subdisciplines. Second, to understand the evolutionary implications of sex, we must see fairly deeply into the process of natural selection itself. Answers to the questions: Why is there sex?, and: What difference does it make?, probably contain much of the answers to the more general questions: How does natural selection work?, and: What units does it work on?

Some historical perspective will place the papers that follow in context. At the time that Fisher[15] and Muller[24] first published their ideas on the adaptive advantages of sex, most biologists thought there was little genetic variation in natural populations, that mutants were rare, and that variation at most loci could be described by the contrast of 'wild type' and 'mutant'. In 1966, Lewontin and Hubby[22] showed that there was much more variation in electrophoretically detectable isozymes than had been expected. Their discovery was followed by a deluge of papers applying electrophoresis and other techniques to the measurement of genetic variation[21,25]. Recently there has been a comparable development in quantitative genetics: many more metrical traits than expected, including components of fitness, show measurable heritabilities in natural populations[13,30]. As a result, an important and often implicit assumption about the genetic structure of natural populations has changed during the period in which hypotheses about the advantages of sex were multiplying. Since there is a great deal of genetic variability in natural populations, the impact of recombination in a single generation on the progeny of a single outcrossed female is now expected to be much greater than what one might have predicted in 1930 or even in 1965.

To return to Fisher and Muller: ideas on the evolutionary reasons for the existence of sex were dominated for 40 years by the alleged advantages to *species* that result from the genetical consequences of recombination within populations. Recombination greatly accelerates the rate at which combinations of selectively advantageous genes are fixed in Fisher's[15] and selectively disadvantageous genes are eliminated from Muller's[24] populations. All explanations claiming that sex evolved because sexual species could adapt more rapidly to changing environments and were therefore less likely to go extinct than asexual species rely in some way on these features of recombination. While such explanations do not necessarily require species selection, a particular form of group selection, they were originally presented as arguments cast in terms of benefits accruing to species. Fisher's and Muller's inclination to invoke species selection was probably influenced by their implicit assumption that there was not much genetic variation in natural populations, and what there was could be characterized by the 'wild type' vs 'mutant' dichotomy. There might be enough variation in a gene pool to generate some advantage for recombination, but at that time it scarcely seemed likely that there was enough variation to generate some significant advantage to recombination among the progeny of a single female (van Noordwijk, personal communication).

2. Five books on sex

Group selection was common in biological thought before 1962, but it came under intense scrutiny after it was uncritically used by Wynne-Edwards[34] to explain many puzzling patterns of animal behavior. It is no coincidence that three of the strongest critics of group selection also published important books explaining the evolution of sex through advantage to the individual: Ghiselin[16], Williams[32], and Maynard Smith[23]. They did so because sex was the outstanding example of a widespread adaptation of arguable importance that had until then *only* been explained through group selection, and which therefore came into direct conflict with the individual selection that they emphasized. Dissatisfied with the explanations they offered, Bell[4] recently undertook a complete review of the evidence and critique of their hypotheses, and Shields[29] has offered an alternative explanation based on the regulation of recombination through inbreeding achieved by the tendency to remain near or home to one's birthplace. Any brief summay does violence to their thought, which in all five cases has more facets that can be mentioned here. I shall nevertheless give at least a caricature of their main points to orient you to what follows.

2.1 Ghiselin's book: The economy of nature and the evolution of sex

Ghiselin's argument is essentially economic and based on intraspecific competition. He claims that 'sex is a means of *mobilizing genetic variability* ... and, most important, *[of] releas[ing] it at the appropriate time ...: a parent causes his offspring to vary under those environmental conditions in which the parent gains a competitive advantage through doing so over other members of his own species'* (p. 57, his italics).

2.1.1 The Tangled Bank

His idea is that the production of genetically heterogeneous offspring confers a competitive advantage in saturated environments in which diverse offspring can take advantage of opportunities that identical offspring could not utilize. In Bell's hands (ref. 4 and below), this becomes the Tangled Bank Hypothesis, named after the famous last paragraph in Darwin's Origin of Species.

2.2 Williams' book: Sex and evolution

Williams[32] first established that the existence of sex posed problems for individual selection and then proposed possible solutions based strictly on individual selection. He starts, as does Maynard Smith, with the observation that sexual reproduction entails a 50% genetic disadvantage. Other things being equal, a sexually reproducing female contributes only half as many genes to the next generation as her asexually reproducing competitor. (Several authors have since pointed out that where sex is involved other things are rarely equal.)

Williams notes that we normally consider a 1% selective difference to be large, and that a 50% difference will be hard to explain. Sexual reproduction must, however, pay the individuals that use it, because there are organisms that reproduce both sexually and asexually. Some of his examples are confounded by other factors that may confer advantages having nothing to do with sex – diapause or dispersal morphs, for example – but there are cases in which sexual and asexual reproduction co-exist in apparent selective balance in a single individual with relatively few confounding factors present (the grass *Dicanthium aristatus,* for example[23]).

2.2.1 Sib-competition

Williams concludes that we have good reason, therefore, to search for an individual advantage in sex. He suggests that the solution lies in competition among offspring within the patches of a spatially heterogeneous environment. Because siblings compete with each other, and with other organisms, to acquire the space and other resources necessary for successful reproduction, and because they occupy a habitat in which these resources vary among patches, genetically diverse progeny outcompete cloned progeny because they are successful in more different types of patches. Williams' sib-competition model is a particular form of Ghiselin's Tangled Bank hypothesis. It takes several forms sharing a common weakness that he recognized: they only work for organisms with high fecundity, whereas many sexually reproducing species, ourselves included, have low fecundity. His book ends on this note of uncertainty.

2.3 Maynard Smith's book: The evolution of sex

Maynard Smith reworked many of Williams' arguments to give them a stronger mathematical basis. He did not find the sib-competition model convincing because the conditions under which it worked were restrictive. He then considered an additional hypotheses based on individual advantage: negative correlations between generations in the fitness of genotypes. In other words, the genetic combinations that are successful in this generation will be unsuccessful in the next. He rejected this idea as unlikely because it requires not only considerable temporal heterogeneity of an unusual form, but strong genotype x environment interactions as well.

2.3.1 The Red Queen

I suspect he was a bit hasty in rejecting this idea. It now travels under the name of the Red Queen hypothesis. The name comes from a character in Lewis Carroll's *Through the Looking Glass*[8], a Victorian fantasy in which a young girl, Alice, encounters the characters of a chess game. One of them, the Red Queen, takes Alice on a dreamlike chase in which they run as fast as they can but get nowhere, to Alice's bewilderment. The Red Queen comments: 'Now, *here,* you see, it takes all the running *you* can do, to keep in the same place. If you want to get somewhere else, you must run at least twice as fast as that.' (The passage is often quoted to describe political situations.) This metaphor was used by Van Valen[31] to describe his observation that the probability that a family of marine invertebrates will go extinct has not changed appreciably during the last 600 million years (see also Raup[26] and Sepkoski[28]). He argues that the biotic environment is continually evolving, and that organisms must themselves evolve as fast as possible simply to keep up with their competitors, predators, and disease organisms. Therefore their probability of extinction remains the same even though their apparent 'adaptation' – complexity, efficiency – has increased.

This notion has been used by Jaenike[18], Hamilton[17], Rice[27], and Bremermann (this issue) to explain why sexual reproduction can have an immediate advantage to the individual if mortality from disease organisms is at all significant. Disease organisms and parasites have a fundamental advantage in an evolutionary arms race. Their shorter generation time and high reproductive rate enable them to undergo significant evolutionary modification within the lifetime of a single host, and thus adapt themselves to a specific host genotype. Although the ecology of nonhuman disease is not yet well-studied, all the evidence at hand indicates that parasites and disease cause much of the juvenile mortality suffered by the world's organisms[2]. Since fitness is often more sensitive to change in juvenile mortality than to changes in other traits[11], and since the transmission of disease results plausibly in negative fitness correlations between parental and offspring genotypes, I find it a reasonable mechanism deserving the closer experimental examination that both Bell and Bremermann (this issue) recommend. Bremermann shows that sex can evolve as a defense against disease under quite general conditions, with no direct parent-offspring transmission, and that recombination may well be essential to the functioning of the immune system.

2.4 Bell's book: The masterpiece of nature

Bell opened his book[4] with a delightful series of quotations describing the varied reactions of eminent biologists to the problems posed by the existence of sex: Darwin (1862): 'We do not even in the least know the final cause of sexuality ... The whole subject is as yet hidden in darkness'; Weismann (1889): '... the part that amphigony has to play in nature ... is not only important, but is of the very highest imaginable importance'; Muller (1932): '... genetics has finally solved the age-old problem of the reason for the existence ... of sexuality and sex': Williams (1975): 'The main work of providing a workable theoretical structure for understanding the enormous diversity of life cycles remains to be done'; Maynard Smith (1976): 'One is left with the feeling that some essential feature of the situation is being overlooked.' (See Bell[4] for references.)

Bell gave us the most thorough review of patterns of sexuality in the metazoa that has yet been made. He confirmed a number of correlations between asexuality and various environmental patterns mentioned by Ghiselin[16]. Some of these are reviewed by Bierzychudek (this issue) for the plants. Asexuality is found more often in fresh water than in the sea, nearer the poles than in the tropics, and among smaller animals than among large ones. These trends are confounded in animals by life-history traits other than sex, and in plants by polyploidy (Ghiselin[16] and Bierzychudek), but they devalue some hypotheses and suggest others that can be tested in field manipulations.

Bell's major conclusion was that Ghiselin's Tangled Bank hypothesis came closer to explaining the comparative evidence than any other, including the Red Queen and the sib-competition hypotheses. His own views have changed since he wrote the book, and I can certainly do no better than let him speak for himself (this issue). Work in progress indicates that models based on negative fitness correlations between generations – one form of the Red Queen hypothesis – may not explain the evolution of sex (Bell, personal communication). I do not believe, however, that his recent work conflicts with selection for host sexuality by pathogens.

Comparative evidence of the sort that Bell used in his book, and that Bierzychudek uses in her article (this issue), does effectively rule out the idea that sex is primarily an adaptation to unpredictable environments. As Bierzychudek points out, however, comparative evidence is usually confounded by factors not involved in the hypotheses under test. This conclusion leads us to consider experimental manipulations of natural populations to test hypotheses directly, rather than indirectly, and with data gathered for the purpose of the test, rather than for other purposes. The group working most actively on such experiments is led by Antonovics at Duke University[14], and if Bell's and Bremermann's proposals for experiments are taken seriously, there will soon be others.

2.5 Shield's book: Philopatry, inbreeding, and the evolution of sex

Shields' thesis is cast in terms of the costs and benefits of recombination. The disadvantage of recombination is that it breaks up coadapted gene complexes particularly suitable to local ecological conditions. The benefits are those discussed by Fisher, Muller, Ghiselin, Williams, and Maynard Smith. The level of recombination is regulated to an intermediate optimum by inbreeding achieved through philopatry. Thus, Shields argues, restricted dispersal is an adaptation that has evolved to regulate recombination to an intermediate optimum through inbreeding. His case is clearly argued. Although the hypothesis is not readily tested, and not yet supported in quantitative detail by proper models or convincing data, it is plausible. People studying the evolution of sex should be familiar with his perspective.

3. Sex allocation and sex determination

Given that sex has evolved, and both male and female functions are present in a population, another question naturally presents itself: How should an organism allocate its effort between male and female function? If it is a species with two separate sexes, this question is about the sex ratio of the offspring. If the species is a sequential hermaphrodite, then the question is about the sex at birth and the age and size at which the organism changes into the other sex. If the species is a simultaneous hermaphrodite, then the question is about the relative production of male and female gametes.

3.1 Charnov's book: The theory of sex allocation

In an incisive recent book on the subject, Charnov[9] showed that these apparently different questions are in an important sense essentially the same question. The underlying principle is: *'Selection favors a mutant gene which alters various life history parameters if the percent gain in fitness through one sex function exceeds the percent loss through the other sex function'* (Charnov[9], p. 17, his italics). Where there is no within-sex frequency dependence, it is equivalent to say that selection maximizes the product of fitness gained through male function times fitness gained through female function[9].

Charnov's book is stimulating a great deal of research, and sex-allocation theory will probably become a speciality in its own right within a few years. Two papers in this issue contribute to that process. Lloyd shows how sex-allocation theory is a special case of much more general allocation theories. Leigh, Herre, and Fischer analyze the current status of sex-allocation theory by using the heuristic perspective of contrasting the interests of the genome with those of outlaw genes that skew sex allocation to their own interests. They conclude that 'a theory whose main triumphs concern the loves of coral reef fish and the curious sex ratios of fig wasps tells us rather a lot about which factors direct evolution'.

4. Constraints on the evolution of sex ratios

Sex-allocation theory, like other types of optimality and game theory in evolutionary ecology, assumes either that the phenotype is unconstrained, or that if there are constraints on evolution, they are represented implicitly in boundary conditions. The most striking observation about primary sex ratios is that they do not vary from 50:50 in most outcrossed vertebrates[33]. In some of these, such as Uganda kob, elephant seals, baboons, lions, bighorn sheep, and all others with polygynous or polyandrous social systems, it would be advantageous to evolve equential hermaphroditism: in the cases mentioned, to be born female, gain a certain amount of fitness through female function, then change sex and undertake the more risky but potentially more rewarding struggle for male dominance and access to many female mates.

4.1 Bull's book: Evolution of sex-determining mechanisms

To explain this invariance, we must look to constraints arising in the mechanisms that determine sex. Bull[6] recently published a book reviewing both theory and evidence on sex determination, and in this issue he gives us his most recent views. They are an essential complement to the theoretical framework discussed by Charnov, Leigh et al., and Lloyd.

5. Sexual selection

In 1871 Darwin[12] isolated one of the reproductive components of fitness and explained its evolution through a particular type of selection, sexual selection. In making this move he drew attention to the great strength of selection operating on traits that determine access to mates, in particular, male combat and female choice. He sought to explain the evolution of traits, such as the stag's antlers and the peacock's tail, that pretty clearly decrease the survival chances of the males that possess them. From our current perspective, this separation of sexual selection and natural selection was artificial and based on a simplified notion of fitness. Darwin saw fitness primarily in terms of survival. Fitness is now usually defined as reproductive contribution to the next generation: it has both a survival component and a reproductive component. Sexual selection has to do with just one part of the reproductive component – access to mates. It is clearly part of natural selection, not a different type of selection to be contrasted with natural selection. One wonders why we have not created a special terminology to deal with selection acting on other components of fitness: juvenile survival selection, nest site selection, reproductive investment selection, and so forth.

There are at least three reasons why not. The first is simply historical. Darwin called attention to a particularly important component of fitness, and his terminology has precedence. The second is a matter of emphasis and perception: selection operating on access to mates has created some of the most spectacular adaptations visible in vertebrates, the most intensely studied group and the group to which we belong. The third is in fact based in the logic of the process: some of the hypotheses of sexual selection involve tight interactions between the male and the female genotypes. These can lead to a particularly intimate kind of intraspecific coevolution between characters born by two different individuals that requires genetic and developmental coordination of genes working in different directions. This is the best reason for preserving the term 'sexual selection'.

Ghiselin[16] gave a good recent overview of sexual selection, and the two multi-author volumes edited by Campbell[7] and Blum and Blum[5] each contain excellent chapters. Fisher[15] (chapter 6) remains essential. The best single field study of sexual selection in a large mammal is in progress on the Isle of Rhum, where the red deer have been kept under close observation since 1973. Clutton-Brock, Guinness, and Albon[10] report their progress to date in an excellent book combining ecological and behavioral approaches to sexual selection and life-history evolution.

One major recent theoretical effort to understand sexual selection has been centered on quantitatitve genetical approaches initiated by Lande[20] and extended by Arnold and Wade[3] and Kirkpatrick[19]. In this issue, Arnold gives a comprehensive review of the new insights attained with these methods, which claim the demise of some prominently discussed hypotheses (the 'handicap mechanism' and the 'sexy son').

6. Conclusion

Research centered on why sex evolved and what difference it makes has made great strides in recent years. Previously dominant hypotheses have been devalued, in some cases through confrontation with evidence, in others through careful theoretical analysis. The field is in a period of rapid growth and major change, with many opportunities for decisive experiments that have only recently become clear and have not yet been seized. The articles in this issue give an excellent summary of the state of the art. May they stimulate further advance.

1 My thanks to Ric Charnov, who helped organize these reviews, to the authors, who have performed magnificently, and to Arie van Noordwijk, whose suggestions improved this introduction. Geoff Parker was kept from participating by circumstances beyond his control. I regret the circumstances especially, and I am sure that they cost us a fine paper.
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Two theories of sex and variation

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Key words. Sex; evolution; the Tangled Bank; the Red Queen; recombination experiments; genotype × environment interactions.

For almost the whole history of evolutionary biology, sex has been thought of as creating preadaptation to an uncertain future, either permitting species to adapt more quickly or enabling individual females to produce a few unexpectedly fit offspring. The demise of this powerful idea dates from theoretical difficulties noted by Maynard Smith[73], and was completed by the overwhelming hostility of the comparative evidence: it is parthenogenesis, and not outcrossed sexuality, that prevails in harsh, uncertain, disturbed and novel conditions[10]. The comparative evidence points instead to a quite different role for sex, concerned with the efficient exploitation of the full range of possibilities presented by a diverse environment. Two theories of this sort have been especially prominent. The first is the Tangled Bank[10], which descends from the economic analogies of Ghiselin[38] and is related to the sib-competition models introduced by Williams[105] and elaborated by Maynard Smith[74] and Price and Waser[86]. In its simplest form, the Tangled Bank holds that the state of the environment varies widely from place to place on a very local scale, such that different genotypes are optimal at different sites. Since each site can support only a few individuals, the uniform progeny of an asexual female will compete intensely with one another for the same set of resources, while the progeny of a sexual female, which by virtue of their diversity will be able to exploit a much wider range of sites, will compete amongst themselves less intensely and thus achieve greater overall success. In