

The Paradox of Sexual Reproduction and the Levels of Selection: Can Sociobiology Shed a Light?

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The rejection of group selection in the 1960s left the evolutionary maintenance of sex bereft of its previous explanations and turned it into an anomaly or paradox. While the levels of selection debate advanced towards multilevel selection theory as a tentative resolution, the paradox of sex became increasingly decoupled from it. Only differential extinction or speciation of sexual and asexual taxa have been considered in relation to the maintenance of sex. This agrees with multilevel selection scenario 2 (MLS2) in which the groups have their own component of fitness. In multilevel selection scenario 1 (MLS1), however, groups can structure selection without having their own component of fitness. Moreover, MLS1 defines trait-groups via social interactions. Here I suggest that MLS1 can be applied to the maintenance of sexual reproduction against the twofold cost of sex. This neither denies the existence of other costs of sex nor the legitimacy of other hypotheses concerning these costs.

KEYWORDS

Evolutionary maintenance of sexual reproduction • Group selection • Inclusive fitness • Kin selection • Multilevel selection • Sociobiology

1. Introduction

The group selection controversy largely focuses on altruism (e.g., Wilson 1983; Lloyd 2001; Shavit 2004; Okasha 2006, 173ff; Borrello 2010; Leigh 2010; Rosas 2010; Hamilton and Dimond in press). Multilevel selection theory is a resolution of this controversy. Whereas kin selection partitions inclusive fitness into direct and indirect components (via influencing the replication of copies of genes in other individuals), multilevel selection considers within-group and between-group components of fitness (Gardner et al. 2011; Lion et al. 2011). Two scenarios of multilevel selection are often distinguished (Damuth and Heisler 1988; Okasha 2006; Pigliucci 2010): (1) group structure only divides individual fitnesses into within- and between-group components (MLS1); and, (2) groups get their own component of fitness and also, in most definitions, a group-level adaptation (MLS2).

As a by-product, the rejection of group selection in the 1960s left the evolutionary maintenance of sexual reproduction bereft of its former explanations and turned it into an anomaly (Williams 1971, 13ff; Maynard Smith 1978, 2; Hamilton 1996, vii, 354). It even became the major paradox of evolutionary theory—the “queen of problems in evolutionary biology” (Bell 1982, 19). Though this resulted from the rejection of group selection (i.e., for reasons related to sociobiology), research on this paradox is rarely

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connected to the levels of selection issue anymore. The only multilevel selection scenario that has been applied to the paradox of sex is MLS2, with differential extinction and speciation of sexual and asexual taxa (Maynard Smith 1971, 164; Williams 1975, chap. 13; Nunney 1989; Williams 1992, 35). The social interactions of asexual and sexual individuals are no part of this scenario.

In the following I argue that:

- The rejection of group selection as a mechanism of sociobiology in the 1960s turned the maintenance of sexual reproduction into a major anomaly or paradox; current research on the issue largely ignores social interactions.
- If sexual interactions between males and parthenogenetic females are included, then a fitness benefit from social interaction can balance the cost of sex.
- Beyond dissolving a historic paradox at its roots, this perspective has merits for both empirical and theoretical research into the evolutionary maintenance of sex.

Several closely related issues must be disentangled at the outset in order to avoid confusion.

2. Disentangling Related Issues

Different hypotheses for the maintenance of sex emphasize different effects of recombination, including the generation of new combinations of genes, error correction, or the transfer of selfish DNA (Michod and Levin 1988, 5). For simplicity the latter two alternatives will not be considered in the following.

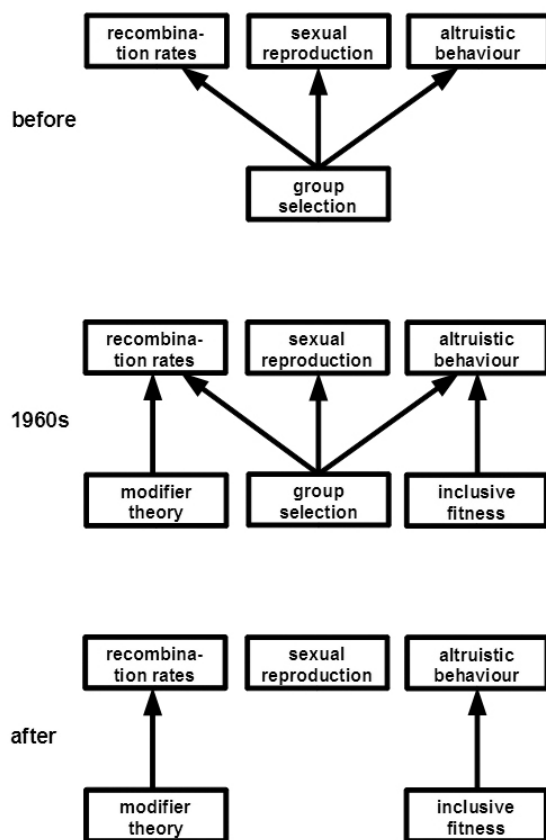


Figure 1 — How rejecting group selection rendered sexual reproduction an anomaly. (Arrows indicate which theory explains which fact.)

Top panel: Before the 1960s, explaining the maintenance of recombination rates, sexual reproduction, and altruism involved some form of group selection reasoning.

Middle panel: Individualistic explanations of recombination and altruism became available during the 1960s.

Lower panel: Without an individualistic explanation, the maintenance of sex became an anomaly after the rejection of group selection. Plugging multilevel selection into the void left by group selection could resolve the paradox, as well as expanding other theories.

2.1 *Recombination rates ≠ sexual functions*

The maintenance of recombination rates is an issue dating back to R. A. Fisher:

The discovery of an agency which tends constantly to increase the intensity of linkage, naturally stimulates inquiry as to the existence of other agencies having an opposite effect, and under the combined action of which [...] linkage intensity could have become adjusted to its observed value. Such an agency appears to be at hand in the constant spread of advantageous mutations through the populations in which they occur. For unless advantageous mutations occur so seldom that each has had time to become predominant before the next appears, they can only come to be simultaneously in the same gamete by means of recombination (Fisher 1999 [1930], 103ff).

Fisher saw the maintenance of recombination as due to natural selection within a species for the purpose of combining advantageous mutations and the maintenance of sexual reproduction as due to competition between sexual and asexual taxa in an evolutionary race.

The comparative rates of progress of sexual and asexual groups occupying the same place in nature, and at the moment equally adapted to that place, are therefore dependent upon the number of different loci in the course of descent. From what is known of the higher animals, this number must be at least several thousands; but even a sexual organism with only two genes would apparently possess a manifest advantage over its asexual competitor [...] from an approximate doubling of the rate with which it could respond to Natural Selection (Fisher 1999 [1930], 123; see also 122).

This would agree with MLS2, where within- and between-species selection work in the same direction but the benefit accrues in the long term.

These two issues—the maintenance of recombination and sexual reproduction—did not remain closely tied together; however, only one became an anomaly (see below and Figure 1). Therefore the relations between these issues need clarification. Sexual recombination poses the root problem in both cases. It mixes genes and thereby destroys genotypes that have proven their mettle by phenotype survival to maturity. In uniform environments the rates of recombination should gradually sink to zero because recombination destroys combinations of genes that have proven to be adaptive (e.g., Fisher 1930, 103ff; Turner 1967; Maynard Smith 1978, chap. 5). As an end result, the genome should congeal leaving an organism with male and female functions but no recombination except for the segregation of homologous genomes (chromosomes being linked).

A logical argument highlighting the problem with the maintenance of recombination rates could go something like:

- (1) Environments are uniform.
- (2) Certain combinations of genes are advantageous over others.
- (3) Recombination destroys combinations of genes that natural selection has favored.
- (4) Therefore, recombination rates should decrease to zero.

Observation: recombination rates in natural populations remain variable and considerable.

The paradox of sexual reproduction arises when males provide nothing in terms of offspring care, breeding territory, etc. The advantage of a mutant female is to save the cost of sex by producing eggs that develop without fertilization (parthenogenesis) and become all female (thelytoky). A logical argument highlighting this paradox could go something like:

- (1) Sex allocation is even.
- (2) The contribution of males to reproduction is negligible in comparison with females (referred to as the negligible-male-contribution assumption).
- (3) A mutation for parthenogenesis and nothing else occurs (referred to as the all-else-equal assumption).

(4) Therefore, parthenogenesis should replace sexual reproduction quickly, even if it was doomed in the long term, because all offspring will contribute to population growth.

Observation: Sexual reproduction prevails in nature, and not only in long-term competition between taxa; sex is evolutionarily maintained in the short term as well.

Decreasing recombination rates cannot be taken as an advantage of an asexual mutant. Conversely, the advantage of an asexual mutant “cannot be invoked as an argument for gradual reduction of recombination rates in a sexual species” (Felsenstein 1985, 217). Starting from the same point of departure, different processes should lead to different end results. “The problem of sex and the problem of recombination are closely related, but they are not simply two names for the same thing. Given that a population reproduces sexually, there still remains the vexing question as to why its recombination rates do not evolve downward toward zero” (Seeger and Hamilton 1988, 177). For simplicity both issues will be treated separately below.

2.2 *Cost of males or cost of meiosis*

The cost of sex arises because, all else being equal, an asexual mutant should gain an immediate twofold advantage. Other costs of sex exist (e.g., the cost of cellular machinery or the time required for meiosis, fertilization, and mate searching) but are not central to this paradox. In 1971, George C. Williams conceptualized the evolutionary cost of sex as the cost of reducing the genome during meiosis:

in meiosis, the number of chromosomes and constituent genes is reduced by half. Each resulting gamete, and zygote that is formed by fertilization, will have a sampling of half the genes of the individual that provides the gametes. In the usual mitotic divisions, each resulting cell preserves the entire genome intact. [...] These parthenogenetic eggs would each contain twice as much of the mother’s genotype as is present in a reduced and fertilized egg. Other things being equal, the parthenogenetic female would be twice as well represented in the next generation as the normal one. [...] Sexual reproduction is analogous to a roulette game in which the player throws away half his chips at each spin. The game is fair as long as everyone behaves in this way, but if some do and some don’t, the ones who keep their chips have an overwhelming advantage and will almost certainly win (Williams 1971, 13).

Here, Williams starts with a 50% vs. 100% genome transmission argument, also known as genome dilution, but ends up allowing sociobiological notions of cheating to slip in. The following makes this shift in the meaning of the term ‘cost of meiosis’ more explicit:

Only Maynard Smith (1971a, b) has attempted to give the short-range problem an exact formulation and to consider the possibility of an individual advantage in sexual reproduction. He concluded that sexual reproduction (except in internalized hermaphrodites) has, roughly, a 50% disadvantage in relation to asexual reproduction. This corresponds to the 50% loss of genetic material in meiotic oogenesis. There may be other disadvantages, such as the generation of recombinational load, and some possible minor advantages in genetically diverse, rather than uniform progenies, but what might be termed the *cost of meiosis* must be the overwhelming consideration (Williams and Mitton 1973, 546).

In 1975, the 50% reduction of the genome has become a 50% hazard of genes coding for sex (the gene’s eye view) with some added qualifications:

Each “sex gene” suffers a 50% hazard per generation, relative to asexual alternatives [...] The 50% cost of meiosis applies to outcrossed but not to self-fertilizing hermaphrodites [...] If males assist females in raising the young, the cost of meiosis is reduced (Maynard Smith 1971a), unless it is possible for a female to get a male to help raise parthenogenetic young. The primary task for anyone wishing to show favorable selection of sex is to find a previously unsuspected 50% advantage to balance the 50% cost of meiosis. (Williams 1975, 9–10).

However, Maynard Smith argued against genome dilution:

No such immediate two-fold disadvantage is associated with sexual reproduction in organisms with isogametes, as is apparent if one considers the biomass associated with each genome rather than the number of cells. Since sex and meiosis almost certainly preceded anisogamy, this disadvantage of sex need not be taken into account when considering the origin of sex, although it is highly relevant when considering its maintenance in higher organisms (Maynard Smith 1974, 300).

Some of the confusion which has arisen over this came, I think, for the phrase ‘the cost of meiosis’. In a species with isogametes there is no necessary twofold cost associated with meiosis, although the time taken to complete the meiosis division might constitute a cost. In a sense, a gene in a primary oocyte is running a 50% chance of being eliminated in a polar body, and could therefore gain a twofold selective advantage by suppressing meiosis. But I believe that the twofold advantage of parthenogenesis is best seen as the advantage of not producing males (Maynard Smith 1978, 3).

This cost of males is now the prevalent conception (Lively 2010; Lehtonen et al. in press). Nevertheless, Williams continued to pursue another route that led him to an increasingly sociobiological conception: 50% vs. 100% transmission turned into coefficients of relatedness (0.5 vs. 1).

Much of the importance and complexity derives from variation in degrees of relationship arising from sexual reproduction, in which a halving of the chromosome number (meiosis) in eggs and sperm, and subsequent fertilization, are the essential features. Without this chromosome cycle, all the coefficients of relationship would be one or zero (complete genetic identity or total independence), and much of the complexity of interactions among organisms would presumably disappear. [...] What would be gained by an individual, in an otherwise sexual population, who cheated by eliminating meiosis and fertilization from its production of an offspring, but remained otherwise the same? [...] If the fusing gametes are equal, neither parent seems to be subsidizing the reproduction of the other. In a more important sense this conclusion is wrong. Given that one cell fuses with another, we can then ask about the consequences of whether it plays the sexual game (meiosis) in its next cell division, or cheats (mitosis). It then becomes clear that the 50% cost of meiosis is still very much a reality (Williams 1980, 371, 372, 377).

In a ‘Retrospect on sex and kindred topics,’ Williams (1988) reasserts his claim that isogamy still involves a cost of sex and thereby arrives at an entirely sociobiological conception.

I do not agree with Felsenstein that there would be no cost of meiosis without the prior evolution of anisogamy. At the least I would suggest that the modeling Felsenstein has in mind is not the most instructive that can be devised. I have already published some arguments to this effect (Williams, 1980), but will try another here. Perhaps it is just a matter of time before someone discovers (or invents in the laboratory) an all-male species. It makes diploid sperm that inseminate eggs of a related species and give rise to diploid nuclei that exclude the egg pronuclei. [...] The point of the story is that any male of any species that refrains from such egg piracy is paying a cost of meiosis as a direct result of the haploid and cytologically cooperative behavior of its sperm. [...] It should be noted that while a cost of meiosis is readily recognizable in my all-male species, a cost of males is not, at least not as an aspect of selection at the individual level (Williams 1988, 294).

Williams’s reference to Felsenstein, here, means there is a chapter in the same volume that denies a problem with the evolution of sex beyond recombination (Felsenstein 1988, 74). Given the role that inclusive fitness played in the rejection of group selection and, in turn, the role this played in bringing forth the paradox of sex, the sociobiological conception of the cost of sex seems to correspond more closely to the root problem that initially perplexed these pioneers. The following will refer to it as the cost of cooperation among unrelated gametes (not meiosis). In conclusion, Maynard Smith defined the cost of sex at the individual level and Williams at the cellular level of gametes. Males and females do not exist in isogamous species and the cost of males does not exist either. The cost of cooperation among unrelated gametes, however, also exists in out-breeding isogamy.

2.3 *The turmoil of the research field*

As shown above, there are two or even three issues sailing under a paradox-of-sex flag: the maintenance of recombination rates, of out-crossing sex, or of male functions respectively. A further source for confusion lies in difficulties associated with trying to expand the explanatory power of a successful theory. For example, research on modifier genes was rather successful and attempts to expand the explanatory power of modifier theory to cover the larger cost of sex are only natural (e.g., Otto 2003; Dolgin and Otto 2003). For the sake of clarity, however, the subsequent discussion will keep these issues strictly separate.

3. Departure from Group Selection and Current States

Given the above disentangling of issues, the following two questions can be addressed more specifically:

- (i) Did the rejection of group selection in the 1960s render the maintenance issue in question an anomaly (i.e., a problem with no acceptable explanation)?
- (ii) What is the current state of research on the maintenance issue in question?

3.1 *The maintenance of recombination rates*

3.1.1 Rejection of group selection caused no anomaly

Feldman et al. (1996) reviewed research on the maintenance of recombination rates and regarded all optimality arguments as “actually couched (usually tacitly) in terms of group selection.” The tacit implication of group selection lies in the parameter being optimized in these models, which are group traits like the speed of adaptation or the time to fixation of two advantageous mutations occurring independently. However, Nei (1967; 1969) proposed a gene’s eye view on this problem, in the form of genes modifying recombination rates but with no other effect. Therefore the rejection of group selection reasoning did not turn this issue into an anomaly (see Figure 1). That is, there was no time-lag between the refuting of the old explanation and the availability of an acceptable alternative conforming with the new perspective.

3.1.2 Current state: theory expansion

Nei (1967; 1969) proposed the existence of genes that modify the rate of recombination between other genes but have no further effect on phenotype or fitness and showed that selection should favor recombination rates above zero. Modifier theory has been very successful. On the one hand, modifier loci could be identified empirically (e.g., Brooks 1988; Petes 2001; Esch and Horn 2008). On the other hand, modifier theory is being expanded to cover migration rates, meiotic drive, and sex ratios, as well as, in some approaches, to cover the cost of sex. Therefore, the terms ‘paradox’ and ‘recombination’ often occur together in publications (e.g., Barton and Charlesworth 1998; Otto and Lenormand 2002). The pure problem of the maintenance of recombination rates above zero, however, is usually not seen as an anomaly (Felsenstein 1985; 1988) and not called a paradox (for an exception see Ghiselin 1988, 13–15). Seger and Hamilton (1988) call it a “vexing question.”

3.2 *The maintenance of sexual reproduction*

The following shows that the paradox of sex was precipitated when the rejection of group selection was applied to reasoning about the evolutionary significance of sexual reproduction.

3.2.1 Rejecting group selection caused an anomaly

Before 1960, group selection explanations for the maintenance of sex were common (Fisher 1930, 123; Muller 1932, 121; see also Ghiselin 1988, 7; Mooney 1993, 1995; Meirmans 2009). Fisher and Muller implied group benefits in an evolutionary race between asexual and sexual taxa. “[S]exless beings, although often at a temporary advantage, can not keep up the pace set by sexual beings in the evolutionary race and, when readjustments are called for, they must eventually lose out” (Muller 1932, 118; see also the above quote

from Fisher 1999 [1930]). Crow and Kimura (1965) showed that Fisher's and Muller's explanations provided no immediate benefit of sex for individuals and that it was due to intergroup selection. Maynard Smith noticed the similarity with Wynne-Edwards's idea of group selection.

I was led to think about these questions after being involved in a controversy with Professor Wynne-Edwards on a quite different problem [...] There is however one property, that of sexual reproduction, which is almost universal, and for which the generally accepted explanation involves, implicitly or explicitly, a process of group selection (Maynard Smith 1971, 163–164).

His own rejoinder to Wynne-Edwards suggested that asexual mutants should undermine the long-term advantages of sex in the same way that cheats should undermine the group selection proposed by Wynne-Edwards (1971). However this theoretical prediction failed to correspond with reality.

The argument in this section seems to lead to the conclusion that [...] metazoan animals would be expected to give rise frequently to parthenogenetic varieties. Since in fact this conclusion is false, the argument must leave something out of account (Maynard Smith 1971, 172–173).

This failure of nature to obey theory, the failure of asexual 'cheats' to take over in the short term, eventually turned the maintenance of sex into an anomaly (Williams 1975; Maynard Smith 1978). The origin of this paradox in the group selection controversy of the 1960s has been documented by Williams in the collection of articles called 'Group Selection: A Controversy in Biology.'

I see in recent years a change in discussions of group selection [...] The emphasis at first was on seemingly altruistic behavior. Because of Wynne-Edwards' work the emphasis today is on the regulation of population density. Prophecy is a hazardous exercise in science, but I will venture to suggest that in the future the controversy will center increasingly on the phenomenon of sexuality [...] Yet only after group-related adaptation had been recognized in social behavior, and a controversial theory proposed to explain it, did the paradox of sexual reproduction begin to be recognized as relevant to the problem. This sequence of developments will someday be recognized as a curious feature of the history of biological thinking in the twentieth century (Williams 1971, 12, 14; see also 161).

Others also recollected the connection between the group selection controversy and recognizing the maintenance of sexual reproduction as an anomaly:

My own active interest in the evolution of genetic systems dates from around 1964, when I recognised that it was illogical to reject Wynne-Edwards's (1962) views in ecology as group selectionist, if at the same time I accepted a group selectionist explanation of sex (Maynard Smith 1978, 2).

In my own case two developments had been helping to bring sex into focus. One was the publication by J.F. Crow and M. Kimura in the mid-1960s of two papers challenging a certain long-accepted orthodoxy, which I will call the Weissmann-Muller-Fisher theory. Essentially, Crow and Kimura had pointed out the uncharacteristically 'groupish' natural selection that had been invoked for the case of sex by these three normally very 'individualistic' originators. Although allergic virtually since my school days to ideas of 'group benefit' and equally to 'species benefit' reasoning about evolution, I had somehow let my awe of R.A. Fisher slip this one argument, or lack of argument, past me without serious question (Hamilton 1996, 354).

When this anomaly turned out to be recalcitrant, Williams (1975, v) proclaimed a crisis, Ghiselin (1988, 19–20) called some decisions of his peers "acts of desperation," and Hamilton described a veritable loss of perspective: "It is as if we are all in a wood—a wood on a hillcrest. We scramble around seeking the gap that will let us look out on the landscape of the other side, which we glimpse tantalizingly through the trees" (Hamilton 2001, xxviii).

This apprehension of crisis is comprehensible from the historical sequence. Just when the argument against group selection had been successful, the paradox of sex popped up like a jack-in-the-box from the

succeeding perspective. Although general observations suggest an advantage of sex (e.g., the taxonomic distribution of obligate parthenogenesis or ecological correlates of facultative sex), a phase of mainly theoretical investigation followed and a lament about a lack of empirical tests arose.

Despite the wealth of theoretical work, the question of the maintenance of sex has received little attention experimentally [...], we are not aware of any experiments reported to date which directly address the major hypotheses (Antonovics and Ellstrand 1984, 103).

There is a continuing flow of new theories and variants of existing theories, but there seems to be no major new source of data, no illuminating new experiment (Felsenstein 1988, 75).

We have enough, even more than enough, possible solutions [...], but we do not have facts to decide which solutions are actually relevant. [...] we need data that explicitly test different hypotheses in various natural populations (Kondrashov 1993, 382–383).

As has been the history of this debate for many years now, most of the work on the evolution of sex is theoretical, and the past 20 years have seen a veritable bloom of ideas and subsequent modifications of these. [...] One of the great struggles in the evolution-of-sex literature is to find a prediction that is truly discriminating between hypotheses (Hurst and Peck 1996, 46, 51).

Critical tests to discriminate between the alternative theories have been hard to devise (Barton and Charlesworth 1998, 1989).

The problem of indecisive tests can be illustrated using two major hypotheses for the short-term maintenance of sex. The mutational deterministic model (Kondrashov 1982) considers detrimental mutations, whereas the red-queen model (Hamilton 1980) considers co-adapting parasites. Both models are designed to make these factors impinge on individual fitness and sexual recombination provides an immediate benefit. Although both factors may have long-term effects that would undermine the fitness of asexual populations and drive them to extinction, the goal to be met is a twofold short-term advantage of sexual recombination accruing to individuals.

The mutational deterministic model requires mutation-rates of at least one new mutation per individual and a synergism between mutations reducing individual fitness disproportionate to the mutation number. The red-queen model requires a particular cycling of parasite co-adaptation that renders adaptive host genotypes maladaptive in the next generation. These distinctive predictions have been hard to test and evidence has been indecisive, while both models are indistinguishable in other predictions (Hamilton et al. 1990). For example, an asexual clone may be moribund either because of mutation accumulation or because of parasite infestation.

3.2.2 Current state: towards integration

Differential extinction of sexual and asexual taxa has been admitted as higher level selection by Williams (1975) and Maynard Smith (1978), and elaborated by Nunney (1989). As it is not based on social interactions, however, it agrees with the MLS2 scenario. Neither MLS1 or inclusive fitness inform current research on the paradox. Many researchers turned to an integrative approach that tries to combine the effects of mutations and co-adapting parasites in one research model and testing design (Howard and Lively 1994; West et al. 1999 and following comments; Cooper et al. 2005; Killick et al. 2006; Meirmans and Neiman 2006; Park et al. 2010). This integration considers different processes or mechanisms as interacting causes (e.g., mutation accumulation and adaptation of parasites) and looks for their combined effect on one level of aggregation (e.g., the genotype). “Interactions between mechanisms may greatly increase the advantage of sexual reproduction” (West et al. 1999, 1005).

West et al. (1999) titled their seminal paper ‘A pluralistic approach to sex and recombination’; “To philosophers, this terminology might be surprising because one of the central ideas of the paper was an integration of models rather than pluralism in explanation” (Meirmans and Strand 2010, S8). Therefore, a

‘process integrator’ is not necessarily a ‘perspective pluralist.’ While Sober and Wilson (1998, 331) endorse both, West et al. (1999) endorse process integration for the maintenance of sex, but they regard the (between-)group selection perspective on altruism as useless for professionals and outright confusing for laypeople (West et al. 2007; 2008). That is, they refute perspective pluralism or at least want to exclude one perspective. Finally, Kondrashov (1999, 1031) even dislikes process integration: “I do not like this possibility because such a beautiful phenomenon as sex deserves a nice, simple explanation and messy interactions of very different processes would spoil the story.”

Intuitively, one might regard parasites and mutations as levels of selection above and below the individual, respectively. This is not true, however, because the models to be integrated are designed to provide the benefit of sexual recombination to individual fitness (see above).

4. Updating the Paradox to Multilevel Selection

4.1 Multilevel selection and sexual interaction

In MLS1 scenarios, between-group selection acts with the frequency of group dissolution. As that is usually linked to a breeding season, it is often shorter than a life-cycle. Hence it should be possible to come up with an MLS1 explanation for the maintenance of sex, whose benefit is also evolutionarily immediate. The classic assumptions of the paradox, however, would lead one to expect within-group selection to favor parthenogenesis and between-group selection to favor sexual reproduction. The following inverts this reasoning by assuming that sexual interactions within groups suppress parthenogenesis and asexual females can only realize their reproductive advantage in patches without males.

4.2 The evidence on sexual interactions with parthenogenetic females

The classic paradox assumes a population with females reproducing sexually or parthenogenetically, with half the offspring of sexual females being males that contribute nothing but DNA to offspring production. Parthenogenetic females gain a two-fold reproductive advantage given that males do not interfere. In nature, male interaction with parthenogenetic females takes different forms that can only be evaluated empirically. Male New Zealand mud snails readily copulate with asexual females and do not strongly bias copulations towards sexual females (Neiman and Lively 2005, see also Nelson and Neiman in press). It is necessary, therefore, to know the effect of mating on the fitness of asexual females.

In sperm-dependent parthenogenesis (Beukeboom and Vrijenhoek 1998), for example, mating has positive effects on the fitness of parthenogens because sperm triggers the development of parthenogenetic eggs although sperm DNA is excluded from the zygote (gynogenesis) or germ-line (hybridogenesis). The absence of donor males negates the fitness advantage of sperm-dependent parthenogens. That is, asexual females can only realize their reproductive advantage within groups of sexual donors. Kokko and Heubel (2011) modeled the maintenance of this system with males that can refrain from mating with asexual but sperm-dependent females. While this corresponds to the classic assumption that asexual females realize their reproductive advantage in the midst of sexual groups, it only applies to the small number of cases with sperm-dependent parthenogenesis.

Conversely, males are known to interfere with parthenogenesis in some lizards (Darevsky and Danielyan 1968; Cole et al. 2007 and references therein), nematodes (Fisher 1972), grasshoppers (White and Contreras 1978), sunfish (Dawley et al. 1985), and geckos (Dame and Petren 2006). If interference with parthenogenesis occurs, it is probably a side effect of indiscriminate mating. All else being equal, a mutant female may produce parthenogenetic eggs but otherwise behave like a virgin sexual female, that is, be as attractive to and attracted by males.

Williams (1975, 105) already suggested male interference with parthenogenesis:

[Carson (1967)] selected for parthenogenesis in *Drosophila* and increased its frequency from .001 to .064. They seemingly developed from unreduced eggs, because all parthenogenetic offspring were diploid, vigorous, fertile, and female. It may be too much to expect that such eggs would also resist fertilization. I

suggest that, if normally inseminated, the partly parthenogenetic females would produce about 6% inviable triploids.

This is not to be mistaken as suggesting that male interference will sterilize only 6% of the parthenogenetic offspring—an entirely arbitrary prediction with no empirical basis—but as the testable hypothesis that the same offspring developing parthenogenetically (frequency .064) in the absence of males will become sterile triploids (about 6%) in their presence.

In contrast, male interference is restricted in strains of *Drosophila mercatorum* that are obligatorily parthenogenetic and also strongly reluctant to mate (Ikeda and Carson 1973; Takenaka-Dacanay and Carson 1991). All else being equal, a mutant female may not be like a virgin but like a fertilized sexual female and, therefore, be repelled by and repelling to males. This may indeed be the cause for the behavior of asexual *D. mercatorum* in comparison with the asexual grasshoppers, lizards, geckos, or nematodes mentioned above. Maynard Smith (1978, 41) even saw the possibility of reproductive interference in parthenogenetic plants with sexual competitors through the maintenance of a male function (pollen). Lynch (1984, 259ff), as well as Gröning and Hochkirch (2008), review reproductive interference in general but this has been of interest primarily to those working in conservation biology.

Given the wide range of interactions between males and parthenogenetic females occurring in nature, it is impossible to predict whether parthenogenetic females will be able to realize their hypothetical twofold advantage over sexual females without further knowledge of the male contributions to sexual reproduction (see Table 1) or male interference with parthenogenesis (e.g., disruptive sperm penetration or negative effects of seminal compounds on parthenogenetic eggs). In conclusion, assuming that asexual females can realize their reproductive advantage in the midst of a sexual population is as justified as the opposite assumption. It is therefore critical to consider the consequences of male interference.

4.3 Reproductive interference could repress parthenogenesis within groups

According to Sober and Wilson (1998) the trait-group is defined as:

a set of individuals that influence each other's fitness with respect to a certain trait but not the fitness of those outside the group. [...] groups are defined exclusively in terms of fitness effects and everything else about groups, such as their duration and the manner in which they compete with other groups, follows from the nature of the interaction (92ff).

Hence, the trait-group relevant to the maintenance of sex is the set of individuals that affect each other's fitness through reproductive interactions. That is, the trait-group is the group of females (sexual and parthenogenetic) and males that can actually mate.

Suppose a population goes through cycles of group establishment and dissolution. Further, let sperm be cheap, with males incurring a negligible cost from mating, and let mating be indiscriminate and interference with parthenogenesis an accidental side effect. In the simplest case, a single mating will reduce the reproductive success of parthenogenetic mutants from 1 to 0 but raise that of sexual females from 0 to 0.5 (Table 2). Selection should favor sexual reproduction in each cycle if:

$$c < b \cdot (p_s/p)$$

where c is the cost of sex incurred by sexual females, b is the cost of mating incurred by asexual females, p_s is the number of sterilized parthenogens, and p the number of all parthenogens.

Assuming for simplicity that every sexual female gets fertilized (or sexual individuals could be hermaphrodites resorting to selfing in the absence of mating partners), the cost c of sex will be 0.5. The benefit of sex b equals the harm that mating incurs on a parthenogenetic female (Dagg 2006). In the present case, this equals 1. Sex will maintain itself if $p_s/p > 0.5$. This maintenance of sex would not be a case of between-group selection trumping within-group selection because a group of parthenogens would always out-reproduce a sexual group and the repression of parthenogenesis would inevitably occur within groups with males. Nevertheless, this depends on the portion of parthenogenetic females that end up in groups

containing males (i.e., on group structure and dynamics). Kriebler and Rose (1986, 437) provided genetic models of male interference with parthenogenesis that analyzed various genetic conditions (e.g., dominance, recessiveness, heterosis), but not group structure and dynamics, and concluded that male interference with parthenogenesis could maintain sexual reproduction even “in the absence of any additional selective advantage accruing to sexual recombination.”

Table 1 — Potential contributions of males to reproduction

Sperm functions beyond genetic information	Epigenetic information: DNA-methylation differs between mammalian eggs and sperm. This imprinting could be a reason for the absence of parthenogenesis in mammals (Jaenisch and Wilmot 2001, Engelstädter 2008). Various hypotheses about the adaptive significance of DNA-methylation exist (e.g., Wolffe and Matzke 1999; Gorelick and Carpinone 2009).
	Various kinds of sperm RNA exist. Their functions, if any, are still unknown as research on sperm RNA is still in its infancy (Nanassy and Carrell 2008).
	The sperm centrioles assemble the sperm-aster that guides the pronuclei towards each other. Complementary degradation of centrosome proteins in sperm and centrioles in eggs may serve to prevent parthenogenesis (Manandhar et al. 2005, Engelstädter 2008).
Ejaculate functions beyond sperm	Seminal fluid compounds have various effects (Poiani 2006). Some suppress female immune responses (Quayle et al. 1989, Emoto et al. 1990) and promote tolerance of male antigens. Some promote the implantation of embryos (Robertson 2007). Some suppress the proliferation of pathogens (Mueller et al. 2007), including eukaryotic parasites of the female genital tract (Krieger and Rein 1982). Some suppress the proliferation of cancer cells, especially in female mammals (e.g., Park et al. 2004), though others promote prostate cancer in old male mammals as a by-product of high fecundity at younger age (Summers and Crespi 2008). If cancer is promoted in males rather than females, and cell-growth inhibition acts on tumors, pathogens, and parthenogenetic eggs alike, then seminal fluid will interfere with parthenogenesis.
Male functions beyond ejaculates	Behavioral stimuli trigger responses of the female reproductive system (Neiman 2004).
	Paternal care is usually taken to annul the advantage of parthenogenesis (e.g., Maynard Smith 1971, 171). Nevertheless, Bednekoff (1996) modeled an exception where males cannot discriminate between females and also care for parthenogenetic offspring (see also Williams 1980, 380ff). This should be unlikely, however, because it requires that mating does not interfere with parthenogenesis and results in viable offspring to care for in the first place.

Table 2 — Fitnesses of sexual and parthenogenetic females depends on group composition (S: sexual females; P: parthenogenetic females)

Composition of Females in Group	(Average) fitness f of females in group	
	<i>with male</i>	<i>without male</i>
S	0.5	0
P	0	1
S + P	$0 < f < 0.5$	$0 < f < 1$

5. Discussion

5.1 *The root problem and its homegrown solution*

The paradox of sexual reproduction emerged out of the context of sociobiology when group selection was rejected in the 1960s. As the levels of selection issue has advanced far beyond these rejected models, so also should the paradox of sex be considered from the perspective of multilevel selection theory. A scenario referred to as MLS2 has been considered extensively in relation to the maintenance of sex (Maynard Smith 1971, 164; Williams 1975, chap 13; Nunney 1989; Williams 1992, 35). This, however, cannot meet the target of providing an immediate benefit for individuals/genes set by Williams (1975). MLS1 with sexual interactions can provide such an immediate benefit, though the maintenance of sex is not necessarily due to between-group selection. In the above model, it would be due to within-group selection against asexual females in combination with a group structure and dynamics that prevents asexual females from remaining isolated for too long. Moreover, reproductive interference is sociobiological and cancels the cost of males by a benefit of males and the cost of cooperation between unrelated gametes by a benefit of it (at the expense of parthenogenetic gametes), whereas other hypotheses are not based on social interactions and recoup the cost of sex by a benefit of recombination.

5.2 *Expectations for research*

Some constraints on the rule $c < b \cdot (p_s/p)$ can be expected. First, an asexual female needs to behave like a receptive sexual female and to be perceived like one by males in order for mating to occur unimpeded. This constraint should apply to cyclic parthenogenesis and other life cycles with facultative sex, where parthenogenetic females are a specially adapted morph, because a mutation abandoning the sexual phase will only leave the parthenogenetic females in the life cycle. As a specially adapted morph they should be unlikely to be perceived as and behave like sexual females before mating. Second, mutant females could actively repulse males as in *D. mercatorum* (Takenaka-Dacanay and Carson 1991). If so, sexual dimorphism with big females and small males or mating behavior that requires cooperative females will limit reproductive interference. Third, in species with strongly female biased sex ratios the frequency of reproductive interference with parthenogenesis should be constrained by the rarity of males. Finally, male interaction may not amount to interference but simply switch females between different modes of reproduction according to their fertilization status. For example, parthenogenesis only occurs in unfertilized females of some *Drosophila* species and mating renders them properly sexually reproducing (e.g., Stalker 1954). These constraints apply to many taxa with known asexual lineages and may explain them.

All the alternative hypotheses assume that an asexual mutant female can arise in the middle of a sexual population and realize a large reproductive advantage; they tacitly assume that reproductive interference cannot occur. Whereas the red queen hypothesis, for example, requires that asexual clones reach considerable frequencies, in order to allow for the co-adaptation of parasites, male interference can eliminate parthenogenesis immediately. Therefore, asexual mutant females should often remain cryptic in appearance, like sexual females that are sterile for some unknown reason. Under conditions of male interference, many origins and eliminations of parthenogenesis would remain beneath the radar of unsuspecting researchers. Some sterile sexual females may turn out to be ‘sterilized’ parthenogenetic ones. Fortunately some cases of male interference with parthenogenesis have been recorded (Cole et al. 2007 and references therein; Dame and Petren 2006; Darevsky and Danielyan 1968; Dawley et al. 1985; Fisher 1972; White and Contreras 1978). The above model predicts that the presence of males should strongly reduce the fitness of asexual females in these cases.

5.3 *Implications for multilevel selection theory*

Male interference with parthenogenesis inverts the widely held idea that within-group selection necessarily favors the selfish strategy and between-group selection the altruistic one because gamete-cooperation (sex) is favored in groups with males and recurrent group dissolution, mixing, and group establishment is needed to prevent asexual groups from ousting sexual ones. This case also has interesting

implications for multilevel selection theory. In conventional scenarios, within-group selection works uniformly in one direction, between-group selection works uniformly in one direction, and the relevant cases arise when these selective pressures are opposed (Okasha 2006). With male interference, however, within-group selection no longer works uniformly in one direction. Instead, within-group selection favors sexual females in the presence of males and asexual ones in their absence. In conclusion, selection is not only structured into vertical levels, but also into horizontal patches (male-occupied versus male-free). These unconventional cases may contribute to resolving ongoing debates surrounding group selection.

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