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Genetics 453

Evolutionary Genetics

Evolution of Genetic Systems

Joe Felsenstein

Department of Genome Sciences
University of Washington, Seattle

email: joe@genetics.washington.edu

Evolution of the genetic system

How well various things have been explained

Very well

Sex ratios of 1/2 (R.A. Fisher, 1930, W. D. Hamilton, 1967)

Degeneration of Y chromosomes (B. Charlesworth, 1978; Orr, 1998)

Anisogamy and sexual dimorphism (Parker, Baker, and Smith, 1972)

Recombination
(Fisher, 1930; Muller, 1932; Sturtevant and Mather, 1938)

Diploidy

Mutation rates

Poorly

Some sex–determination systems

1) XX – XY

♀ \ ♂	X	Y
X	XX ♀	XY ♂
X	XX ♀	XY ♂

many dioecious angiosperms

many animal species

most vertbrates

2) ZW – ZZ

♂ \ ♀	Z	W
Z	ZZ ♂	ZW ♀
Z	ZZ ♂	ZW ♀

some flatworms
" crustaceans
" insects especially
lepidopterans
diptera (some)
" some fish, amphibians, lizards
" most birds

Some more sex–determination systems

3) XX – XO

♀ \ ♂	X	O
X	XX ♀	XO ♂
X	XX ♀	XO ♂

many insects

4) XX – XY1Y2

♀ \ ♂	X	Y1Y2
X	XX ♀	XY1Y2 ♂
X	XX ♀	XY1Y2 ♂

e.g. the Muntjak deer

Some more sex−determination systems

5) Arrhenotoky (haplo−diploid sex determination)

♀ \ ♂	haploid	no sperm
haploid gametes	diploid ♀	haploid ♂

hymenoptera (ants, bees, wasps)
thysanoptera (thrips)
mites and ticks
rotifers

6) Environmental sex determination

more ♀♀ if	better nutrition	nematodes
	colder temperature	lizards, alligators
	hotter temperature	most turtles
	extreme temperatures	snapping turtles, crocodiles

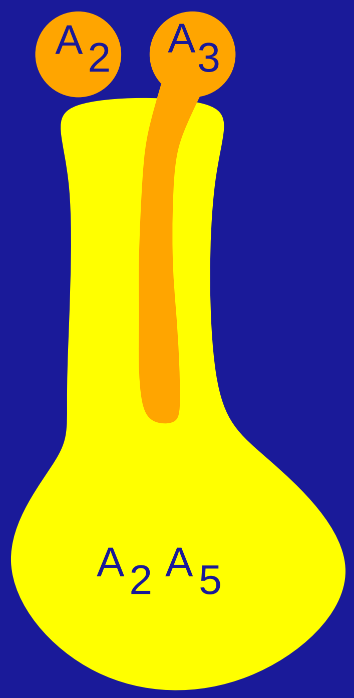
Yet more sex−determination systems

7) Sequential hermaphroditism
(start life as one sex, usually male, and switch later)

oysters, shrimp, some fish

8) Self−sterility systems

In some angiosperm plants, multiple alleles which allow pollen to succeed only if it does not contain any allele at that locus which is found in the female parent (gametophytic self−incompatibility) or the male does not contain any allele at that locus found in the female (sporophytic self−incompatibility)



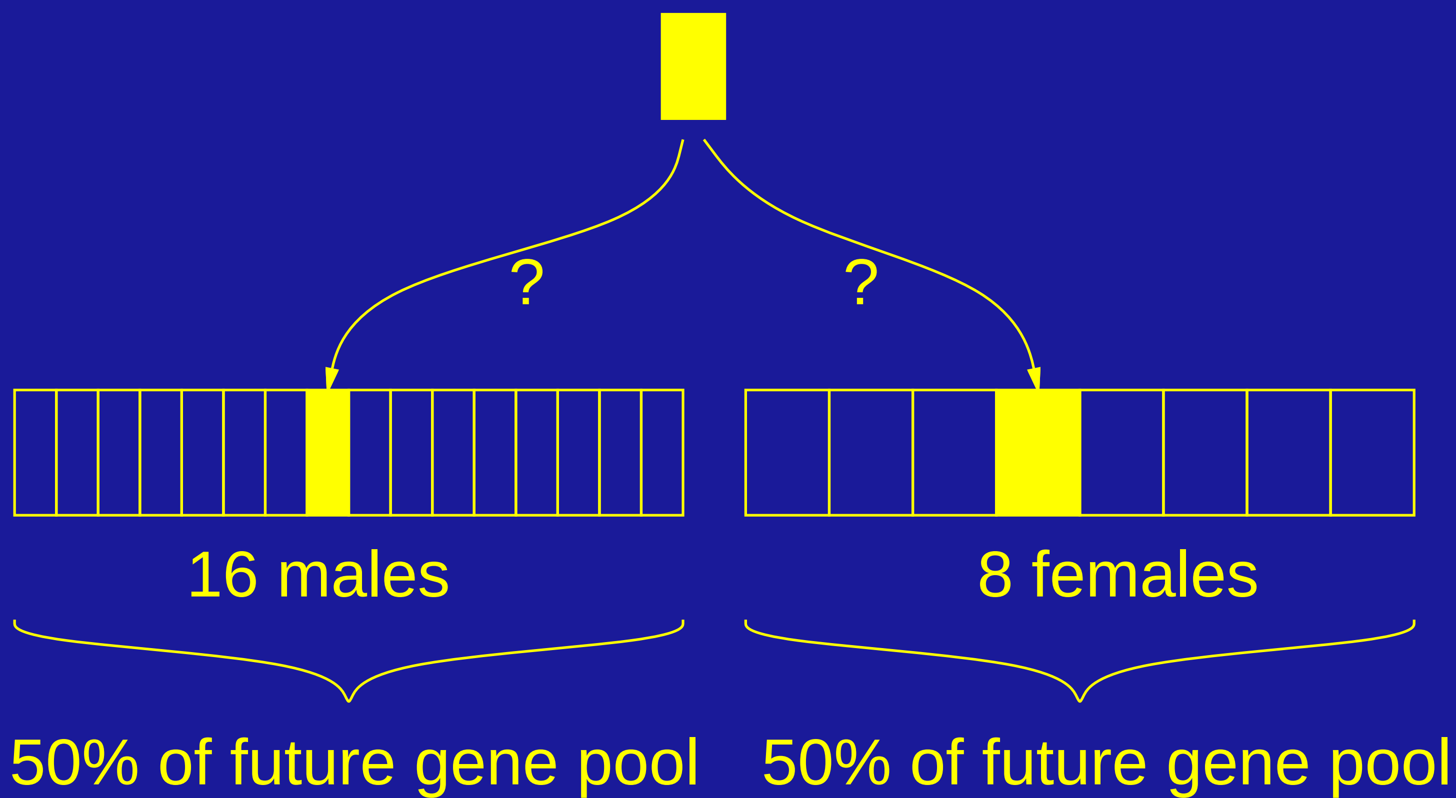
The Evolution of the Sex Ratio

In a work usually mistakenly attributed to R. A. Fisher (1930), Charles Darwin (*Descent of Man* (1871), 1st edition only) and Carl Düsing (1883 and 1884) put forward the modern theory of why sex ratios tend to be 1:1:

> The females as a whole and the males as a whole contribute equally to the next generation, and to the ancestry of all future generations. If one sex is in short supply, an individual will contribute more to the future gene pool if it is of that sex (as then it is a bigger fraction of that half of the gene pool).

Düsing, C. 1884. *Die Regulierung des Geschlectsverhältnisses bei der Vermehrung der Menschen, Tiere und Pflanzen.* Fischer, Jena.

Why an individual should "want" to be a member of the minority sex



Numerical Example

Consider an allele that affects the probability that its bearer is a female.

	females	males
aa	100,000	50,000
Aa	100	100

Frequency of A among everybody $= \dfrac{200}{300{,}400} = 0.00066578$

Frequency of the A allele (counting copies of genes)

among females $= \dfrac{100}{200{,}200} = 0.0004995$

among males $= \dfrac{100}{100{,}200} = 0.000998$

increase!

The frequency in the next generation is the average of
the frequency among males and the frequency among females: 0.00074875

When males are rare, a male offspring will have more descendants

When females are rare, a female offspring will have more descendants

A driven Y chromosome – a nightmare scenario

Suppose there is a Y chromosome that causes all offspring of a mating to be Y-bearing males, without reducing the total number of offspring. We then expect, if p of the males have this Y* chromosome: Males: $\frac{1}{2}(1-p_t)+p_t$ Females $\frac{1}{2}(1-p_t)$

and the frequency of the Y* chromosome among Y's should follow the equation:

$$p_{t+1} = \frac{p_t}{\frac{1}{2}(1-p_t)+p_t}$$

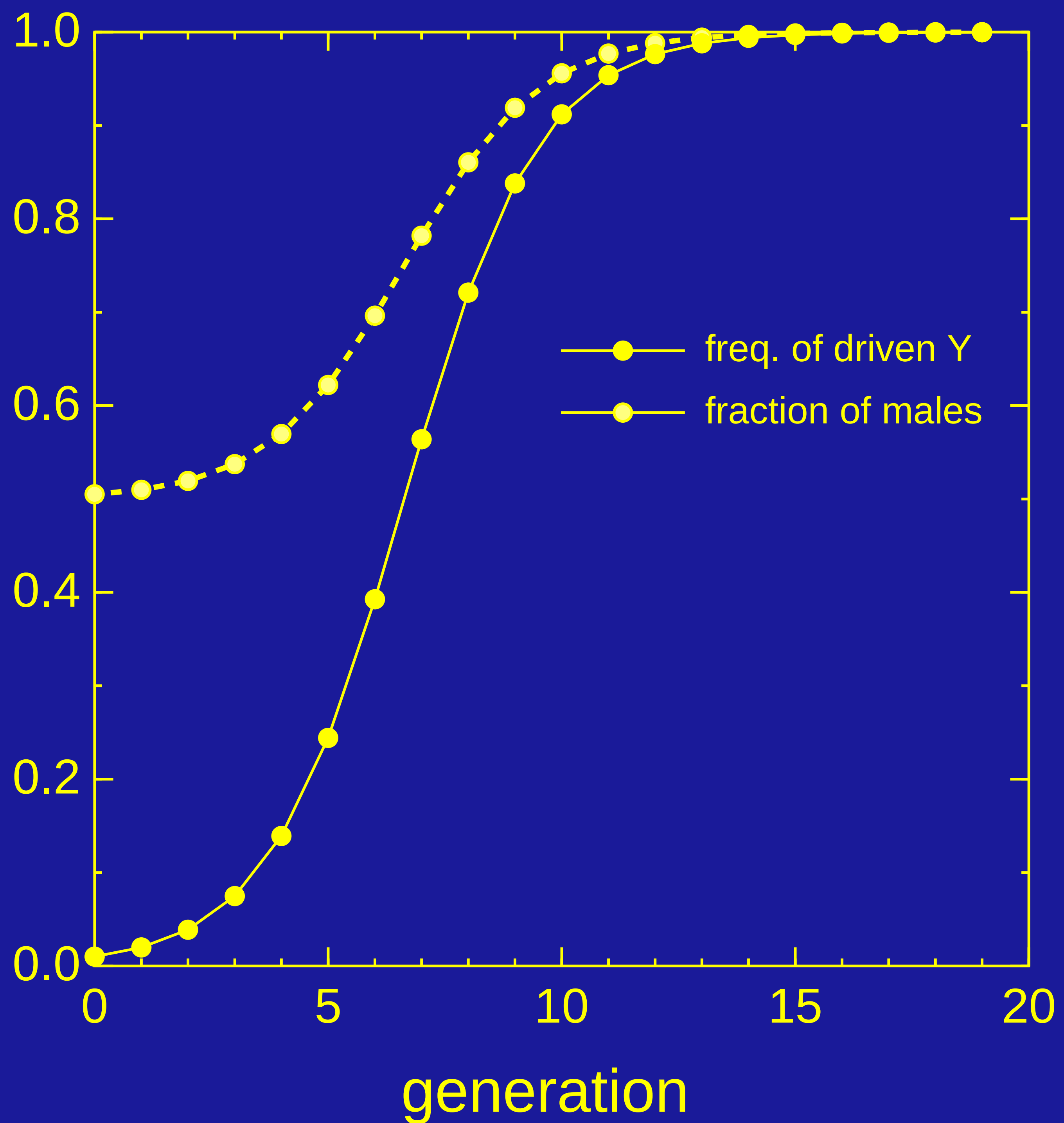
while the sex ratio among the offspring will be

$$\frac{\frac{1}{2}(1-p_t)}{\frac{1}{2}(1-p_t)+p_t}$$

Here are values, starting at 0.01 frequency of Y* among Y's:

generation	p_t	fraction of females
0	0.01	0.5
1	0.0198	0.495
2	0.03883	0.4901
3	0.07476	0.4805
4	0.13913	0.4626
5	0.24427	0.4304
6	0.39364	0.3779
7	0.56387	0.3037
8	0.72113	0.2181
9	0.83797	0.1394
10	0.91184	0.0810
11	0.95389	0.0441
12	0.97640	0.0231
13	0.98806	0.0118
14	0.99399	0.0059

The population is evolving its way to extinction!


1.0
0.8
0.6
0.4
0.2
0.0
0
5
10
15
20
generation
freq. of driven Y
fraction of males

Major Explanations for the Evolution of Recombination

1. It creates variation (East and Jones, 1919). Unfortunately it is easy to show that it destroys just as much variation, so this one doesn't even work.

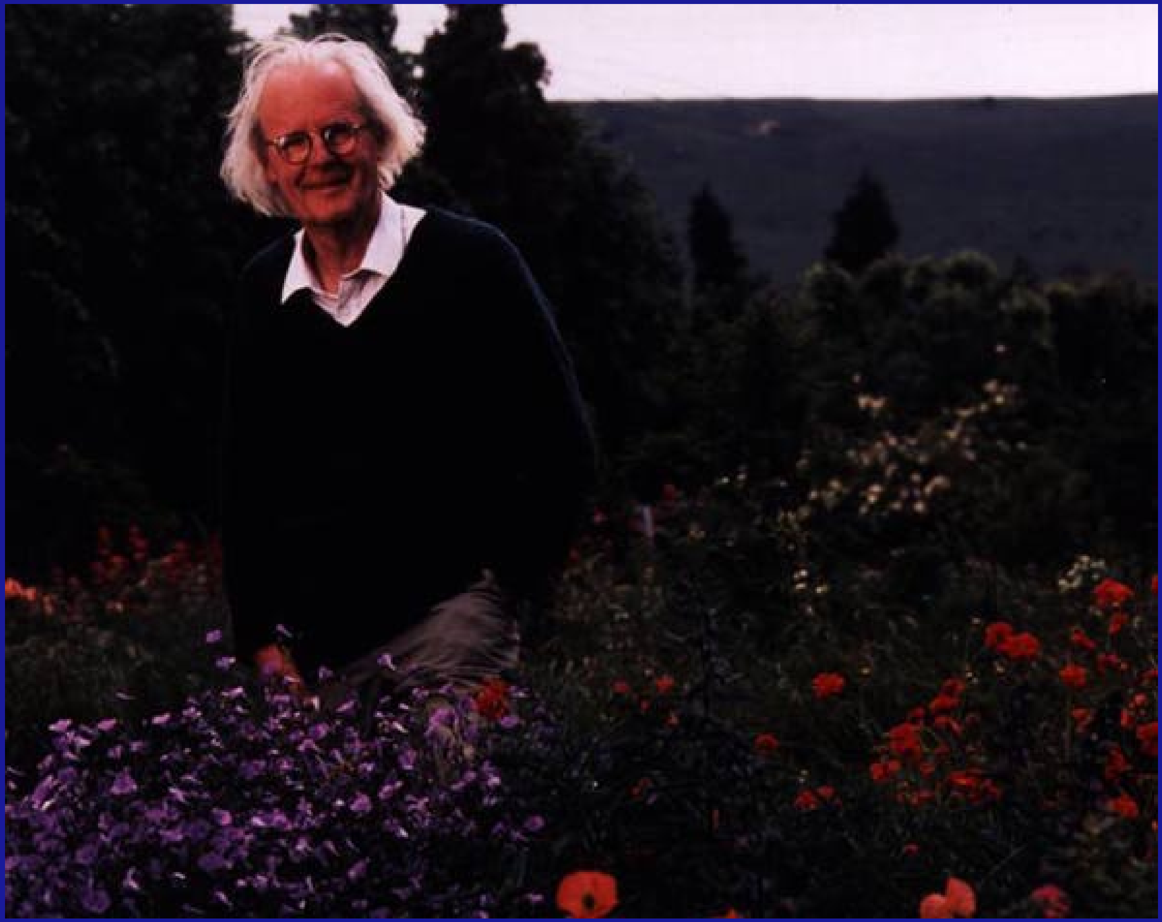
2. It breaks down random linkage disequilbrium which slows down response to selection (Fisher, 1930; Muller, 1932; Muller, 1958, 1964) Major variants:

   - Fisher and Muller's argument that recombination allows advantageous mutants to get into the same descendant.
   - "Muller's Ratchet", that recombination allows deleterious mutants at many loci to be eliminated even when haplotypes that have no deleterious mutants have been lost by genetic drift.

3. Sturtevant and Mather's (1938) argument that recombination helps the pattern of linkage disequilibrium change rapidly in response to changes in the pattern of multi-locus selection. This has been the basis of Hamilton's "parasites and sex" explanation.

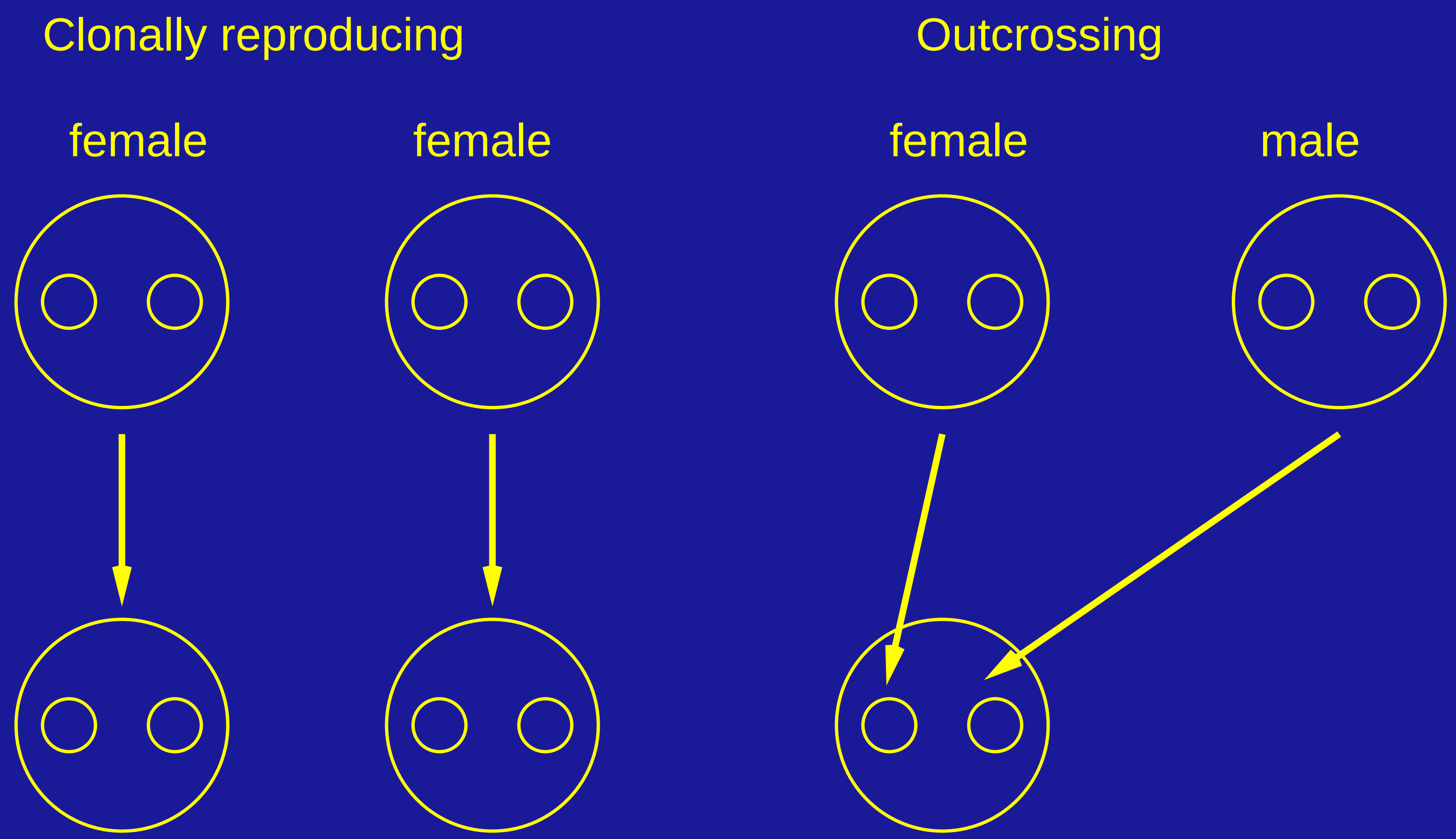
4. Michod and Bernstein's argument that recombination is not needed for long-term evolutionary reasons, but is a byproduct of a system for repairing double-stranded breaks in DNA.

Many other explanations reduce to one or another of these (e.g. Williams's "sibling competition" scenario or Bell's "tangled bank" scenario). They are in effect biological scenarios in which these combinations of evolutionary forces act.



John Maynard Smith

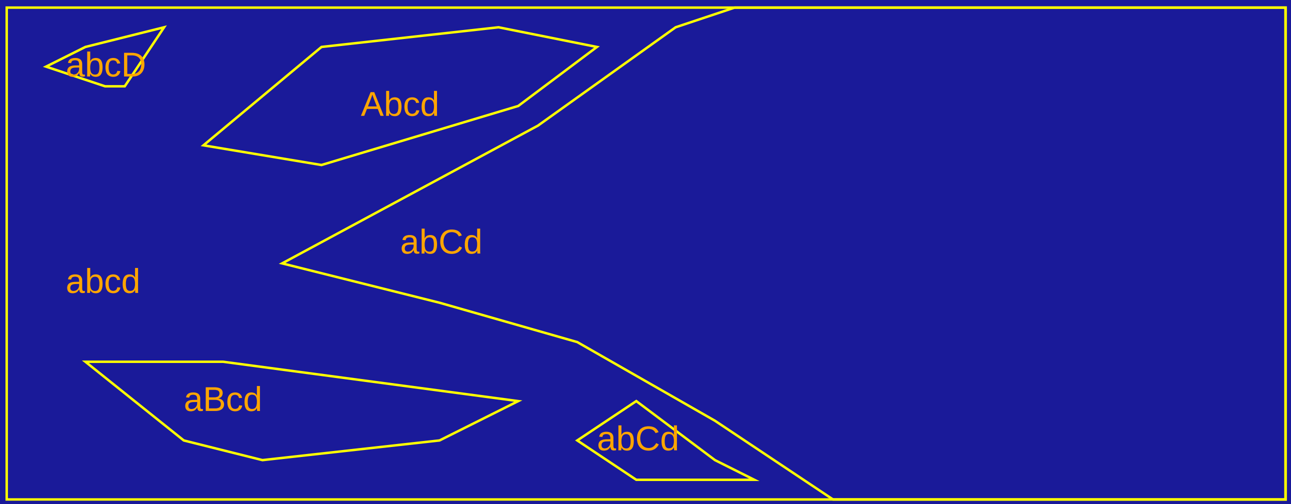
Maynard Smith's argument for the twofold cost of sex



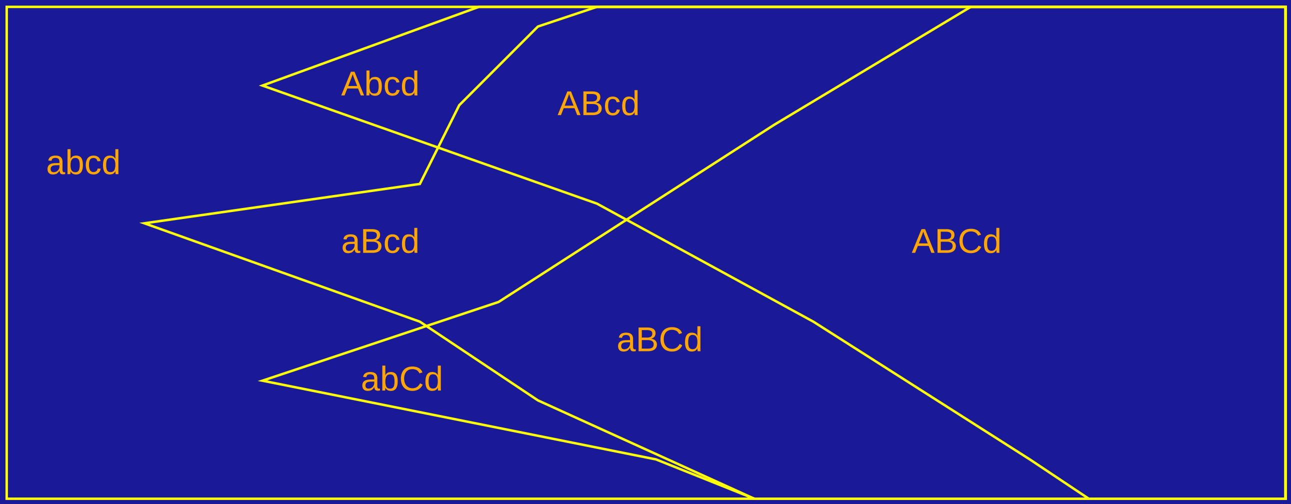
Fisher and Muller's mechanism for the evolution of "sex"

(i.e. really recombination with outcrossing)

no recombination

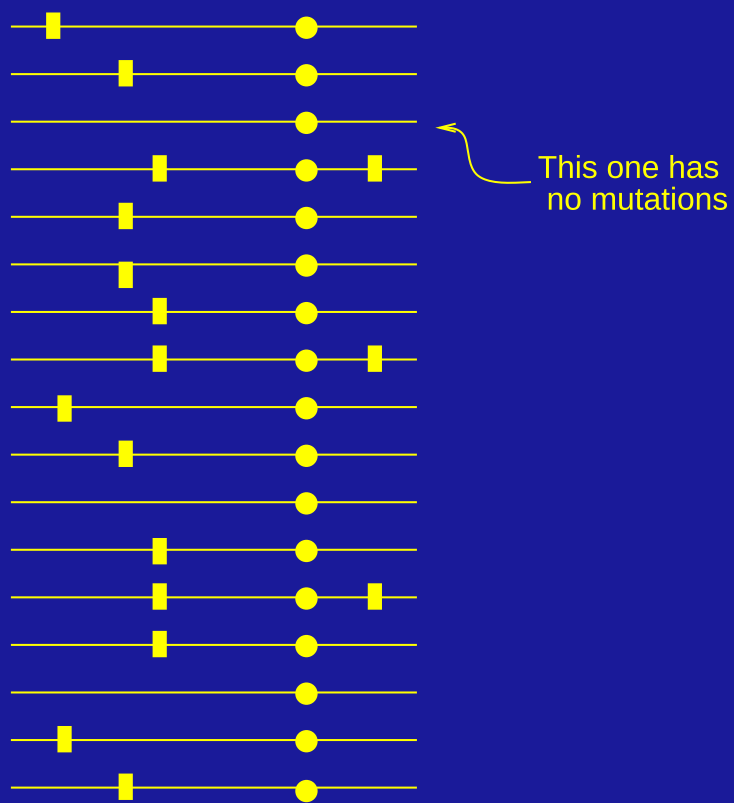


with recombination

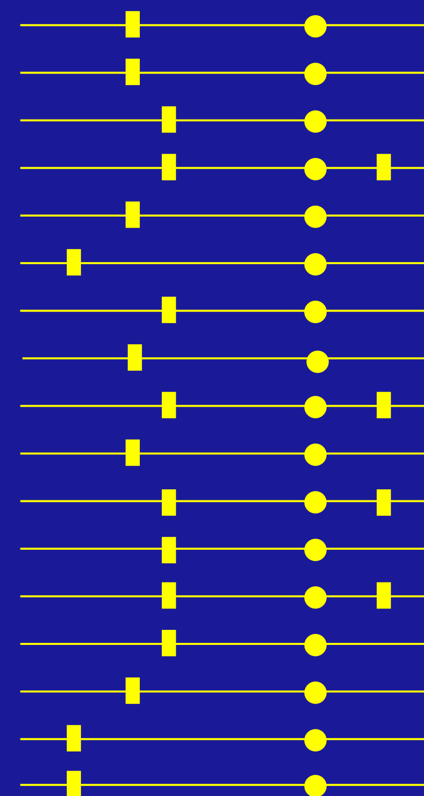


Muller's Ratchet (1958, 1964)

Suppose we have a population in which chromosome copies have deleterious mutations



Suppose genetic drift loses the chromosome(s) with no deleterious mutations:



The population can recover "wild−type" chromosomes by recombination.

Otherwise it has to wait for reverse mutation. The ratchet has moved one notch.

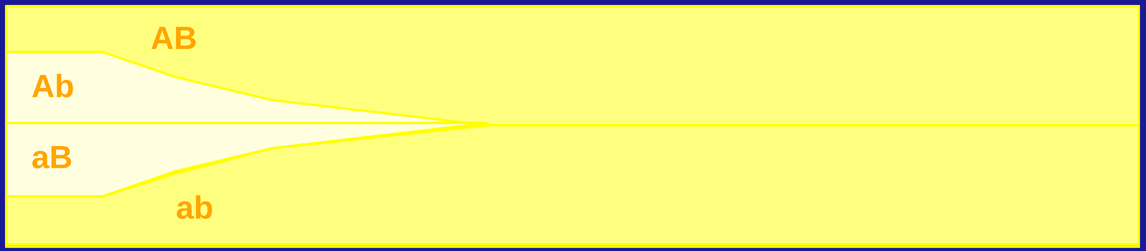
Gradually the mutations accumulate.

Sturtevant and Mather's theory of the evolution of recombination (1938. 1942)

Suppose that in one period the population favors haploid genotypes AB and ab:

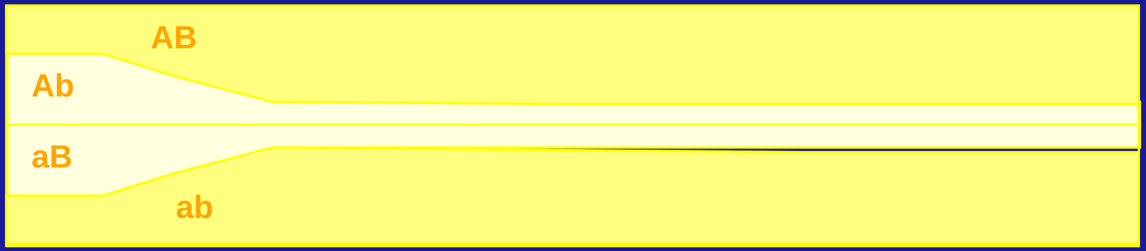
AB	1.0
Ab	0.9
aB	0.9
ab	1.0

Then the population will, if there is no recombination, become composed almost exclusively of AB and ab genotypes:



AB and ab haplotypes are eliminated by natural selection

but will not become so well–adapted if there is recombination:



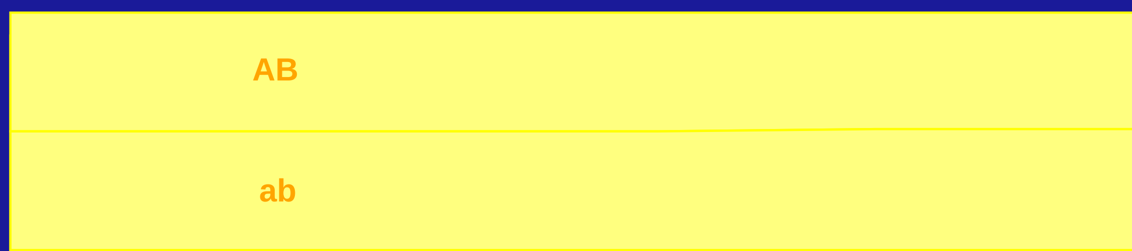
Ab and aB are continually produced by recombination in this case

Sturtevant and Mather's theory of the evolution of recombination (1938. 1942)

... but in another period soon after, selection favors Ab and aB:

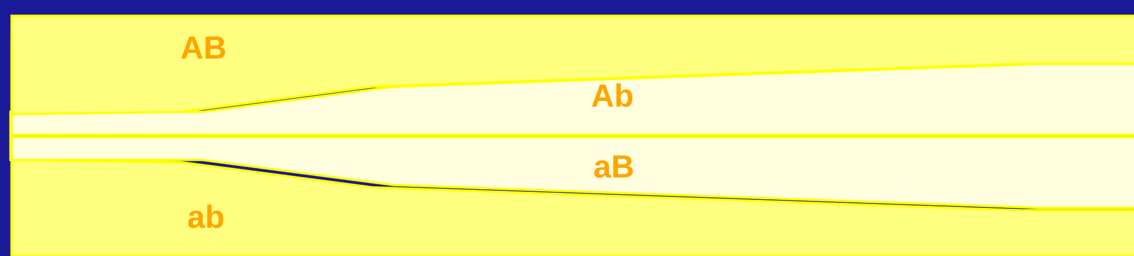
AB	0.9
Ab	1.0
aB	1.0
ab	0.9

the population without recombination will have a hard time getting Ab and aB



Ab and ab are not created by recombination in this case

but the case with recombination is better adapted during this period



Ab and aB are re−introduced by recombination in this case

Hamilton's scenario for the Sturtevant-Mather mechanism

or: "Sex and parasites"

Suppose there are two kinds of parasites:

Genotype	Parasite #1	Parasite #2
AB	grows	can't grow
Ab	can't grow	grows
aB	can't grow	grows
ab	grows	can't grow

Then when parasite #1 is widespread and Parasite #2 is rare, AB and ab are favored. Once they become common, Parasite #2 spreads and Parasite #1 declines.

Then Ab and aB are favored. As they become common Parasite #2 declines and Parasite #1 spreads.

This provides a biological scenario for the Sturtevant-Mather mechanism.

This freeware-friendly presentation prepared with

- Linux (operating system)
- PDFLaTeX (mathematical typesetting and PDF preparation)
- Idraw (drawing program to modify plots and draw figures)
- Adobe Acrobat Reader (to display the PDF in full-screen mode)

(except that we had to use Microsoft Windows to project this as the X server I have in Linux is not too great)