

Evolutionary stability of sex and recombination. [You will need to fill in the graphs from lecture](#)

1. Motivation. Sex and recombination are anomalies for theory, and, from a pedagogical point of view, these anomalies “capture” many of the ideas we have been studying (e.g.: [mutation selection balance](#), geometric mean fitness, stable limit cycles, frequency-dependent selection).

2. Cost of sex (or the 2-fold advantage of obligate asexual repro.)

a) the all-else-equal assumption.

b) the grandchildren asymmetry

c) time to extinction for a sexual population

3. The advantages of sex (meiosis and syngamy) (i.e., all else is not equal).

a) the macroevolutionary hypotheses

i) Stanley (1975): sex species speciate faster

ii) Nunney (1986): obligately sexual species are less prone to extinction.

b) the microevolutionary hypothesis

i) mutation clearance:

ii) adaptive variation (or ecological genetic) hypotheses

4. Mutation Clearance as an advantage to sex

a) Muller's Ratchet.

i) some history

ii) independent effects of mutations in graphical form

let U be the mutation rate per genome per generation

let k be the number of mutations.

Individual fitness is $(1 - s)^k$

Mean fitness at mutation selection balance is e^{-U} , assuming s is small. This is true for both sexual and asexual population (Kimura and Maruyama 1966).

The mean number of mutations at [mutation-selection balance](#) is equal to U/s

Muller (1964) realized that Kimura and Maruyama must be assuming an infinite population size. He stated that if population size is finite, the asexual population incorporates a ratchet-like mechanism (Muller 1964).

In other words, individuals containing the fewest number of mutations can be lost, and not replaced, in the asexual population. But through sex and recombination, this class of individuals can be replaced, giving an advantage to sex.

b) Kondrashov's hatchet

Kimura and Maruyama were worried about the consequences of mutations having independent effects: the genetic load at mutation-selection balance could be very high. They therefore considered a different way to map mutation number onto fitness. Specifically, they considered the case for when there is a negative synergism among mutations. In graphical form...

K&M also realized that fitness at mutation-selection balance would be **greater** in a sexual population **than** for the case when mutations had independent effects. Specifically,

$$\bar{W}_{sex} > e^{-U}$$

But fitness for the asexual population would be **the same**:

$$\bar{W}_{asex} = e^{-U}$$

Alexy Kondrashov knew of this result, and he asked the question: What would the mutation rate have to be for a given level of negative epistasis for sexuals to overcome the two-fold advantage of producing males (Kondrashov 1982; Kondrashov 1988)?

Kondrashov constructed the simplest model, for which fitness was truncated at a threshold number of mutations. He assumed an infinite population size, so drift was not a problem. He found that sexuals would be favored under these conditions, if

$$U > 1.$$

That is the mutation rate per genome per generation is greater than one. That is a fascinating and testable prediction, and it launched many labs into frantic action...

- Kimura, M., and T. Maruyama. 1966. The mutational load with epistatic gene interactions in fitness. *Genetics* 54:1337-1351.
- Kondrashov, A. S. 1982. Selection against harmful mutations in large sexual and asexual populations. *Genetical Research, Cambridge* 40:325-332.
- Kondrashov, A. S. 1988. Deleterious mutations and the evolution of sexual reproduction. *Nature* 336:435-440.
- Muller, H. J. 1964. The relation of recombination to mutational advance. *Mutation Research* 1:2-9.