COMMENT
Hybrid theories of sex

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West *et al.* (1999) propose that we should examine the situations when more than one mechanism works to protect a sexual population from invasion by asexual clones. They think this pluralistic view is better than trying to choose only one theory for the advantage of sex and drop the others. In particular, they look for the joint action of theories considering mutation accumulation (the stochastic Muller's ratchet, and the mutational deterministic hypothesis of Kondrashov) and the effect of parasites (the Red Queen). As every species must fight against both parasites and deleterious mutations, it is a realistic situation. Note that, taken separately, all the hypotheses have difficulties with assigning a two-fold advantage to sex in the short run irrespective of population size. If two mechanisms act simultaneously, one does not need to assume extremely high mutation rates or severe effects and extreme transmission probabilities of parasites.

West *et al.* argue that different mechanisms may interact *not only simultaneously but synergistically*, i.e. the combined effect of the two mechanisms is greater than the sum of their contributions. We would like to comment on this aspect of the pluralistic view.

We think there are three main reasons why this synergism can exist: (i) the action of one mechanism supports the key assumption of the other, so the latter can work better; (ii) one mechanism slows down the spread of the clone in the short run so that the other has more time to render it a disadvantageous strategy; (iii) the selective forces assumed in the two mechanisms work against each other in the clone while in the sexual population they act independently, hence the clone cannot climb onto the adaptive peak. We comment below on some (maybe not all) possibilities for these types of synergistic interaction between theories.

(i) The Red Queen helps Muller's ratchet

As all the asexual clones originate from one founder individual and undergo a period with small population size at the beginning, they are prone to accumulate

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deleterious mutations stochastically according to Muller's ratchet. Because of the slowness of this process, the clone can reach a reasonable size well before its fitness decreases to half the average fitness of sexuals (required to counterbalance the two-fold cost of sex), but Muller's ratchet clicks rarely in a large clone. Howard & Lively (1994) showed that the Red Queen can help because parasites depress the size of the clone cyclically, and thus Muller's ratchet can accelerate at the bottlenecks.

We are not aware of any model in which the Red Queen is aided by some other mechanism in the sense of providing better conditions for it, provided the effect of parasites is more serious for the clone. One possibility might be to consider deleterious (null) mutations in the resistance loci of the host (e.g. in Hamilton's model) and then calculate the effect of Muller's ratchet on these loci.

Neither do we know about any model where the Red Queen provides the necessary conditions for the mutational deterministic hypothesis, except the brief note of West *et al.* that parasites might be the factor causing truncation selection against highly contaminated genomes.

(ii) The Red Queen and Muller's ratchet aid the mutational deterministic hypotheses

The problem with the mutational deterministic hypothesis occurs when an asexual clone invades a sexual population of modest size (10^3–10^4), because the clone can win before it reaches its higher equilibrium contamination and lower fitness (even with $U = 1$ and truncation selection when the equilibrium fitness of sexuals is more than two-fold). The effect of parasites slows down the spread of the clone providing more time for the deterministic advantage to develop and at the same time Muller's ratchet speeds up the deterministic process of mutation accumulation stochastically. The odd thing is that the latter aid given by Muller's ratchet is aided further by the Red Queen as we described in (i). Note that while it is true that Muller's ratchet can hardly doom a clone to extinction in case of truncation selection, it does decrease the time required to reach its equilibrium where the mutational deterministic hypotheses kills the clone.

Muller's ratchet helps the Red Queen fighting against repeatedly occurring clones

Lively & Howard (1994) called the attention to the fact that parasites do not select for sex *per se,* but for genetic (clonal) diversity. If the clones occur repeatedly then it can happen that the first one has not yet been eliminated when the second or third one emerges. Thus clonal diversity develops and the sexual population has no further hope except in the case when some mechanism speeds up the elimination of the clones. Muller's ratchet is appropriate for this task because the clones oscillate and mutation accumulation accelerates at every bottleneck causing eventual mutational meltdown. In consequence, the probability that more than one clone exists at the same time decreases. In Lively and Howard's model the size of the sexual population was only 10^3 and they did not ask if the mutational deterministic hypothesis can give a similar aid. We think that it possibly cannot give much aid, because the deterministic mutational load difference develops only slowly, and unlike Muller's ratchet it does not speed up at the bottlenecks. Thus we do not know any model which shows that the Red Queen is helped by the mutational deterministic hypothesis.

(iii) Selective forces

Selective forces eliminating deleterious mutations and spreading a favourable one work against each other in an asexual poplation because of sochastically generated linkage disequilibrium, as Manning & Thompson (1984) and later Peck (1994) described well in the 'ruby in the rubbish' type of model. It is a kind of synergism between Muller's ratchet and the old Fisher–Muller theory.

A similar disadvantage of asexuality can occur if we think further on Manning's (1982) argument that frequency-dependent selection and the spread of a favourable mutation can work again antagonistically. As the Red Queen results in frequency-dependent selection, synergism may exist between it and the Fisher–Muller theory. This possibility has not yet been formally modelled.

What is missing from the picture? For example, the shifting optimum model of Maynard Smith and the models with patchy environment (Lottery, Tangled Bank) have not yet been considered in this pluralistic sense.

Summarizing, one can identify several cases when considering two models we can give a greater advantage to sex than the sum of the separate effects, but note that all the models mentioned above assumed sexual populations of modest size and in the majority of cases at least one of the interacting mechanisms is stochastic. So the aim declared in West *et al.*'s paper to find interactions among deterministic mechanisms working in large populations has not been completely achieved.

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