COMMENTARY

Measuring the benefits of sex

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West *et al*. (1999) identify and encourage a shift in studies of the evolution of sex from hypothesis testing to parameter estimation. While this trend is beneficial, relating parameter estimates to the reasons for the maintenance of sex is surprisingly difficult. This commentary discusses two of the issues involved.

Is there a two-fold benefit of sex?

West *et al*.'s argument for their pluralist view is based on the premise that sex needs a large short-term benefit in order to offset its two-fold cost. An alternative, developed by Nunney (1989) and A. Burt (personal communication), is that sex is maintained by clade selection. Clonal lineages are generally short-lived in evolutionary time (Maynard Smith, 1992). Consequently, if the rate of origination of clones is low, sex can persist even if it is out-competed by asexuality every time it arises. Nunney showed that clade selection would also reduce the rate at which sexual species produce new clonal lineages.

This clade selection hypothesis is sufficient to explain the rarity of obligate asexuality, but does not explain the persistence of systems in which sex and asex coexist (Nunney, 1989). These systems are therefore taken by many (e.g. Williams, 1975) as evidence for a large short-term benefit of sex. The existence of systems in which obligately sexual and asexual forms compete provides a basis for West *et al*.'s argument that sex needs a plurality of benefits in order to offset its two-fold cost per generation. However, these systems are rare (Bell, 1982), possibly because most of those that arise become extinct shortly afterwards (A. Burt, personal communication). Those that we do observe may be atypical in that they posses factors which promote persistence.

Possible factors include: (1) low hatch rates of parthenogenetically produced eggs; (2) residual male function of asexual hermaphrodites; (3) differences in ploidy levels between sexuals and related asexuals; (4) hybrid origins of asexuals; (5) the requirement of asexuals to be fertilized by male sexuals or other hermaphroditic asexuals. Each factor is common amongst sexual/asexual systems, but none is universal (Bell, 1982), an observation consistent with each one being common because it increases the time a system persists.

Each of these factors alters the costs and benefits of sex. The low hatch rate of parthenogenetic eggs, a common trait among facultative asexuals, reduces the fitness cost of sex relative to asex directly. Residual male function has been shown theoretically to reduce the benefit of sex necessary for coexistence in some but not all circumstances (Joshi & Moody, 1995). Ploidy differences can have an indirect effect by ensuring that sexuals and asexuals are morphologically distinct. When sexuals and asexuals inhabit different ecological niches, a wide range of values for the benefit of sex are all likely to be consistent with coexistence. Similarly, niche separation associated with speciation may protect sexual forms in hybridogenic systems. Finally, the necessity for asexuals to be fertilized by sexuals has been shown to give sexuals a frequency-dependent advantage that, in the unisexual fish *Poeciliopsis mollachaoccidentalis*, can be large enough to offset a two-fold cost of sex (Moore, 1976).

Residual male function and the necessity for asexuals to be fertilized by sexuals may also promote persistence by ensuring the creation of new clones through 'contagious asexuality' (Hebert & Crease, 1983). There is direct evidence for contagious sexuality through fertilization of unisexual females by sexual males in salamander hybrids of the Ambystoma system (Hedges *et al*., 1992). Eighteen out of 20 unisexuals, which were otherwise genetically diverse, were shown to share a common mitochondrial genotype. Contagious sexuality through male function has also been suggested as the mechanism of clone creation in a number of systems (e.g. Enghof, 1976; Hebert & Crease, 1983; Pongratz *et al*., 1998). In these systems selection to maximize female fecundity within each clonal lineage may be balanced by the increased ability of clones with lower fecundity to create new lineages. Contagious sexuality plays a multiple role in ensuring the creation and stability of sexual/asexual systems. First, it can facilitate the evolution of asexuality (Jaenike & Selander, 1979). Second it ensures the continued creation on new clones. Third, it reduces the fecundity advantage of asexuals. Fourth, it may allow asexuality to jump between species, counterbalancing clade selection against sexual species which produce asexuals. Consequently, contagious asexuality may

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ensure persistence and a reduced cost of sex in many of the systems that field workers observe.

Should fitness be measured on a log scale?

Several experimental methods have recently been proposed which measure the fitness of individual genotypes before and after sex (Charlesworth & Barton, 1996; de Visser *et al*., 1996; 1997a). This approach has the potential to provide a direct estimate of selection on sex and recombination (Barton, 1995). Unfortunately, most of the proposed methods may prove impractical (West *et al*., 1998). One problem is that each of the methods relies on a logarithrmic fitness scale to interpret data. The scale has many theoretical advantages. The most powerful analysis of the evolution of recombination (Barton, 1995) relies on the scale, treating epistasis as a deviation from multiplicativity. It also tends to make results easier to interpret. For example, under synergistic epistasis, increasing the variance in mutation number always lowers mean log fitness, but may either raise or lower mean fitness, depending on parameters (compare Tables 2 and 3 of Charlesworth & Barton, 1996).

Conversely, use of the scale can bias results, give a misleading indication of selection pressures and, in some circumstances, prove impossible. Barton's analysis, like every other, simplifies reality in order to represent it. In practice, genotypic fitnesses will not obey the relationships the analysis suggests. This is a problem because logarithmic measurements can easily over-emphasize the importance of genotypes with very low fitness. The exact fitness of these genotypes has little effect on recombination modifier dynamics but can alter epistasis estimates substantially. Additionally, measurement error is bound to have a nonlogarithmic component. Unless this source of bias is corrected for it will also exaggerate the contribution of genotypes with low fitness.

In a recent experiment, the use of a logarithmic scale proved impossible. Elena & Lenski (1997) collected *Escherichia coli* mutants in a permissive environment in order to measure the shape of the fitness function. A number of genotypes that they obtained were found to have zero fitness in the more stringent environment in which fitness was measured. For these genotypes, log fitness is undefined. Faced with this difficulty, Elena and Lenski abandoned a true logarithmic scale, calculating the log of mean fitness rather than the mean of log fitness. Better, they should have abandoned logarithms entirely. A fitness function is a statistical construct, designed to summarize the results of a number of measurements in a few parameters. The choice of function should therefore be made on statistical grounds, taking into account both the range of measurements (which in this case disqualifies the use of logarithms) and also their error. Fortunately, in Elena and Lenski's experiment the choice of fitness function did not matter much. However interpreted, the measurements do not indicate significant synergistic epistasis (Elena & Lenski, 1997).

A similar experiment has revealed another problem with the measurement of individual fitnesses. de Visser *et al*. (1997b) attempted to isolate genotypes of *Aspergillus niger* with every possible combination of a set of marker loci before measuring their fitness. They found that those combinations that were not isolated had more low fitness alleles than those that were. This experiment illustrates that some low fitness genotypes will inevitably be lost before being isolated. On a logarithmic scale the resultant bias will be large.

What can be done? One approach is to minimize the importance of low fitness genotypes by ensuring that offspring fitnesses are intermediate to those of the parents (as in the design favoured by West *et al*., 1998). A second approach is to abandon the effort to measure the fitness of individual genotypes and instead perform multigenerational experiments in which aggregate frequencies are followed for a number of generations. In an experiment of this sort, Greig *et al*. (1998) modified the capacity for sex genetically and allowed sexuals to compete with asexuals during and after sex. This approach avoids all problems with biased sampling of genotypes and nonlogarithmic error. The best solution to the problems associated with logarithmic fitness measurement may be to design experiments that do not require it.

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