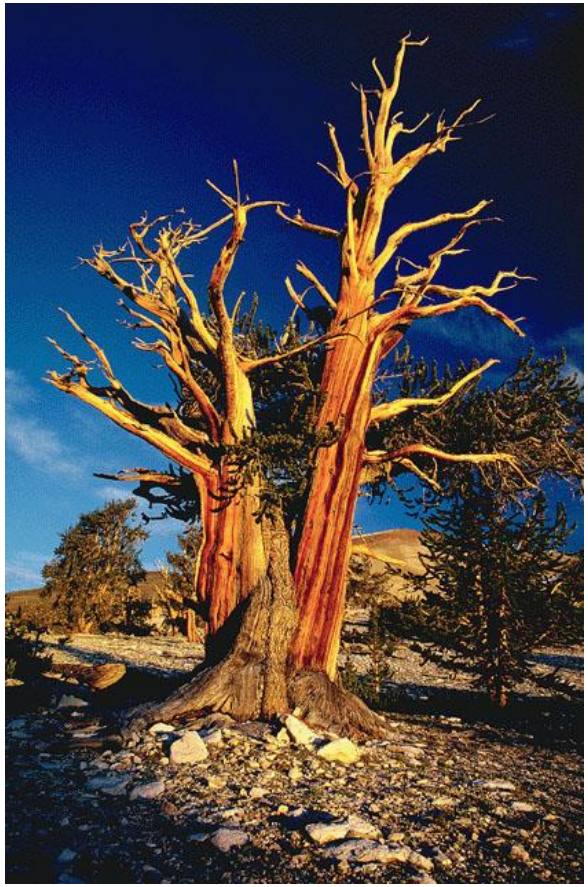
The evolution of sex and death

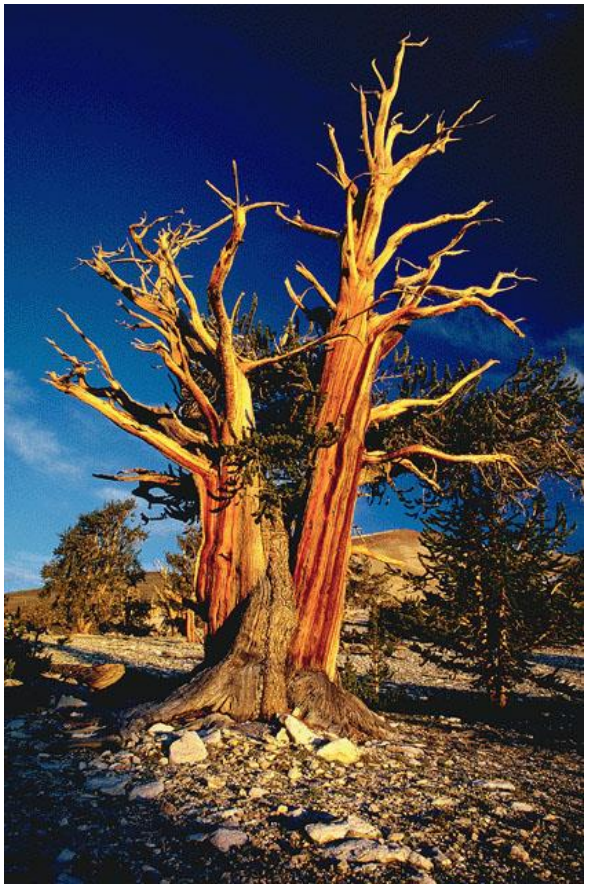
Bdelloids: No sex for over 40 million years
***Science News* 2000**



“Methuselah” – 4767 years old

Part I: The evolution of senescence

The official world record for the oldest human: 122 years, 164 days -- Jeanne Calment of France 113'th birthday party



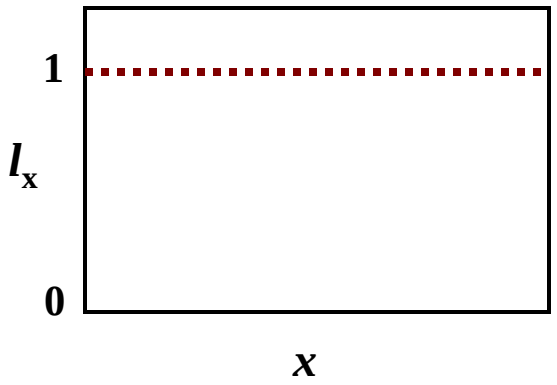
Semi-official world record for oldest organism: "Methuselah" at 4,767 years.

What is senescence?

Senescence – The late-life decline in an individuals fertility and probability of survival that occurs in all organisms in which germ cells and somatic cells are distinct.

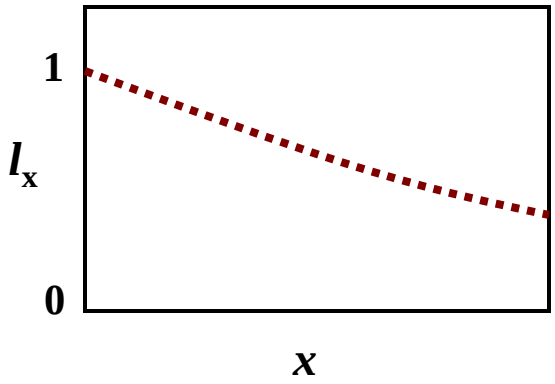
Why not live forever?

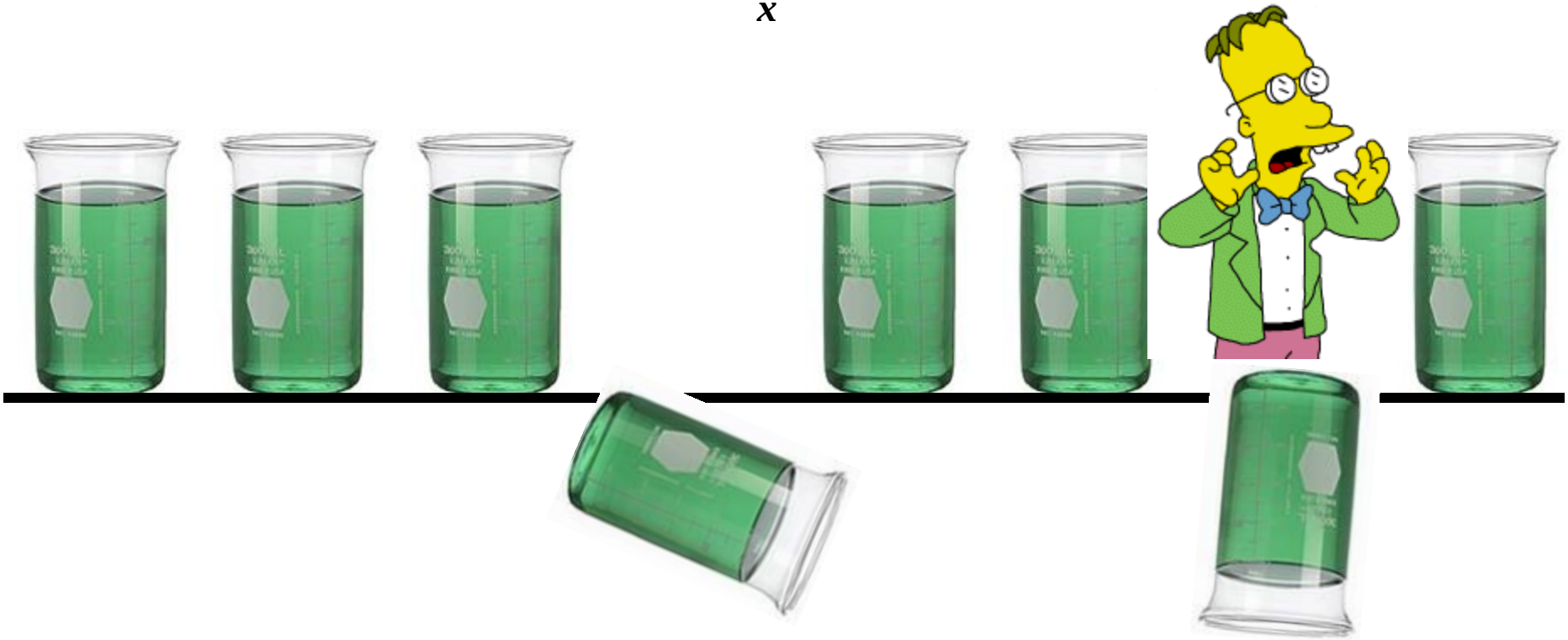
All else being equal, living forever would certainly maximize lifetime fitness!



$$R_0 = \sum l_x m_x = \infty$$

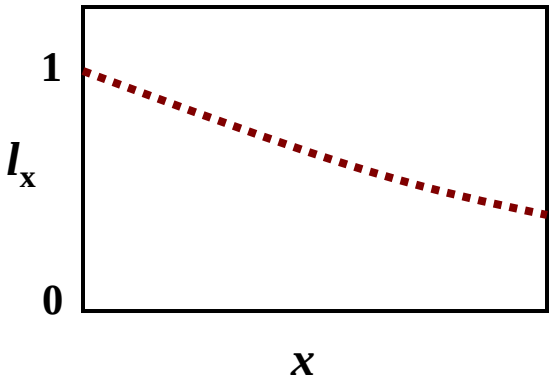
Even organisms that don't age "die"!





This is true even for real organisms

Even if an organism could live forever… it wouldn't!



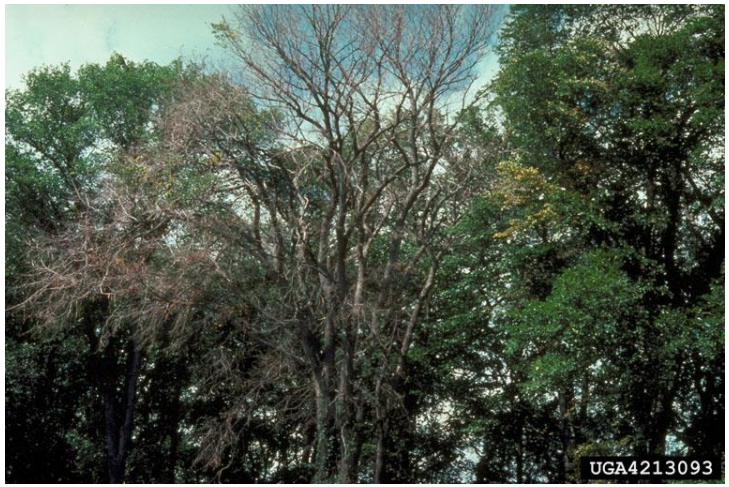
WHY?

Predation

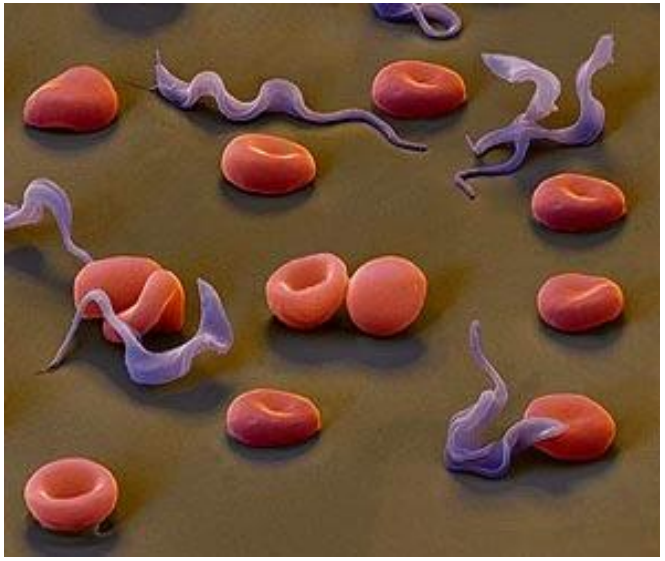
Crab spider eating skipper

Tobacco hornworm with parasitoids

Disease/Parasitism



Dutch elm disease
(*Ophiostoma ulmi*)

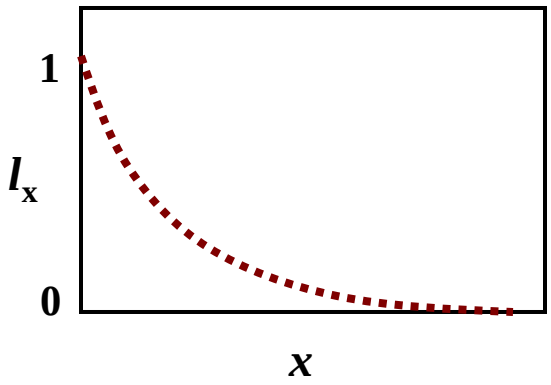


Trypanasoma brucei

Random chance

https://www.youtube.com/watch?v=8bS4fOHzN1U#t=10

What are the consequences of this result?



$$R_0 = \sum l_x m_x$$

An individuals 'reproductive value', R_0, declines with age because FUTURE reproduction is DISCOUNTED by mortality

A numerical example

(60% survive in every generation)

What is the reproductive value, R_0, of an individual of age 1?

x	l_x	m_x	$l_x m_x$
0	1.000	0.00	0.000
1	0.600	0.00	0.000
2	0.360	1.00	0.360
3	0.216	1.00	0.216
4	0.130	1.00	0.130
5	0.078	1.00	0.078
6	0.047	1.00	0.047
7	0.028	1.00	0.028
8	0.017	1.00	0.017
9	0.010	1.00	0.010
10	0.006	1.00	0.006

$$R_0(1) = 0 + .360 + .216 + .130 + .078 + .047 + .028 + .017 + .010 + .006 = .892$$

A numerical example

x	l_x	m_x	$l_x m_x$
0	1.000	0.00	0.000
1	0.600	0.00	0.000
2	0.360	1.00	0.360
3	0.216	1.00	0.216
4	0.130	1.00	0.130
5	0.078	1.00	0.078
6	0.047	1.00	0.047
7	0.028	1.00	0.028
8	0.017	1.00	0.017
9	0.010	1.00	0.010
10	0.006	1.00	0.006

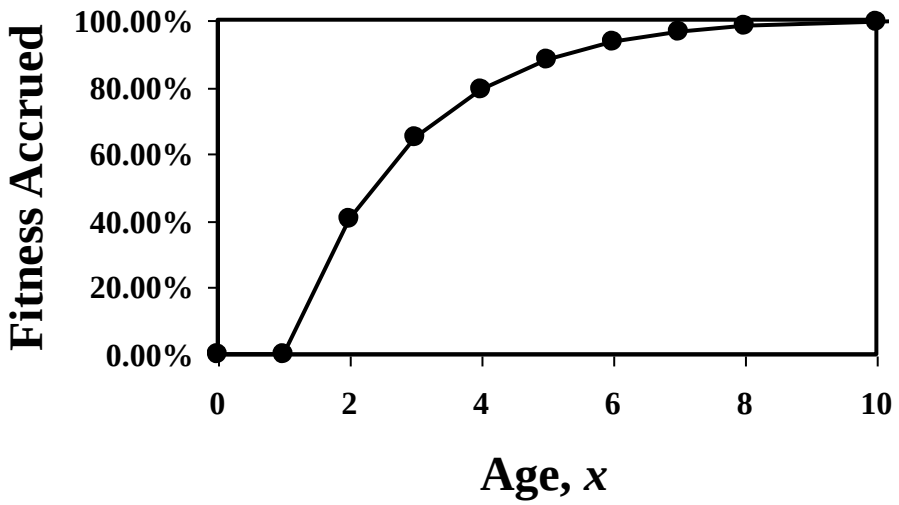
What is the reproductive value, R_0, of an individual of age 6?

$$R_0 = .047 + .028 + .017 + .010 + .006 = .108$$

Why does it matter if R_0 decreases with age?

- **The number of offspring an individual produces, R_0, is a measure of its lifetime fitness**

- **As a consequence, by age *x*, an individual has already accrued R_x/R_0 of its lifetime fitness**



As a result, the strength of natural selection declines with advancing age

This leads to two evolutionary theories of aging

• **Mutation accumulation –** Deleterious mutations that affect later age classes accumulate to higher frequencies in populations than do mutations acting on earlier age classes because selection against them is weak (Medawar, 1952)

• **Antagonistic pleiotropy –** New mutations with beneficial effects in early age classes tend to accumulate even though these same mutations have deleterious effects in later age classes (Williams, 1957)

Mutation accumulation

Imagine a new mutation arises that causes death at age 9

x	l_x	m_x	$l_x m_x$
0	1.000	0.00	0.000
1	0.600	0.00	0.000
2	0.360	1.00	0.360
3	0.216	1.00	0.216
4	0.130	1.00	0.130
5	0.078	1.00	0.078
6	0.047	1.00	0.047
7	0.028	1.00	0.028
8	0.017	1.00	0.017
9	0.000	1.00	0.000
10	0.000	1.00	0.000

Mutation causes early death here

As a result, R_0 decreases from .892 to .876

Because this represents very little change in R_0 this deleterious mutation will not be efficiently removed by selection

Antagonistic pleiotropy

Imagine a new mutation arises that leads to early fertility, but causes death at age 6

Mutation causes early maturation here

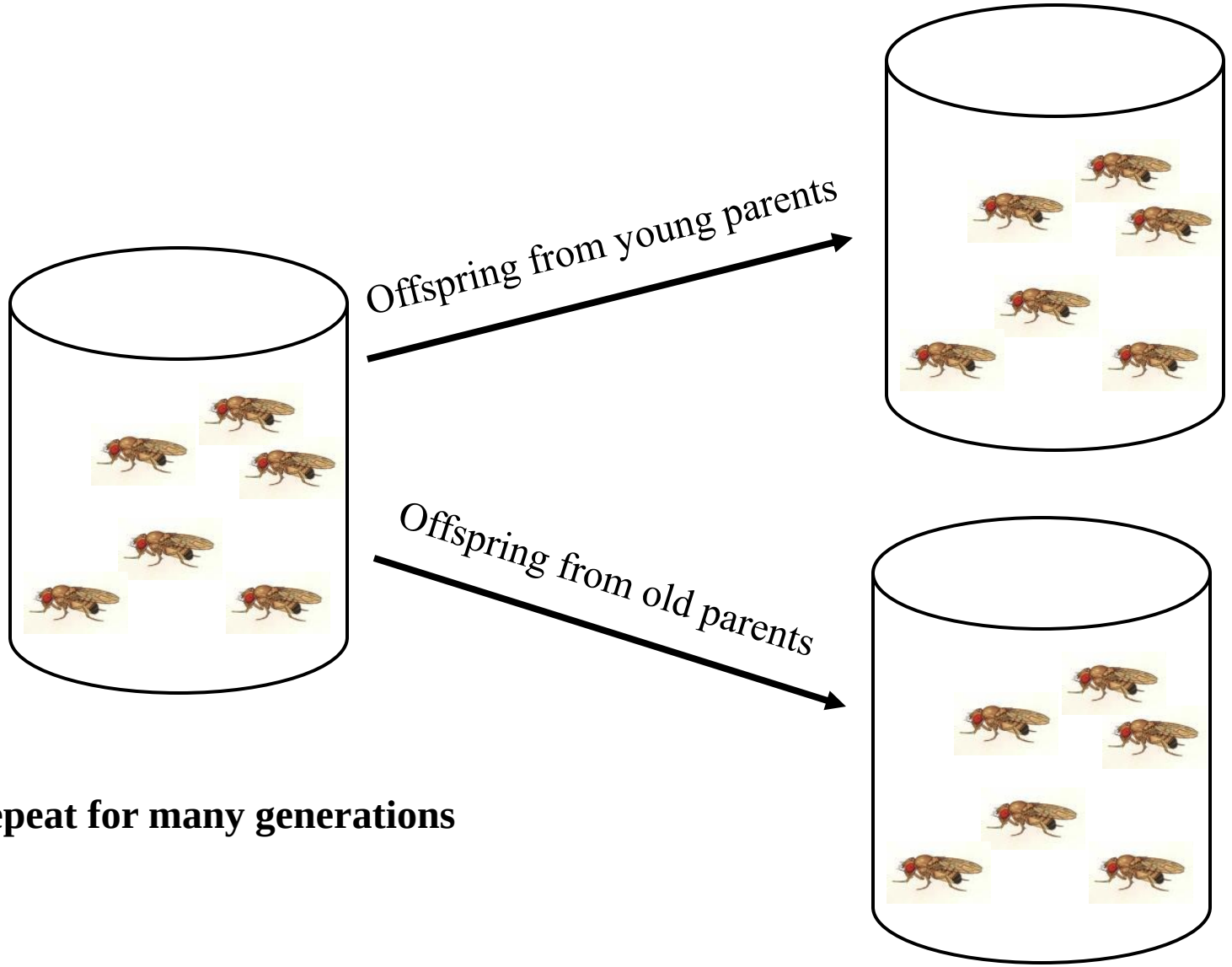
Mutation causes early death here

x	l_x	m_x	$l_x m_x$
0	1.000	0.00	0.000
1	0.600	1.00	0.600
2	0.360	1.00	0.360
3	0.216	1.00	0.216
4	0.130	1.00	0.130
5	0.078	1.00	0.078
6	0.000	1.00	0.000
7	0.000	1.00	0.000
8	0.000	1.00	0.000
9	0.000	1.00	0.000
10	0.000	1.00	0.000

As a result, R_0 actually INCREASES from .892 to 1.384

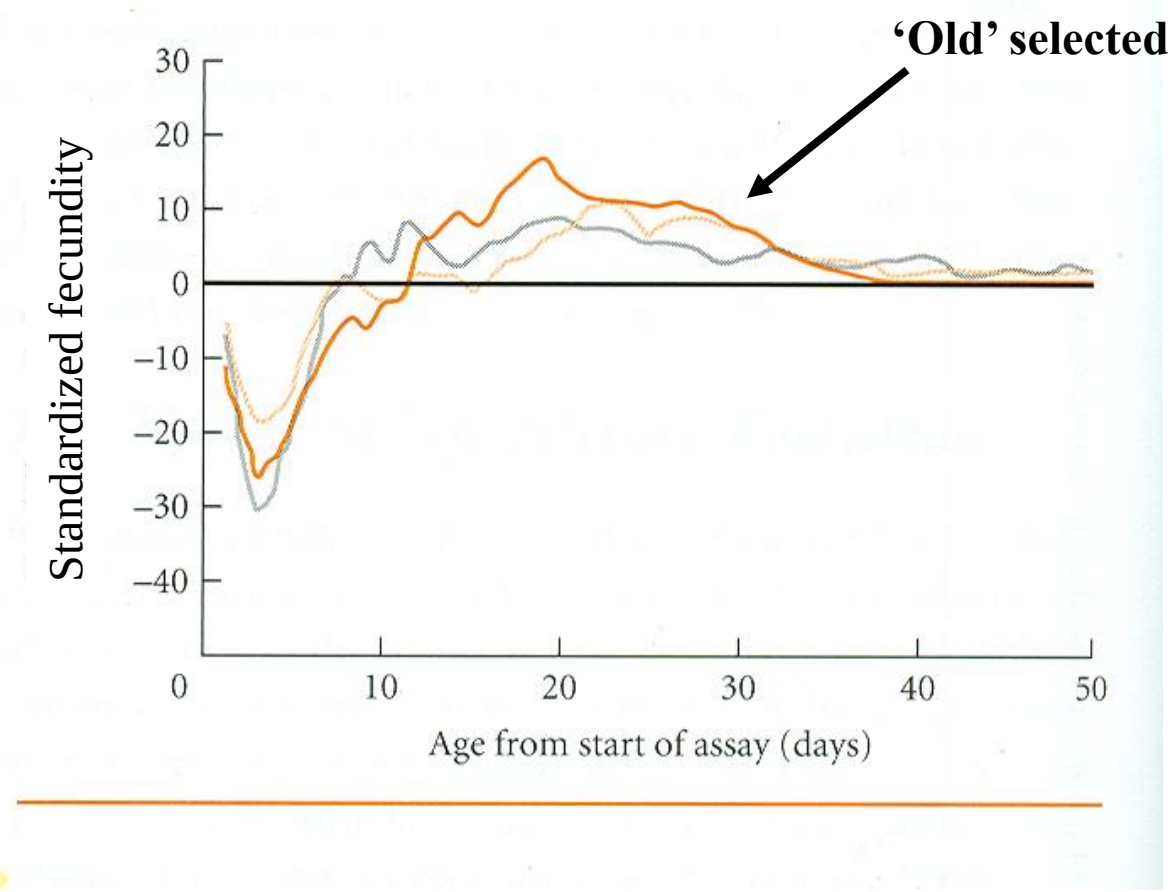
Because this mutation increases fitness, this mutation is likely to reach a high frequency, even though it shortens life.

An experimental test of senescence theory



Repeat for many generations

The result



The 'Old' selected lines have low fecundity in early age classes. Natural selection for increased early reproduction would therefore lead to a decline in later reproduction and fecundity, consistent with the AP hypothesis

From Rose (1984)

So why do we age?

- **Some empirical evidence supports the antagonistic pleiotropy model**
- **Some empirical evidence supports the mutation accumulation model**
- **These models are NOT mutually exclusive**
- **Suggests that both are important for the evolution of senescence**

Practice Problem

A group of researchers was interested in understanding the mechanisms underlying senescence in *Drosophila*. To this end, they established 10 experimental populations. Five of these experimental populations were selected for longevity by allowing only those flies which lived for more than 20 days to breed. The other five experimental populations were selected for early fertility by using the offspring of the first 5% of flies to reproduce to start the next generation. All ten of these experimental populations were propagated for 20 generations. At the end of the experiment, life tables were estimated for the flies in each type of treatment.

Early Selected		
x	lx	mx
1	1	0
2	1	1.2
3	0.95	1.3
4	0.85	1.6
5	0.79	1.8
6	0.76	2.1
7	0.58	2.1
8	0.49	2.0
9	0.38	1.9
10	0.35	1.6
11	0.32	1.4
12	0.21	1.1
13	0.16	0.8
14	0.11	0.3
15	0.03	0.0
16	0.0	0.0
17		
18		
19		
20		
21		
22		
23		
24		
25		
26		
27		

Late Selected		
x	lx	mx
1	1	0
2	1	0
3	1	0
4	1	0
5	1	0
6	1	0
7	0.98	0
8	0.95	0
9	0.94	0
10	0.89	0
11	0.85	0
12	0.84	0
13	0.82	0
14	0.79	0
15	0.75	0
16	0.74	0
17	0.71	0.56
18	0.68	0.78
19	0.65	0.81
20	0.59	1.06
21	0.54	1.25
22	0.49	1.80
23	0.46	2.02
24	0.38	1.84
25	0.29	1.56
26	0.18	1.0
27	0.0	0.0

Which theory for the evolution of senescence does this data support?

Part II: Why have sex?

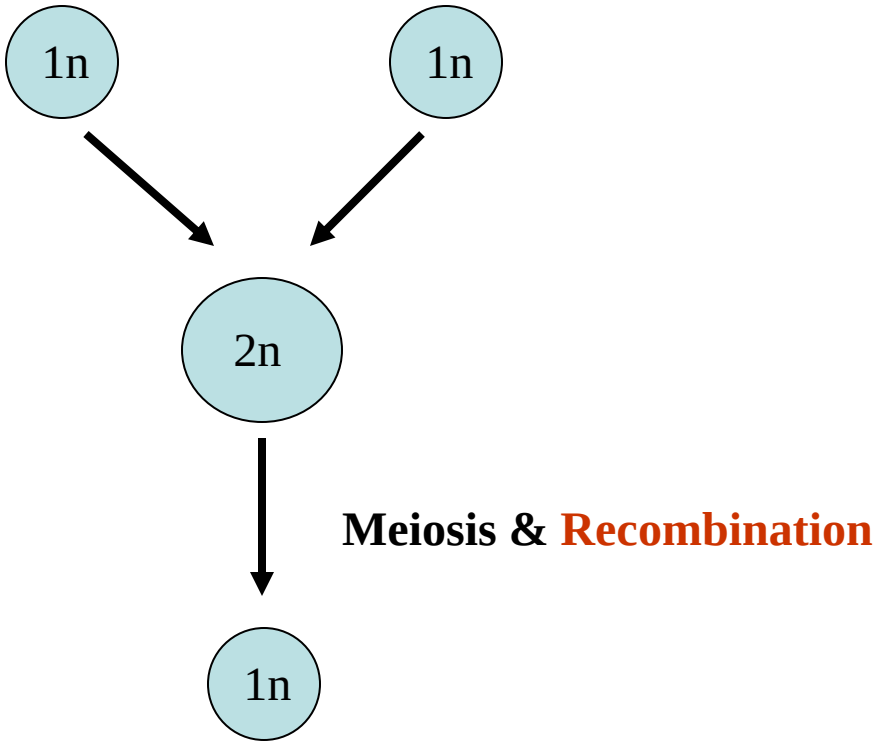
Bdelloids: No sex for over 40 million years
***Science News* 2000**

***Heuchera*: Sex everyday**

What is sex?

For the purposes of this class at least…

Sex is the union of two genomes, usually carried by gametes, followed at some later time by reduction, ordinarily through the process of meiosis



The disadvantages of sex

1. **Recombination breaks apart co-adapted gene complexes**

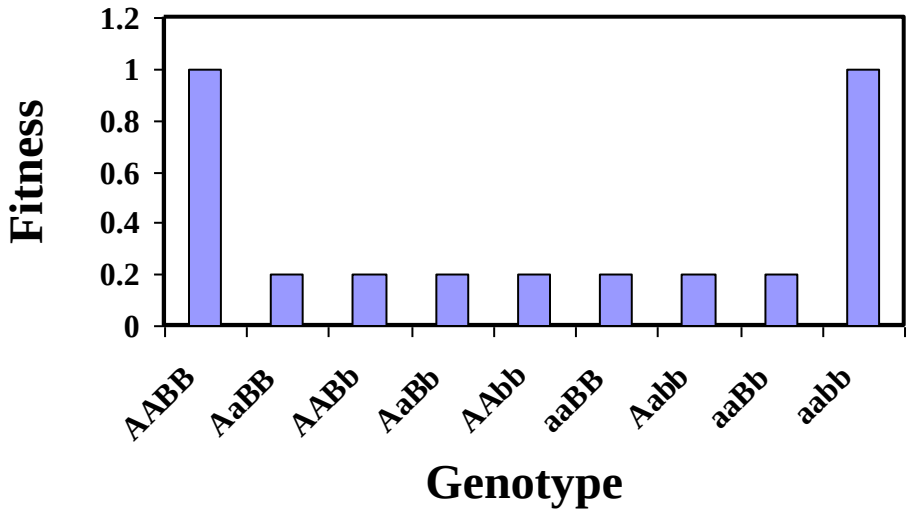
AB X ab → AB ab & Ab aB

Combinations favored by N.S.

Combinations disfavored by N.S.

2. **Sex requires males**

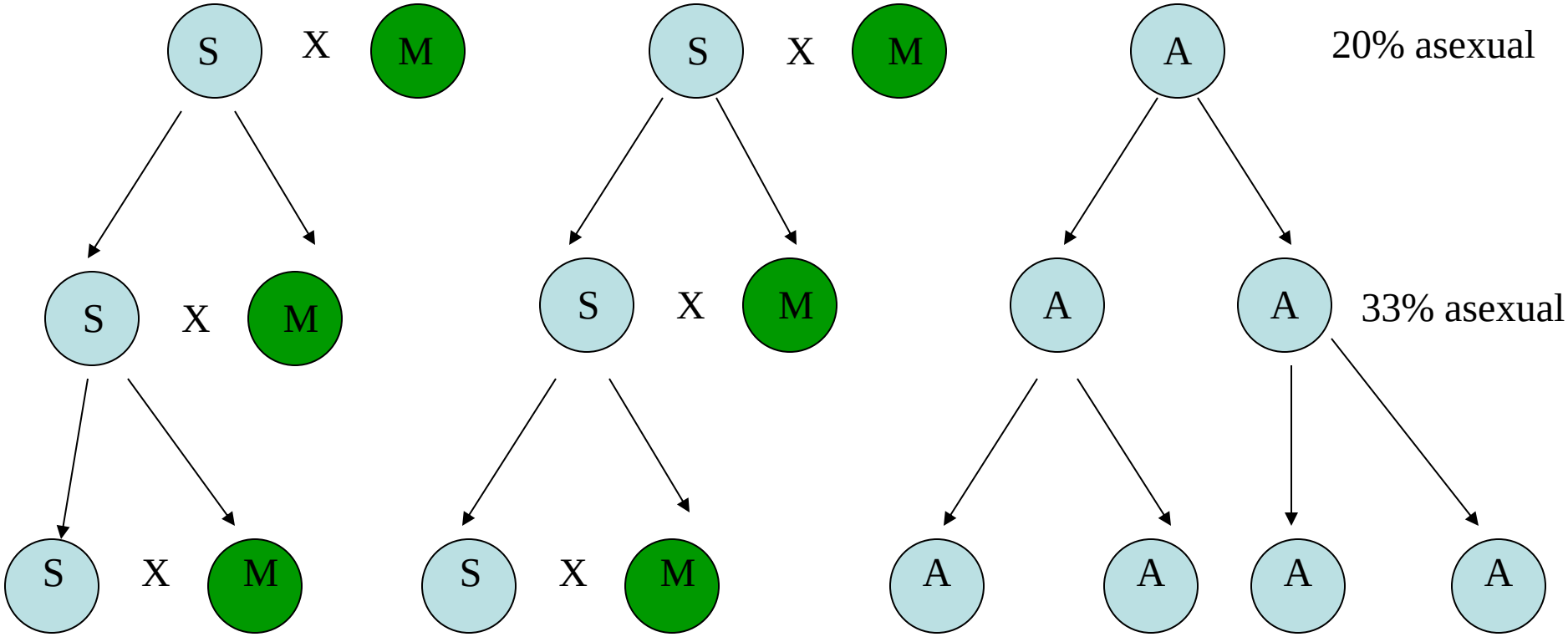
Sex breaks apart co-adapted gene complexes



- In a clonal population (i.e. no sex) only AABB and aabb genotypes would persist

- In a sexual population, however, recombination would continually re-generate the other less fit genotypes

Sex requires males



After just two generations the frequency of asexuals has increased from 20% to 50%!

And yet, the vast majority of eukaryotes are sexual

WHY?

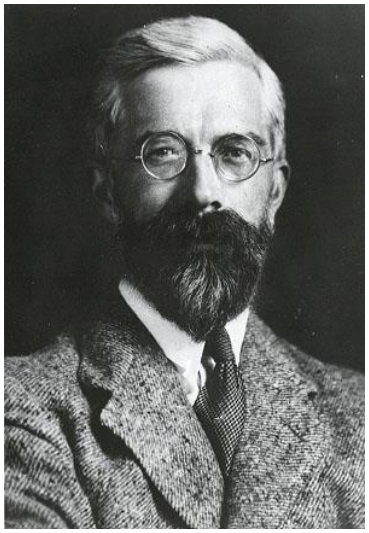
Hypotheses for the advantage of sex

• Fixation of rare beneficial mutations – Sex and recombination brings beneficial mutations that arise in different genomes together.

• Muller's ratchet – Sex and recombination allows deleterious mutations to be more efficiently purged from the genome.

• The Red Queen – Sex and recombination generate new combinations of genes to which parasites are not adapted

Fixation of rare beneficial mutations

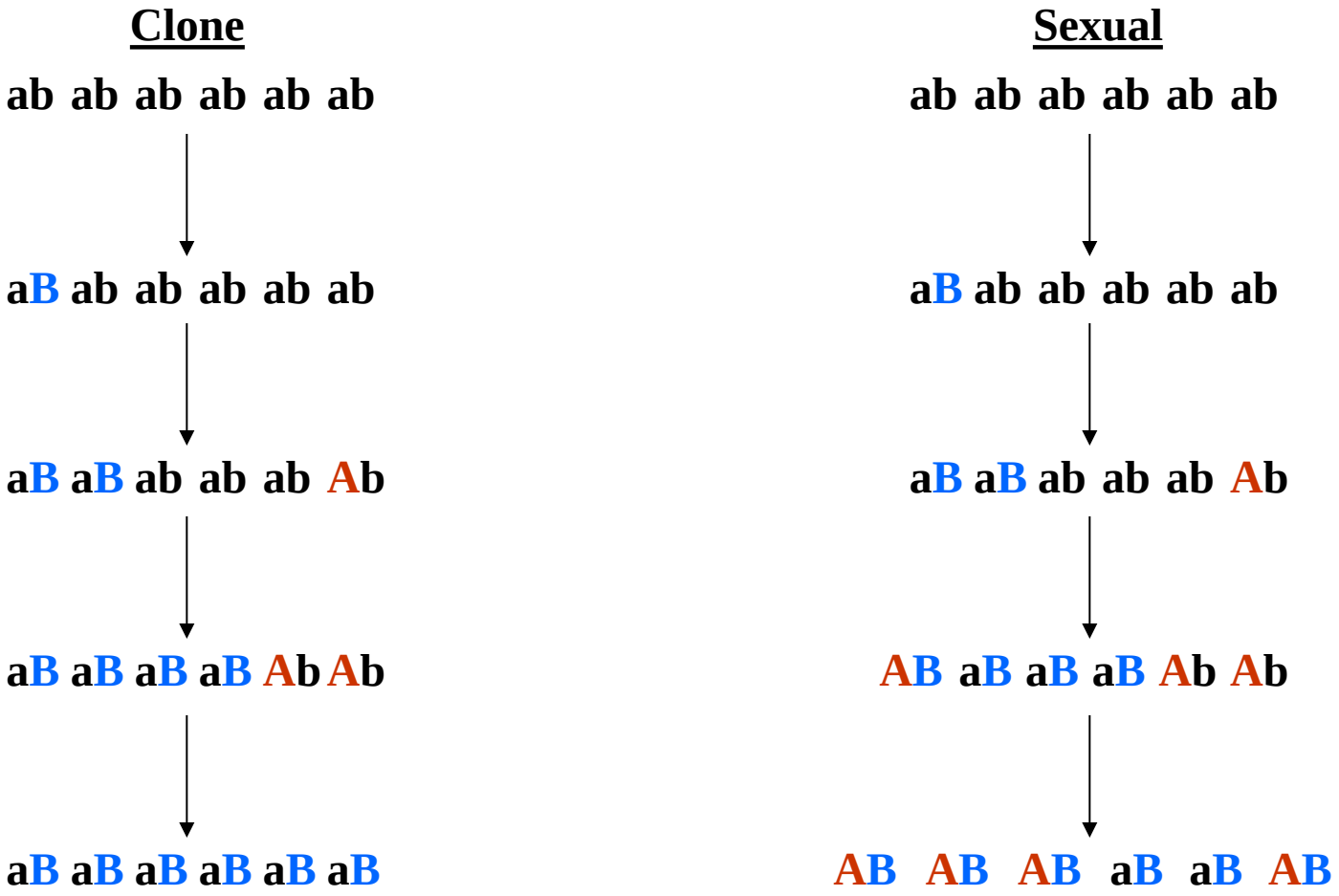


“For, unless advantageous mutations occur so seldom that each has had time to become predominant before the next appears, they can only come to be simultaneously in the same gamete by means of recombination.”

- R. A. Fisher (1930)

Fixation of rare beneficial mutations

(In finite populations: The Hill-Robertson effect)



The beneficial A mutation was lost

Both beneficial mutations remain

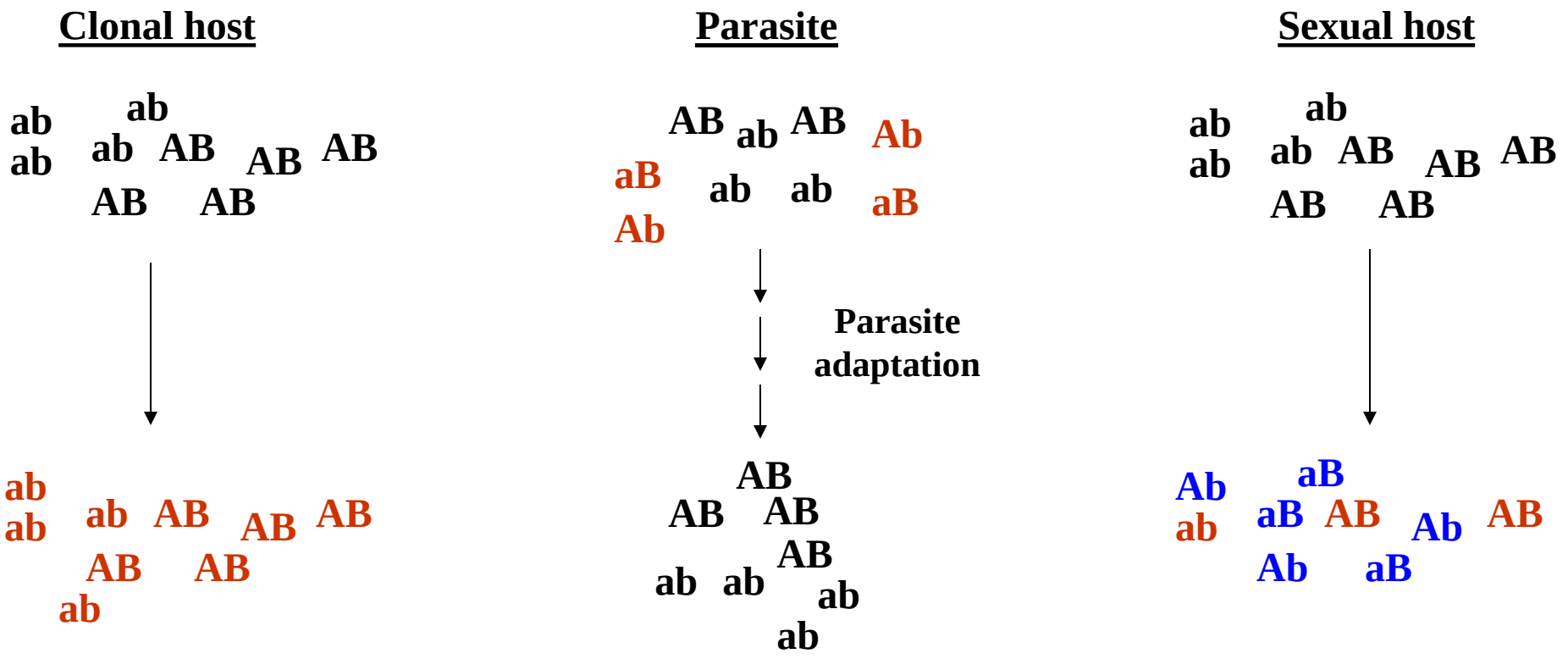
The Red Queen

• All species are continually assaulted by a variety of parasites

• These parasites are continually adapting to the host population

• Sex and recombination may allow the host to produce genetically novel offspring to which the parasites are not adapted

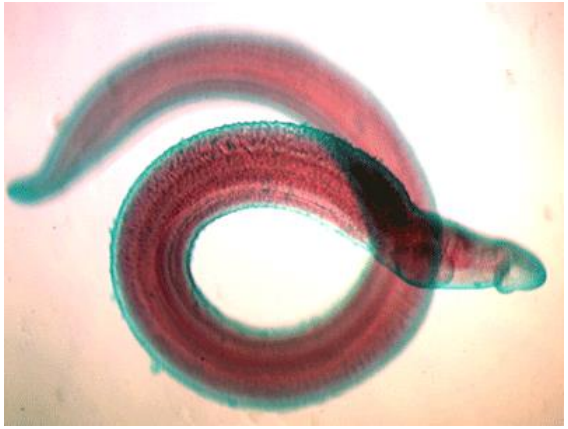
The Red Queen



The Red Queen and some famous snails

Some random lake in New Zealand where this snail lives

Potamopyrgus antipodarum



A castrating trematode

The Red Queen and some famous snails

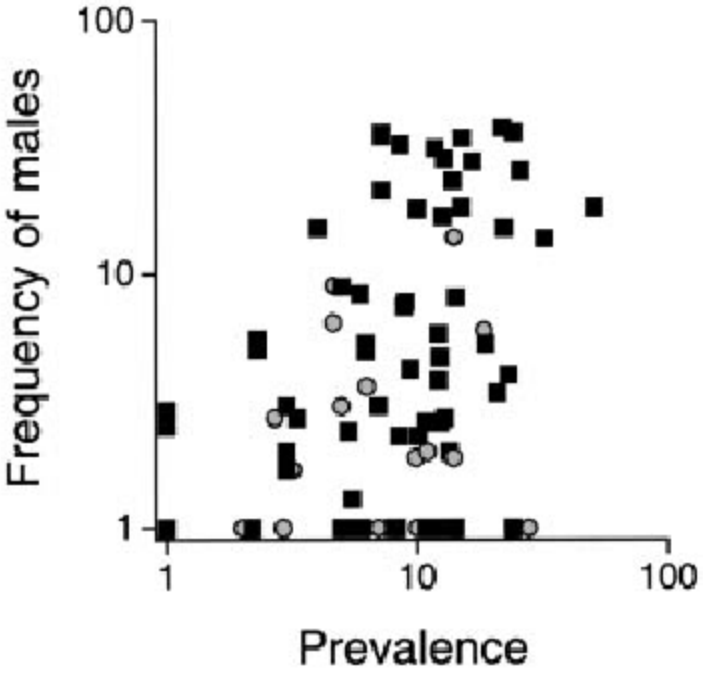


Fig. 4. Relationship between prevalence of infection by trematodes and the frequency of males for 95 populations of the freshwater snail, *P. antipodarum*. Squares represent lake populations (from Lively, 1992); circles represent stream populations (from Lively, 1987).

Lively (2001)

So why do we have sex?

- **The red queen hypothesis:**

  May be important for some groups of organisms, but is not likely to be the general explanation for why so many species have so much sex

- **Hill-Robertson effect:**

  Currently the most likely explanation because it depends only on pervasive factors common to all populations:

  - Genetic drift

  - Advantageous mutations

Practice question

A group of researchers is attempting to evaluate support for the Red Queen Hypothesis. To this end, the researchers started 8 common garden experiments, each of which was initiated by planting 100 asexual and 100 sexual plants at random within a $100m^2$ plot. The researchers added the parasitic rust fungus to 4 of the 8 plots. After ten plant generations, the researchers recorded the proportion of sexual individuals in each plot. Their data is shown in the table below:

Rust fungus present?	Proportion sexual
Yes	0.74
Yes	0.77
Yes	0.66
Yes	0.69
No	0.17
No	0.21
No	0.23
No	0.19

Remember that you can calculate the value of the test statistic, t, using the following formula:

$$t = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\left(\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}\right)\left(\frac{n_1 + n_2}{n_1 n_2}\right)}}$$

and that a table of critical values for the t-distribution is available at the back of your exam (but since this really isn't an exam, just use the table in lab Module 2).

A. Do the data gathered in this study provide support for the Red Queen Hypothesis? Justify your response statistically and verbally.