

A distinction between the origin and maintenance of sex

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West *et al.* (1999) present a reasonable argument for the pluralistic view that multiple adaptive mechanisms may simultaneously, and even synergistically, favour sexual reproduction. However, they ignore a fundamental and potentially important distinction between the adaptive role of sex in extant organisms and the evolutionary origin of sex. If one seeks to explain the current utility of sex, then I am inclined to agree with their view that multiple factors contribute to its maintenance and prevalence. On the other hand, I suspect that one selective factor may have been important in the emergence of sexual organisms from an asexual ancestor (although I do not have a preferred candidate for what that single factor was). Even if several factors were involved in the origin of sex, they may have acted sequentially rather than simultaneously, so that each step along the way provided a solution to one problem (e.g. Maynard Smith & Szathmáry, 1995). This distinction between multiple factors acting simultaneously to maintain sex, versus a single factor or several sequential factors accounting for its origin, is merely a hunch on my part.

It often seems to be the case that evolutionary innovations are initially driven by one primary factor; but after an innovation has been integrated into an organism's way of life, the organism becomes multiply dependent on the continuation of that trait. For example, consider the origin of insect wings during the Devonian period (Kingsolver & Koehl, 1985). Small proto-wings may have been initially beneficial for thermoregulatory capacity. As the size of these structures increased, owing to change either in relative proportions or overall body size, they subsequently acquired aerodynamic properties

that were beneficial in certain settings. Despite the initially one-dimensional selection to acquire the antecedents of wings, a thorough study of natural selection acting on these structures in extant organisms would probably find evidence to support multiple adaptive roles, including not only thermoregulation and locomotion but also courtship display in certain groups. Thus, selection against loss of a derived trait may often be more complex and multifaceted than was selection to produce that trait originally, as a consequence of the subsequent integration of the trait into the whole being.

That this distinction is potentially relevant to the evolution of sex can be seen more clearly by considering the recommendations that derive from the pluralistic viewpoint of West *et al.* (1999). They suggest focusing future research on a few biological systems to obtain a detailed picture of multiple selective forces and their interactions. They then state that it is '... highly important to estimate relevant parameters in sexual species. The form of selection must be different in sexual species than in species which are asexual ...' This advice is quite sensible if one seeks only to understand the selective factors that are responsible for the maintenance of sexual reproduction in extant organisms. But it can be turned on its head with respect to understanding the evolutionary origin of sex. After all, sexual organisms evolved from asexual organisms that experienced the conditions – ecological and genetical – necessary to promote the emergence of sex.

The origin of sex can be addressed not only from a historical perspective (using comparative methods and evidence from palaeontology), but it can also be studied by performing experiments with extant asexual organisms to determine whether they fulfil essential preconditions for the emergence of sexuality according to a particular hypothesis. For example, in our own work

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(Elena & Lenski, 1997), we sought to test the mutational deterministic hypothesis for the evolution of sex. According to this hypothesis, sex is advantageous because it allows deleterious mutations to be more efficiently eliminated from a population, even one that is very large and hence not affected by the random drift that advances Muller's ratchet (Kondrashov, 1988). The validity of the mutational deterministic hypothesis depends on key assumptions being met, including a tendency toward synergistic interactions between deleterious mutations. That is, two or more mutations together should be worse, on average, than would be expected from their individual effects. To test this assumption, we used the bacterium *Escherichia coli*, an organism that reproduces asexually. [In nature, *E. coli* undergoes occasional recombination via parasexual processes, but the effective recombination rate is very low (Guttman & Dykhuizen, 1994).] We chose *E. coli* for this research for two important reasons. First, *E. coli* offers exceptional opportunities for genetical precision and statistical power. We constructed some 250 genotypes with different combinations of mutations, and we measured the fitness of each genotype relative to an unmutated common competitor. Second, and more subtly, we wanted to know whether there exists 'a general tendency for genetic architectures to exhibit synergistic epistasis among deleterious mutations' (Elena & Lenski, 1997). If such a tendency were manifest even in this asexual bacterium (and in other bacteria more generally), then this would fulfil an essential precondition for the evolutionary origin of sex according to the mutational deterministic hypothesis. In our study, we found abundant evidence for epistasis among deleterious mutations, but the interactions were not primarily synergistic in form. Thus, we rejected the general proposition that genetic architectures are structured such that there exists a substantial excess of synergistic interactions.

If one were to perform the same experiment, but using a sexual organism, then one might get a misleading answer with regard to the origin of sex, for the following reason. Imagine that sex evolved originally for some reason other than the one postulated by the mutational deterministic hypothesis. Once sex became integrated into the way of life of early sexual organisms, this may have allowed the subsequent evolution of a higher genomic mutation rate. This secondary change might reflect the fact that mutator alleles, which increase the genomic mutation rate, are penalized more directly in asexual than in sexual organisms (Leigh, 1970), or the fact that the conditions under which higher mutation rates promote more rapid adaptive evolution are restrictive in asexual organisms due to clonal interference (Gerrish & Lenski, 1998). In either case, a higher genomic mutation rate would produce a higher genetic load, which in turn might favour the evolution of a genetic architecture biased toward synergistic epistasis, because such an architecture reduces the equilibrium load of deleterious mutations in sexual – but not asexual –

organisms (Charlesworth, 1990). *Voilà!* If this hypothetical cascade of evolutionary events occurred, then one would find evidence among extant sexual organisms to support the mutational deterministic hypothesis for the evolution of sex, even though the effect that is postulated by this hypothesis only evolved later and had nothing to do with the origin of sex. (Let me emphasize that I am not arguing that this precise sequence of events unfolded in this manner. Rather, I offer this scenario to illustrate how secondary evolutionary change could lead to some mistaken inference concerning the origin of sex, especially if that inference rested entirely on studies of extant sexual organisms.)

West *et al.* (1999) themselves point out that 'The mutation rate ... is generally selected to be lower in asexual species ... [and] the form of epistasis between deleterious mutations is likely to differ between asexual and sexual species.' Indeed, they use these points to bolster their recommendation that parameter estimates used for testing various hypotheses should be obtained in sexual species. But they fail to realize that this recommendation is a two-edged sword, one that may cut differently depending on whether one seeks to understand the present utility or the evolutionary origin of sex.

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