Evolutionary stability of sexual reproduction (defined here as genetic mixing between two parents) and the evolution of meiotic recombination. (see pages 301-313 in Freeman and Heron 4th ed)

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 males** (or the 2-fold advantage of obligate asexual repro. see John Maynard Smith, *The evolution of sex.*) Chalk talk. History of the “cost of males” wrt group selection

   a) the all-else-equal assumption.

   b) the grandchildren asymmetry. (draw on board)

   c) what is the time to extinction for a sexual population? (draw on board)

   d) Ecological view of the cost of sex (per capita growth, $K$)
An ecological perspective on the “cost of males.”
3. The advantages of sex (meiosis and syngamy) (i.e., all else is not equal).

a) the macroevolutionary hypotheses
   
i) Stanley (1975): sexual 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

Results from Kimura and Maruyama (1996)

let $U$ be the mutation rate per genome per generation
let $k$ be the number of mutations.
let $s$ be the selection coefficient (little $s$)

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 $U/s$

note: see L567 lecture 12 ratchet wb.xlxs
Fitness at equilibrium is $e^{-U}$

The equilibrium is the same for both sexual and asexual populations.

So this model cannot favor sexual reproduction!

$U$ is the mean number of new mutations each generation.
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).

“... we find that an asexual population incorporates a kind of ratchet mechanism, such that it can never get to contain, in any of its lines, a load of mutations smaller than that already existing in its at present least-loaded lines.” H.J. Muller. 1964. Mutation Research 1: 2-9

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.
Recombination in sexual populations can restore the least loaded class.
As an aside... Kimura and Maruyama (1966) 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.

\[ W = 1 - \left( \frac{N}{K} \right)^a \]
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:

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

b) Kondrashov’s hatchet.

Alex 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)?

Question: what is $e^{-U}$?
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

\[ U > 1, \]

where \( U \) is the Mean number of new mutations, where the number of new mutations has a Poisson Distribution.

Sex is favored when the mean 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...

Kondrashov’s Hatchet for $U = 1.0$, assuming a threshold fitness function. In this example, the advantage of sex outweighs the cost of males.
The Poisson probability distribution for $U = 1$

The probability of having zero mutations is $e^{-U}$.

Thus $e^{-U}$ is the survival prob.

The probability of having 1 or more mutations is $1 - e^{-U}$.

Note: see L567 lecture 12 Poisson distribution.xls