THE MAINTENANCE OF SEX AS A DEVELOPMENTAL TRAP DUE TO SEXUAL SELECTION[1]

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ABSTRACT

The writings of George Williams challenged biologists to think critically about levels of selection, social behavior, and the paradox of sex, whose maintenance by recombination alone has not been convincingly demonstrated in theory or in fact. A solution is suggested by observations of the dependence of females on interaction with males, as a result of sexual selection. This, along with recombination in changing environments and DNA repair during meiosis, may contribute to a pluralistic explanation for the maintenance of sex.

ONE of the fascinating observations about scientists is the way personality, or personal character, affects the research one does. This is especially obvious in the science of animal behavior. In insect behavior, for example, we have the mild mannered, collaborative Charles Michener. What did he propose as the basis for the origin of insect societies? Mutualism, of course. Then there was the brooding humanitarian William Hamilton, who focused on the phenomenon of altruism; and the feisty verbally combative Richard Alexander whose doctoral thesis was on aggressiveness and territoriality in crickets. I have chosen not to analyze too deeply my own obsession with social wasp colonies full of competitive females.

And then there is George: it was George Williams, a rugged individualist if ever there was one, who insisted on the importance of selective benefits at the *individual* level to explain social phenomena, as a corrective for simplistic and erroneous interpretations in terms of the good of the species or the good

of the group (Williams 1966). At a time when genetic similarity of group members was emphasized as a factor that could favor cooperation, he reminded us that genetic heterogeneity of group members can lead to departures from cooperation or competition within groups.

Among individualists, I classify George as a "soft iconoclast"—he would rather resist than follow a tide, but he does not shout about it. He would rather learn Icelandic than French. He is a quiet, even a sneaky, revolutionary. I suspect that he is suspicious of everything he reads, especially if people are starting to believe it. He will lurk there, cultivating his doubts until he finds the pivotal word, and then he will spring it on us. For example, in analyses of social behavior the pivotal word was "adaptation." If you understood the nature of adaptation, George said, you could properly unravel the nature of groups. The fact that adaptation can ultimately be seen to involve more than one level of selection does not detract at all from George's focus on ben-

[1]Based on a lecture originally titled, "What George Williams said about sex but didn't really believe," for A Symposium in Honor of George C Williams, Stony Brook University, April 24, 2004. The central theme is more thoroughly discussed in Chapter 31 of West-Eberhard 2003.

efit to individuals. It cleared away the rubble of simplistic group selection to pave the way for a proper understanding of how different levels of selection work. As George acknowledged, this insight had been anticipated by David Lack (Lack 1954; see especially Williams 1966:161–164). Through *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (Williams 1966), this point reached a larger audience.

Early in my career, the importance of George's 1966 book was that it showed the relationship between individual selection and the idea of kin selection. He quickly understood Hamilton's (1964) treatment of kin selection because he had already thought about it himself; back in the 1950's George and Doris Williams had written a paper on sibships and the evolution of social insects (Williams and Williams 1957). The Williamses' combination of individual-level selection and kin-selected aid clarified my observations of social wasps and led to discoveries that would have been impossible without it. Before that, as an undergraduate, I had been distracted and confused by other approaches to animal interactions. For example, there was the big book by Wynne-Edwards on epideictic displays, and the inspired writings of Alfred Emerson on the superorganism and social homeostasis. There was also a lot of hype about seeing animal communication in terms of information theory, an ultimately sterile fad that left me permanently disillusioned with merely metaphorical attempts at cross-disciplinary synthesis. (For a more optimistic view of the possibility that cybernetic models will come of age see Amdam and Omholt 2003.) The Williams approach was sensible, organismic, and clear. It applied directly to what I observed occurring in social insects.

George's individualistic approach also led to insights about sex. Before George came along, sex was usually seen in terms of the long-term advantage of recombination for populations. Along with Maynard Smith, George pointed out that there is a cost of sex for individuals, in particular for individual females, whose relatively enormous maternal investment ends up replicating their mate's genes as well as their own. George saw that they would profit more by only duplicating their own genes. The extra burden on females is "the cost of meiosis" (the cost of genome dilution, as it affects the spread of alleles determining sexual versus asexual reproduction), and the twofold cost of sex (the cost of producing males; Maynard Smith 1978).

Given the effects of personality on chosen themes of research, you are now probably expecting me to launch into a fascinating analysis of the reasons for George's longtime obsession with sex. Unfortunately I do not have any data on that, so I have decided to abandon amateur psychology for the moment and turn to the problem of sex itself.

I want to concentrate, as George did in his 1975 book, *Sex and Evolution,* on the *maintenance* of sex rather than on the *origin* of sex. There are two major explanations for the maintenance of sex: the DNA repair hypothesis and the Recombination hypothesis. There is evidence for both, and both could be important: they are not mutually exclusive explanations. Under the DNA repair hypothesis, aberrant chromosomes are eliminated by excision and resynthesis during meiosis (Bernstein and Bernstein 1991). Recombination is the hypothesis more often discussed by evolutionary biologists (e.g., Birdsell and Wills 2003). Recombination is considered advantageous at two levels: at the individual level because it can enable the members of a single brood to have a better probability of survival in a heterogeneous environment; and at the population level because it facilitates persistence over time, which provides a hedge against extinction. Ideas about coevolutionary races between parasites and pathogens are prominent at both of these levels.

This view of sex as recombination has had a tremendous influence on how biologists interpret the interactions between the sexes. If you see sex as recombination, then you are likely to see sexual behavior as having what Hamilton and Zuk (1982) call a "eugenic" function—that is, sexual behavior, such as female assessment of males, is testing for good survival genes. You see female choice and male-male competition as ways of screening for the genetic quality of potential mates in the struggle for survival and ecological success. Agrawal (2001) and Siller (2001) assigned sexual selec-

tion another kind of eugenic function that depicted it as a way of placing the burden of mutation disadvantage on males. By this idea, which we can call "mutational cleansing," the cost of selection against deleterious mutations falls mainly on the more strongly sexually selected sex, usually the males, and this may help to compensate the cost of sex to females.

But there is another way to look at sex. In *The Economy of Nature and the Evolution of Sex* (Ghiselin 1974), Michael Ghiselin pointed out, following Darwin, that sex can be viewed as social behavior. Here we consider not only the ultimate evolutionary interpretation of sex, but also the immediate, or proximate, functions. If you consider sex as social behavior, you see the sexual behavior of males—both fighting and courtship—in terms of social competition for mates. Courtship, however else it may function (e.g., as a demonstration of quality, species identification, or the unaggressive intentions of a potential mate), is part of a contest to see which male can better approach or stimulate a female. Female "choice," no matter how you view its ultimate effects, means that females are differentially responsive to the competitive activities and characteristics of males. This has two important results for the evolution of male sexual signals: it means that they can have stimulatory value per se, above and beyond any significance they may have as signs of good genes. Since stimulatory value sets a premium on female discrimination, there is always the potential for a runaway process involving a coescalation of signal and discrimination (Fisher 1958), and this may cancel any eugenic value the signal initially may have had. It is important to realize that under female choice, male signals can originate as pure manipulations, and good-genes indicators can be exaggerated and become pure manipulations too, with the result that they can lose their value as indicators of good genes. A successful signal is one that elicits a response. Thus, courtship need not have anything to do with genetic quality under natural selection (selection for survival or ecological success). This was the essence of Darwin's (1871) argument regarding sexual selection, which he invented to explain traits that could *not* be explained in terms of their survival

value. The good-genes arguments so much discussed today (e.g., Hamilton and Zuk 1982) turn sexually selected traits into survival traits that evolve under natural selection, bypassing Darwin's distinction.

Finally, if you concentrate on the social aspects of sex, you can see males and females as two divergent, complementary morphs, mutually dependent alternative phenotypes that are similar to the queens and workers of social insects in their mutual dependence; neither can reproduce without the other. This last point needs a little more explanation. The concept of the twofold cost of sex comes from the special burden to females, which has to do with their fat gametes, the eggs. Eggs are specialized for nutrition and packed with influential maternal transcripts, and they are relatively bad at the kind of dispersal that may be required for finding mates. The sperm, by contrast, is a competitive dispersal or mate-seeking form, unsuited to nourish the young. In this sense, there is a reproductive division of labor between the gametes of anisogamous species (that is, species with unlike male and female gametes). This very same difference, of course, leads to sexual selection and the importance of sex as social competition for mates, as well as the opportunity for female choice.

In a way, female choice backfires on females. By being choosy, females are potentially subject to reproductive manipulations of the females' reproductive responses by males. They may then come to depend on males to trigger those responses. In fact, it is known that males can act as:

- releasers of female receptivity;

- stimulators of physiological responses, such as sperm transport in the female reproductive tract;

- stimulators of oviposition (female will not oviposit without seminal products);

- (in mammals) stimulators of uterine preparation for implantation of the embryo; and

- initiators of embryonic development (a well-known function of fertilization).

In addition, genomic imprinting—in which mothers suppress some genes and

fathers suppress others in taxa with large maternal investment in offspring—leads to mutual dependence because normal development of the offspring requires both sets of genes. Similarly, in angiosperms, a plant without a father would lack crucial developmental instructions provided by transcripts originating in the haploid male contribution to the triploid endosperm, as well as organelles contributed by the male (references in West-Eberhard 2003).

The result of these complications is that females need males for normal reproduction. Depending on the species, they may rely upon males to stimulate ovulation, to initiate embryonic development, or to provide essential genetic transcripts, organelles, or genes. A female variant that fails to interact with males has an immediate, and often severe, disadvantage. She may not be able to reproduce at all. Females of sexually selected lineages are in a male-dependent developmental trap that arises due to sexual selection. And that trap alone should often be enough to maintain sex (West-Eberhard 2003).

In summary, the cost to females of giving up sex, or of "asex" as George would say, equals the genetic or "eugenic" good-genes cost plus the social cost. But this is not a straightforward equation because the social cost is immediate. A female who pays the genetic cost may have inferior descendants. A female who pays the social cost in male-dependent reproduction has no descendants at all. She is reproductively dead.

From this sexual-selection hypothesis we can make at least three predictions. First, asexuality or parthenogenesis should be more common in isogamous species, where sexual selection is expected to be absent or less intense, than in anisogamous ones. This is known to be true, even though it is "quite the opposite of what one would predict with knowledge of the costs" (Hurst and Peck 1996:46), since in anisogamous species with large eggs and small sperm, the cost of sex to females is relatively great compared to that in isogamous organisms. An association between asexuality and isogamy is expected under the developmental trap hypothesis, since the trap is created by sexual selection due to differential parental investment by

males and females, which does not occur in isogamous species.

Second, there should be signs of female dependence on males even when sexual reproduction involving recombination is lost. This, also, is known to occur: in some secondarily asexual or parthenogenetic species, females must mate in order to reproduce even though there is no genetic contribution of the sperm to the zygote; the sperm acts only to stimulate embryonic development. Examples include various species of fish, salamanders, lizards, nematodes, planarians, and a beetle (review in West-Eberhard 2003). Nonetheless, it is worth noting that the importance of recombination is indicated by the fact that in some primarily asexual organisms and clonal lineages there is occasional sex (D'Souza et al. 2004) or parasexual recombination, such as by anastomosis or karyogeny, that permits genetic exchange without sex (Tuthill 2004).

Third, loss of sex, including facultative or cyclic parthenogenesis, should be associated with weakness of sexual selection when not accompanied by male parental contributions, even in anisogamous species. This is a new hypothesis and needs to be tested. But some support may come from the psychid moths of the genera *Siederia* and *Dahlica* (Lepidoptera; Psychidae) (Kumpulainen et al. 2004). These genera are very unusual in the Lepidoptera in that asexual reproduction has evolved repeatedly (Kumpulainen et al. 2004). Although moths are noted for their elaborate and often species-specific male genitalia, which are frequently used as taxonomic characters (Eberhard 1985) and remating is common in Lepidoptera (review in Eberhard 1985:130–138), the sexually reproducing species of these genera are also unusual in having relatively simple male genitalia whose morphology is not species-specific and therefore not useful in taxonomy; and there is little opportunity for sexual selection by direct female choice, since the wingless females mate only once (J. Mappes, personal communication; see also Rhainds et al. 1995 on another psychid moth). In further support of the hypothesis that sexual selection is weak in these taxa, sexual populations are very small, genetically isolated, and highly inbred, and

males are severely sperm-limited. So, females that mate with already-mated males lose 30 to 100% of viable offspring (Kumpulainen 2004).

George mentioned in his book, *Sex and Evolution*, that it might be difficult for a lineage to evolve its way out of sexual reproduction. He recognized the need for fertilization to initiate development, and thought that the evolution of asexuality "would seem unlikely in an organism historically committed to exclusively sexual reproduction" (Williams 1975:104). This sounds a little like a developmental trap. But his heart was not really in it—he did not commit himself to a view of sex as a mere legacy of selection past, and spent only a few sentences discussing it. He ended his book with the charming admission: "I really do not understand the role of sex in either organic or biotic evolution" (Williams 1975:169).

In our long correspondence about the maintenance of sex, George and I have arrived at a stalemate. He insists that "only looking at critters that regularly do it both ways (i.e., alternating between sex and asexual reproduction) can provide answers to the question" (letter, 13 May 2004). But I contend that studies of such flexible species will not necessarily reveal what maintains sex in species that are more completely and irreversibly committed to sex. I believe that with this assertion George reveals that the question that most concerns him is not the maintenance of sex—for in facultatively asexual species, sex is not strictly maintained. What concerns him is the primary function of sex, that is, what sex is designed by natural selection to do. By examining the circumstances in which strawberry plants express sexual reproduction rather than asexual cloning, you can discover the *function* of sex in strawberry plants. But the factors responsible for the functional design of a trait are not necessarily those responsible for its maintenance at high frequency: sports utility vehicles were originally *designed* for rugged off-road use, but they are *maintained* at high frequency in many parts of the world for quite different reasons, such as to display signs of wealth and to serve as armored shields against injury in traffic accidents.

Ghiselin (1974:637) has described sex as a kind of legacy or "vestigial feature" implying a useless remnant without current significance. In a letter, George at one point relented slightly, and called sex a "maladaptive legacy." But I think you can call sex an *adaptive* legacy, perhaps at the level of clades. Not only does sexual reproduction contribute to the speciational diversification of a lineage, and thereby perhaps contribute a hedge against extinction (see West-Eberhard 2003: 631), but the trap created via sexual selection keeps sex and recombination going, due to the benefits of sexual interaction, even when genetic benefits would be insufficient. As a result, sex is there when recombination is needed, and this could help to maintain a lineage. Asexuality, by contrast, usually means extinction (Welch et al. 2004; but see their discussion on the Bbdelloid rotifers and Tuthill (2004) on recombination in asexual clades of fungi).

There have been many elegant formulations and simulations to solve the problem of the maintenance of sex as recombination by some of the most powerful intellects of evolutionary biology (review in Birdsell and Wills 2003). But, as David Haig (2003:329) has written, there are lingering doubts. There were too many simplifying assumptions, in spite of incorporating a population of 200 hosts beset by up to twelve species of asexual parasites (also with populations of 200 individuals), host chromosomes with up to fourteen resistance genes and parasites with up to seven virulence loci, and many other factors. This model was described as "a group pursuit around the vertices of an nk dimensional hypercube" by Hamilton et al. (1990:651). The debate continues. A recent simulation attempt arrived at the conclusion that "species interactions typically select against sex" and that "although the Red Queen [hypothesis that sex has evolved in response to fluctuating conditions generated by species interactions] favors sex under certain circumstances, it alone does not account for the ubiquity of sex" (Otto and Nuismer 2004:1018). As George Williams (1975) remarked many years ago, at least the failure to understand the maintenance of sex put him in abundant good company.

The hypothesis I propose can alleviate the difficulty of explaining the maintenance of

sex even if it is designed primarily for recombination or importantly eugenic in function. It turns to another kind of elegance, found in the behavior of living organisms. It requires a new look at the significance of sexual display that goes beyond the search for good genes and pays attention to the purely competitive value of sexual signals. And it encourages "pluralistic" explanations for the maintenance of sex (West et al. 1999), for the primary function of sex, whatever it may be in a particular species, that may not completely balance the twofold cost of sex.

Even when there is a correlation between brightness and health, or between vigorous display and genetic quality, it is important to remember that the strongest social competition is characteristically between the closest contestants, where tiny differences can have enormous consequences for fitness. It is when sexual selection is strongest that a miniscule exaggeration can be detected by the fine-tuned assessment of a discriminating female. It is in this realm that a runaway process, a departure from good-genes honesty, can occur, and it is here that we have to focus our measurements and pay attention to the possibility of purely social functions, of stimulation per se. We cannot assume that all species-specific differences that have probably evolved under sexual selection reflect good survival genes rather than good signaling genes. Consider, for example, the elaborately different plumages of wild male pheasants (Beebe 1926), or the astounding diversity of genitalia in a single genus of male drosophilid flies (Grimaldi and Nguyen 1999). To my knowledge, there is no evidence whatsoever that male genitalia function as indicators of good survival genes. But there is plenty of evidence that their extravagant variants have evolved under sexual selection and that they function to stimulate the reproductive responses of females (Eberhard 1985, 1996).

I conclude with a hypothesis (West-Eberhard 2003): sexual reproduction is maintained as an adaptive legacy of sexually selected and other male manipulations that have produced a reproductive dependence of females on males. This hypothesis should be considered, along with recombination, to explain the maintenance of sex in all anisogamous—that is, all sexually selected—organisms. It is an especially strong hypothesis because the domain of its applicability corresponds exactly to the domain of the paradox of maintenance of sex: the hypothesis is applicable in all species that suffer a cost of meiosis, or the twofold cost of sex, that is, in all anisogamous species. These are precisely the same species that are subject to sexual selection, the context of selection that leads to male manipulations that eventually render females dependent upon males.

I feel quite confident that these social and developmental factors are important for the maintenance of sex. My confidence is grounded upon supportive facts recorded in decades of biological research. As George Williams wrote in 1975: "My reasoning is much less rigorous than the thorough mathematical treatments of others, [but] I think that I have the more reliable conclusion" because "for answering questions on function in biology, comparative evidence is more reliable than mathematical reasoning" (Williams 1975:7).
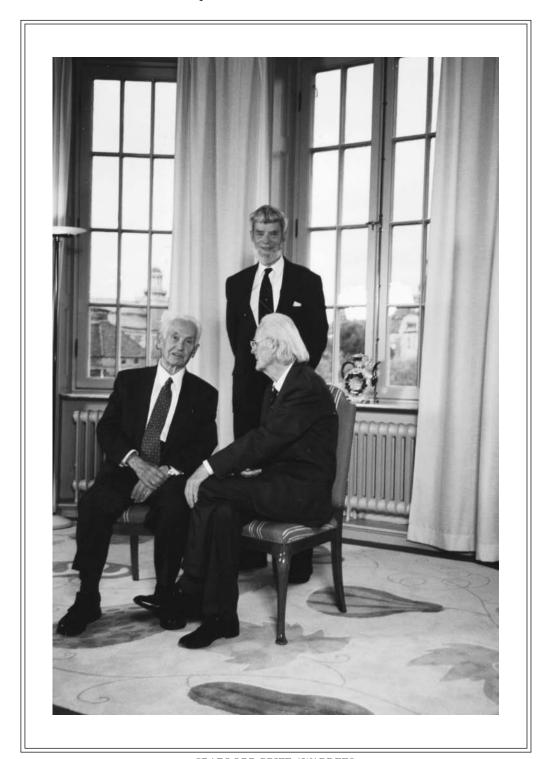
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