Evolution and the Genetics of Structured populations

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Outline

What is Evolution

Evolution and the Reductionist Approach

Fisher/Wright Controversy

Bringing the Fisher/Wright controversy into the 21st century

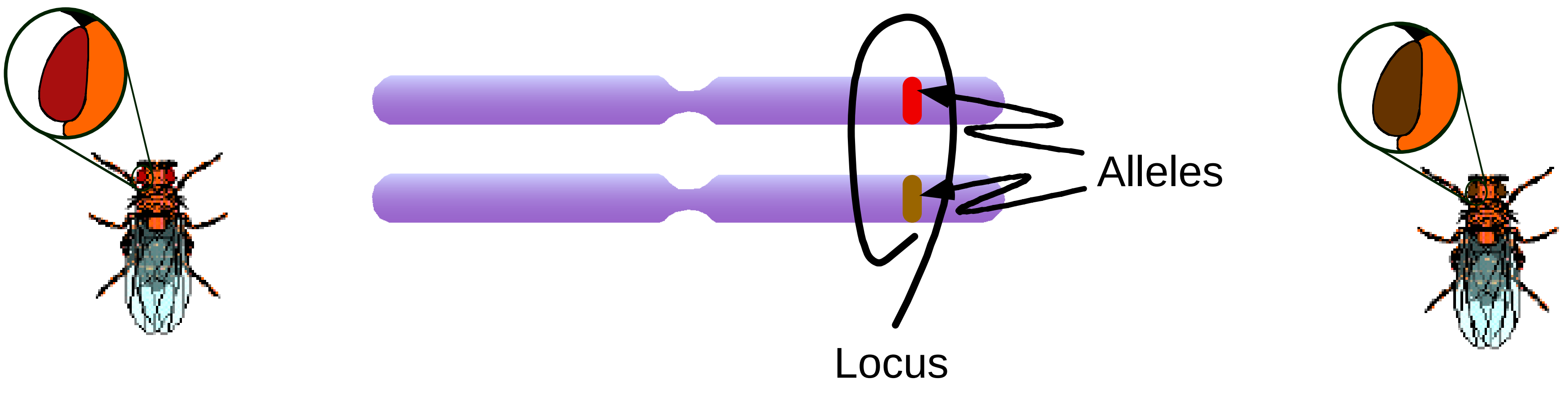
Some Definitions

Phenotype: The appearance of an individual

Genotype: the genetic makeup of an individual

Locus: A location on a chromosome coding for a particular characteristic, e.g., eye color

Allele: different chemical variants of a locus coding for different variations, e.g., brick eye color versus brown eye color



Evolution

One of the most frequently miss-defined concepts in biology

Wrong

Evolution [illegible] the changes that have transformed life on Earth from its earliest beginnings to the diversity that characterizes it today.

Campbell & Reece Biology

Evolution

Some Better Definitions

Evolution:

Descent with Modification

Darwin's term for evolution

Lasting change in the mean phenotype of a population that transcends the life of an individual

Futuyma, Evolutionary Biology

Change in gene Frequency

Several sources

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Evolution
and
Population Genetics

Evolution (usually) is change in gene frequencies

Population genetics is the study of genes in populations
is the study of changes in gene frequency

Population genetics is the study of evolution

(With apologies to those who study macro-evolution)

Most of Population Genetics is "Bean Bag" Genetics

Hardy, Weinberg, Castle Equilibrium

AA	Aa	aa
p^2	$2pq$	q^2

Response to Selection

$$p' = \frac{p + sq(hp + q)}{1 - 2hspq - sq^2}$$

Point: Single locus two alleles.

Williams' Principle of Parsimony

"In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice"

G.C. Williams
Adaptation and Natural selection

Williams on the Reduceability of Fitness

“No matter how functionally dependent a gene may be, and no matter how complicated its interactions with other genes and environmental factors, it must always be true that a given gene substitution will have an arithmetic mean effect on fitness in any population.”

G.C. Williams
Adaptation and Natural selection

Selection can be reduced to choices between alleles at a single locus.

The Reductionist Approach is a Powerful and and Essential Part of Scientific Research

However, it remains an approximation!

The question :

How good an approximation is it?

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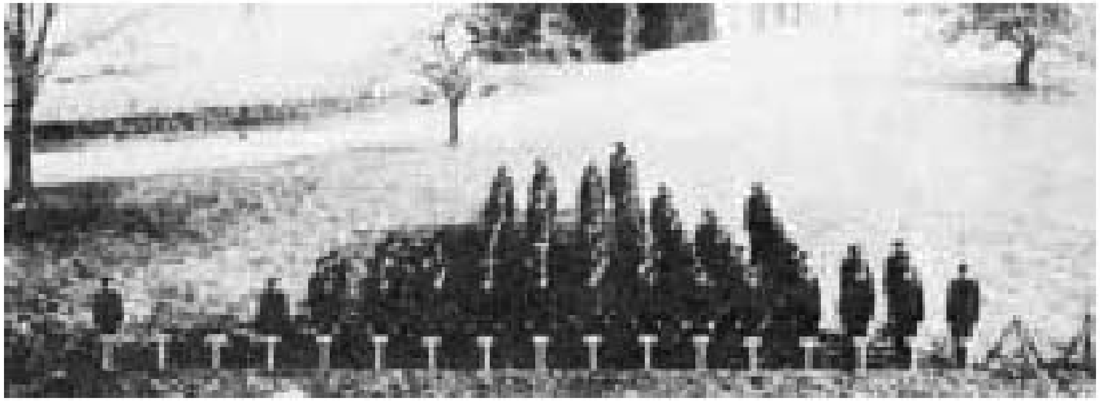
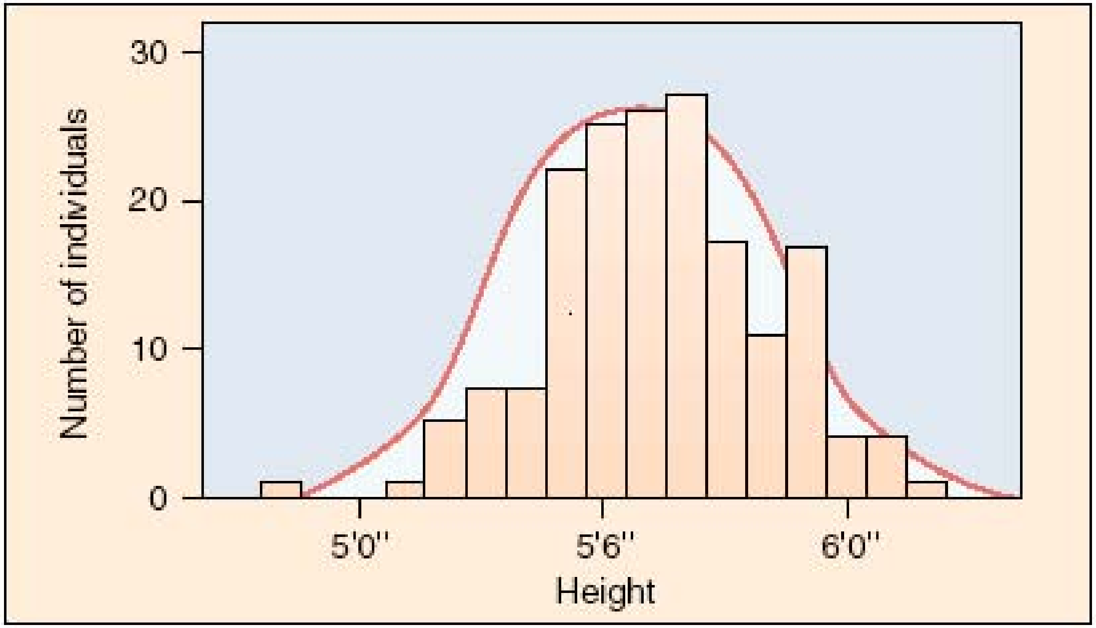
Real traits are more complex!
Connecticut Agricultural College Undergraduates, 1914





Sir Ronald Fisher
And Quantitative Genetics

Sir Ronald Fisher 1890-1962

Assumptions

Traits are determined by many loci of small effect

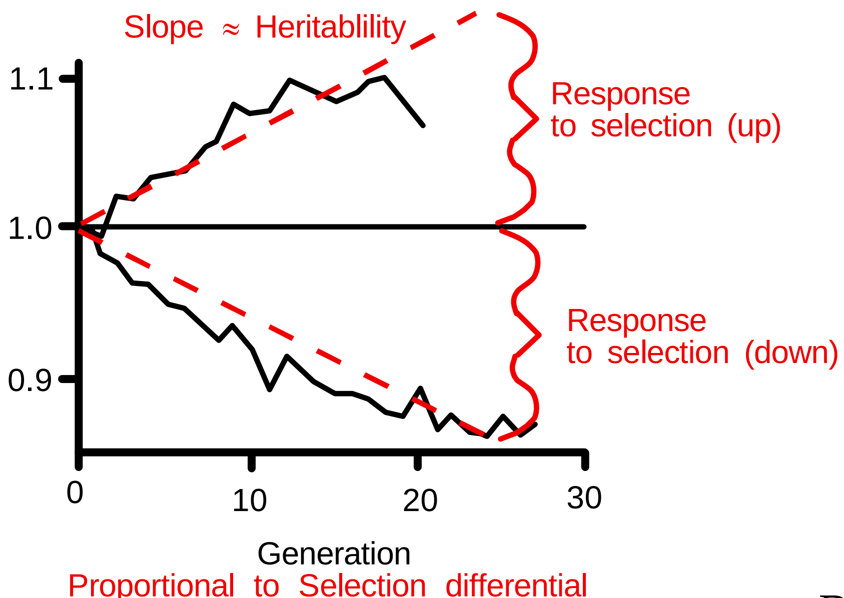
Populations are large and unstructured (well mixed)

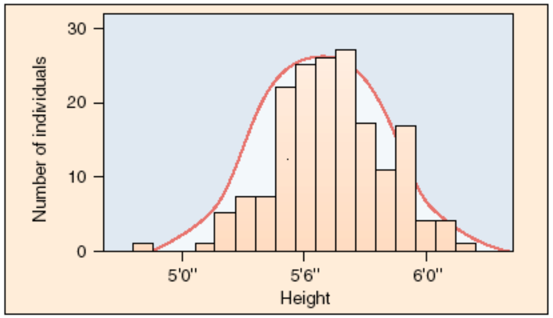
Mating is approximately random

(Yes, he also invented modern statistics)

Fisherian Quantitative Genetics

R	=	h^2		S
Response	=	heritability	*	selection
Change Between Generations	=	portion of total variation that is Genetic	*	Change Within Generations





Robertson's 1955
selection on thorax length in Drosophila

IF

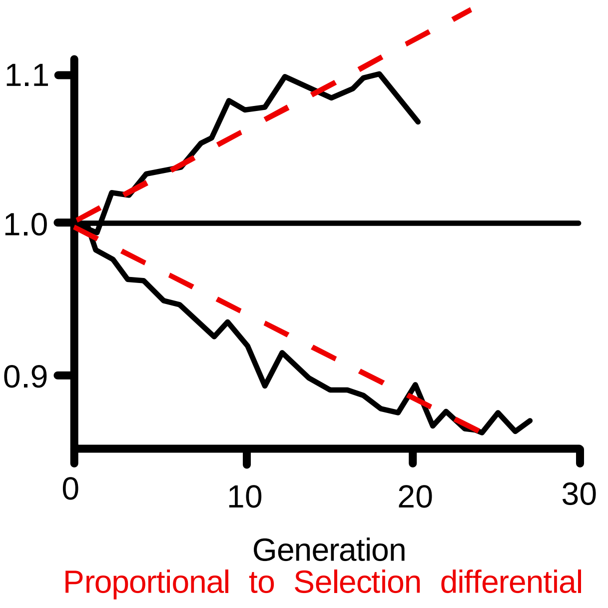
Fisher's assumptions of

A single large population

and

Random mating

are true



THEN

We can ignore Interactions

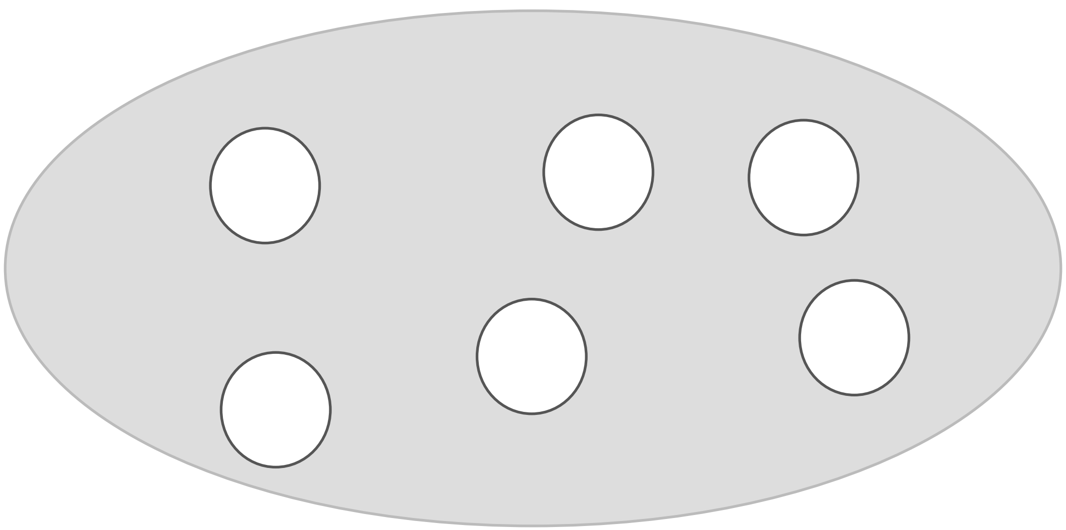
among genes

among individuals

between generations

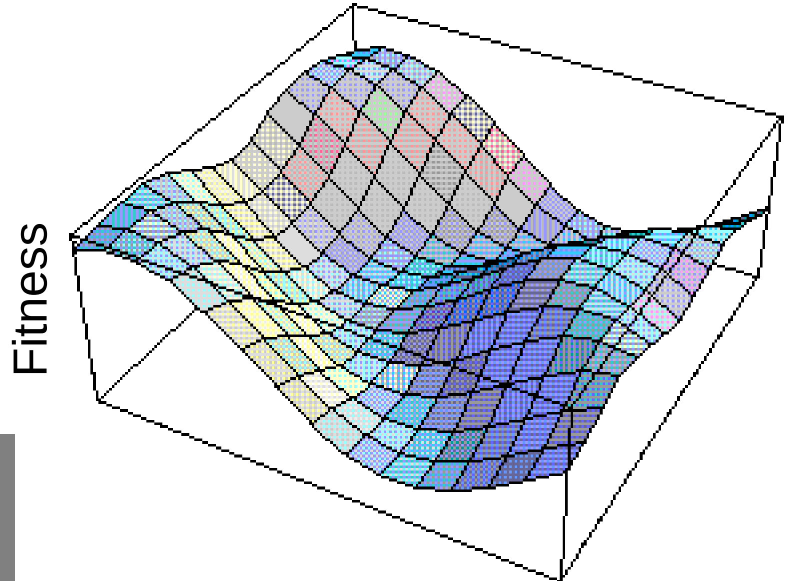
Simplest Way to Relax Fisher's Assumptions

Assume a Metapopulation:
A Population of Populations



Random mating within demes
Random (but limited) migration between demes

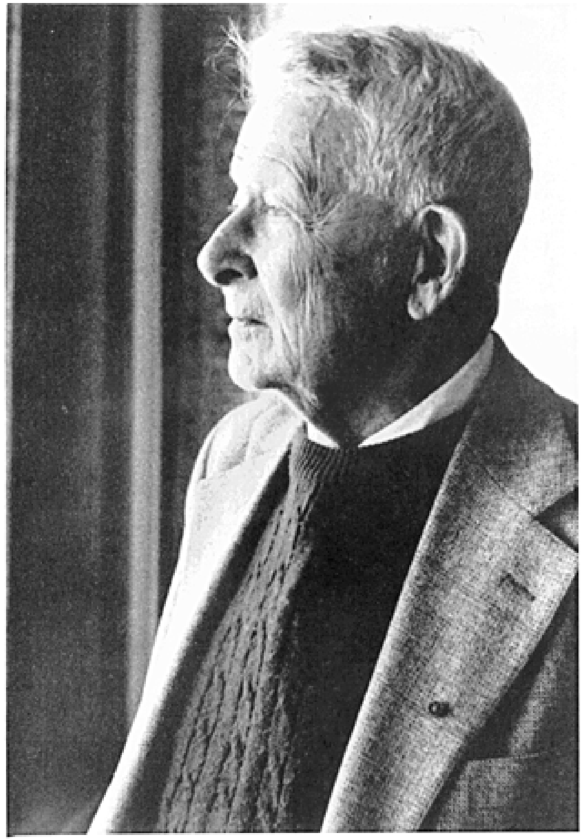
Sewall Wright and the Shifting Balance Theory



Adaptive Topography

Wright's Generalizations:

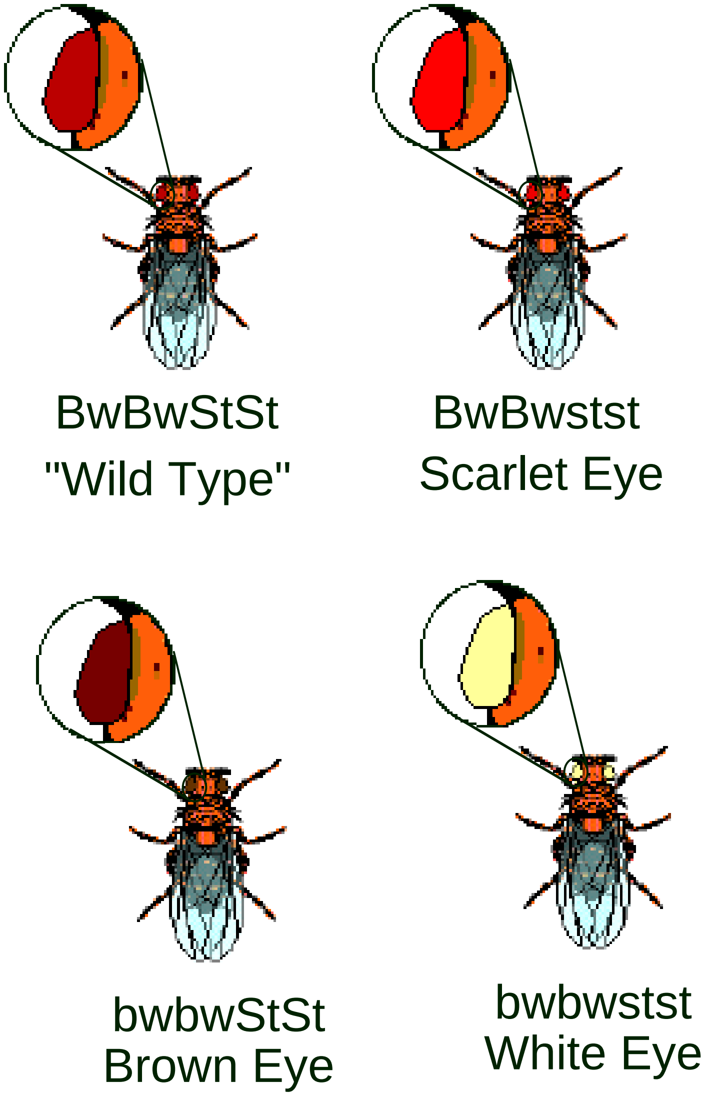
- Traits are Polygenic
- Universal Pleiotropy
- Universal Epistasis
- Multiple Selective Peaks



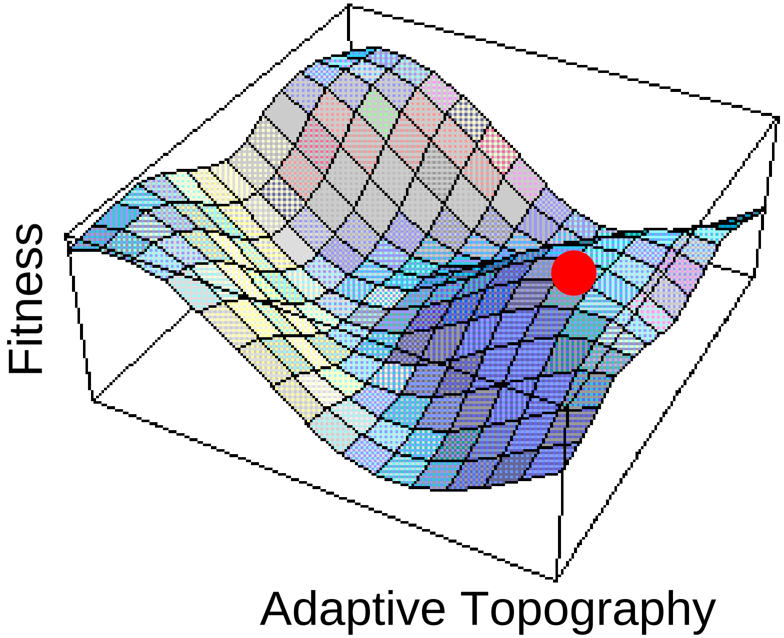
Sewall Wright 1889-1988

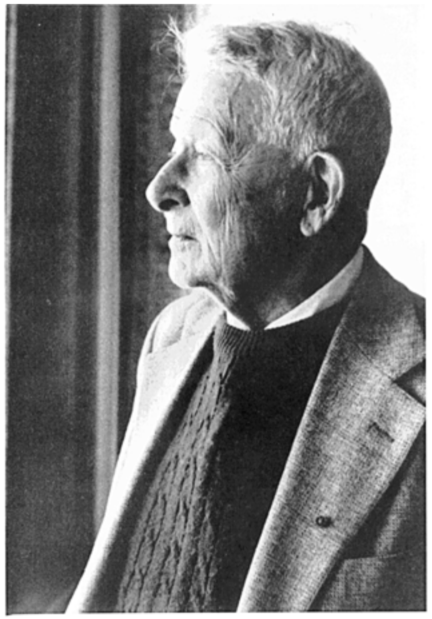
What is Epistasis

Epistasis: Interactions among loci that result in phenotypes that cannot be predicted from the effects of genes considered individually.



Wright's Shifting Balance Theory





Three Phases of Wright's Shifting Balance Theory

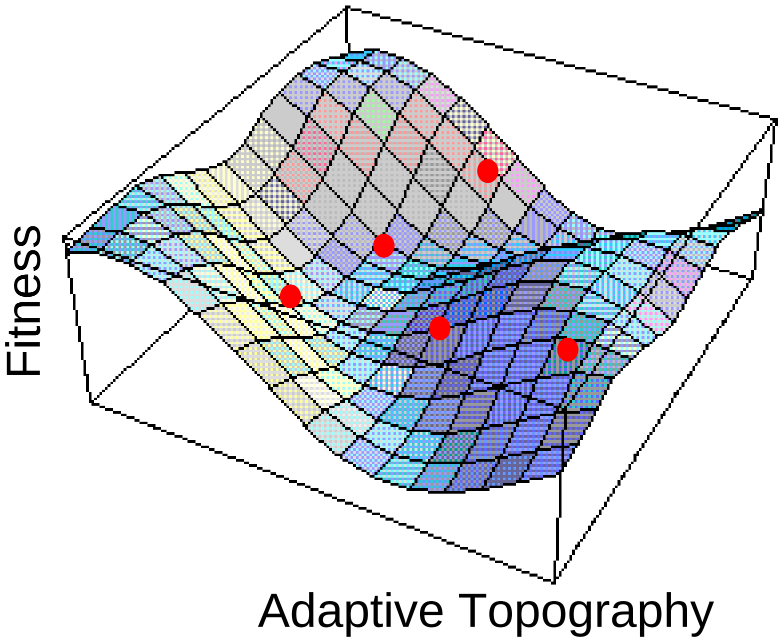
(1) Phase of Random Drift

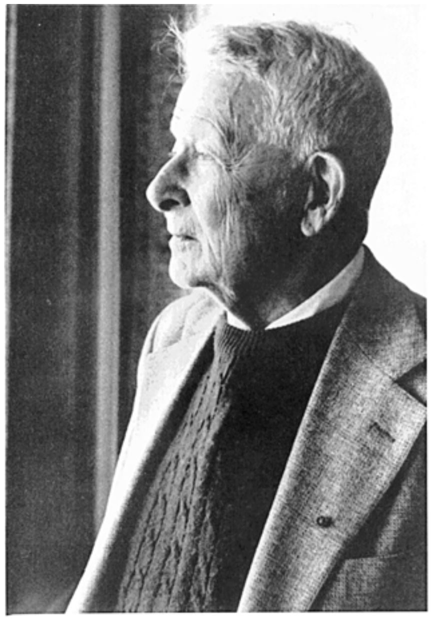
(2) Phase of Mass (Individual) Selection

(3) Phase of Interdeme Selection

Wright's Shifting Balance Theory

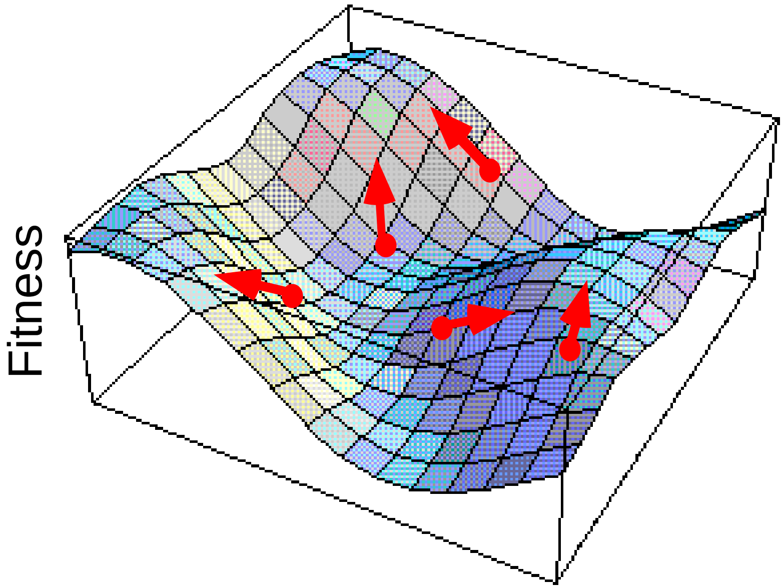
(1) Phase of Random Drift



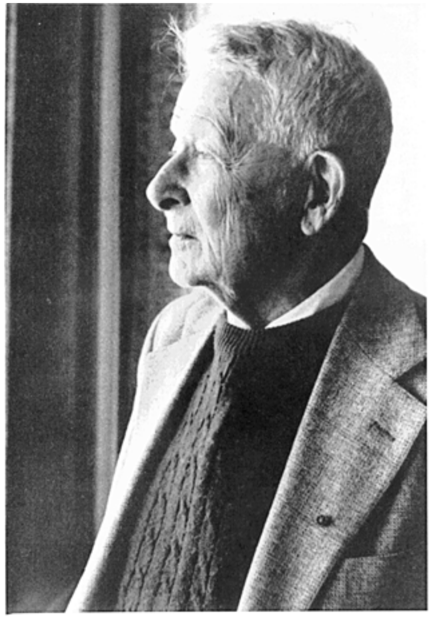


Wright's Shifting Balance Theory

(2) Phase of Mass Selection

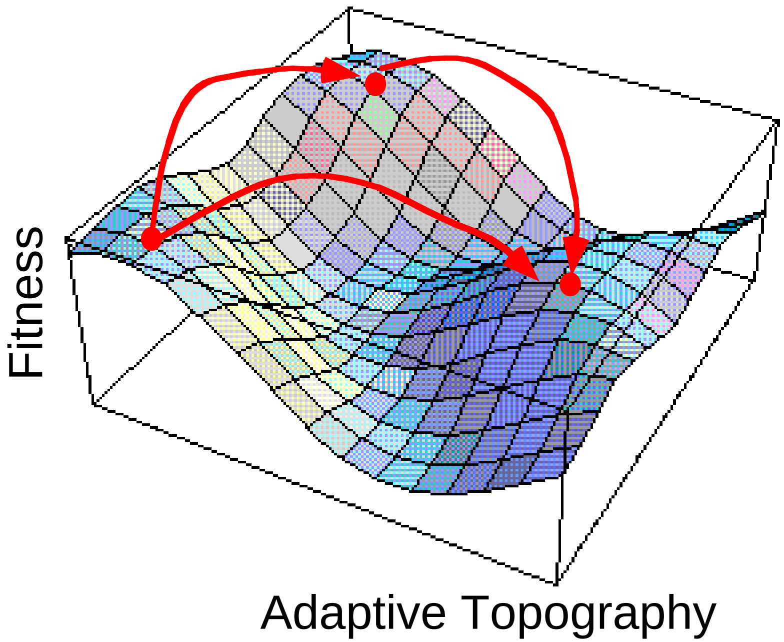


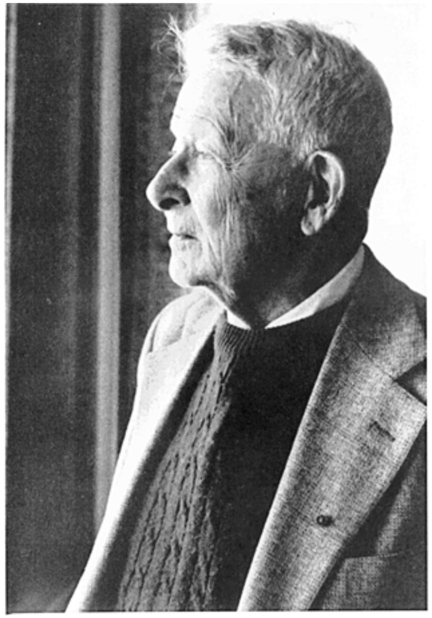
Adaptive Topography



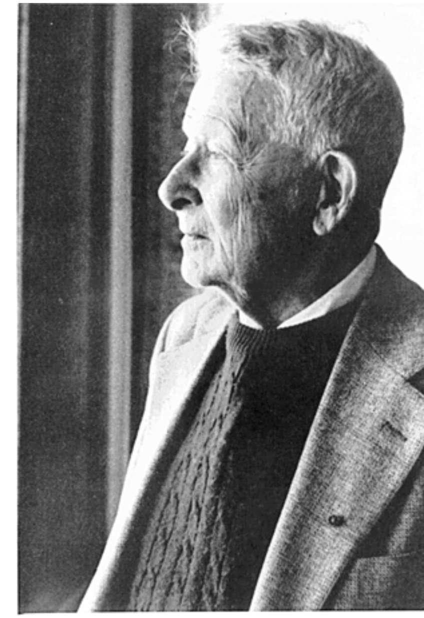
Wright's Shifting Balance Theory

(3) Phase of Interdeme Selection



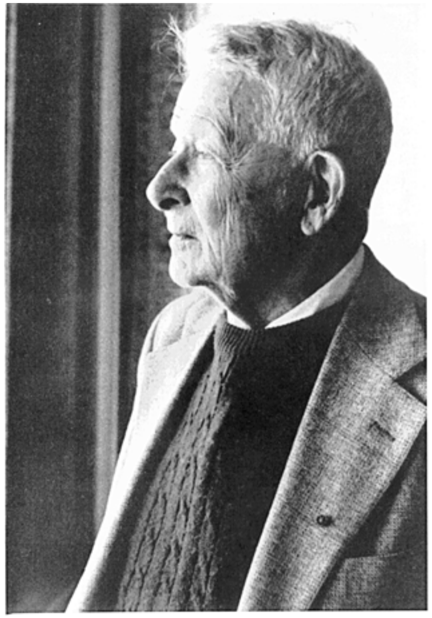


The Fisher-Wright Debate



Refinement of adaptations	**Central Problem in Evolutionary Theory**	Origin of adaptive Novelty .
Mutation and Natural Selection	**Major Process of Evolutionary Change**	Interaction of genetic drift, migration and selection
Large Panmictic Population	**Ecological Context of Evolution**	Small subdivided population
Context independent Genetic Effects	**Genetic basis of Evolutionary Change**	Epistasis and Pleiotropy .
Disruptive Selection	**Process of Speciation**	Inevitable byproduct of local adaptation

The Fisher-Wright Debate



It works.
Well developed theory
No evidence genetic complications important

Why Fisher is right and Wright is Wrong

Not necessary to explain observed adaptations

Model is a metaphor, not a well developed theory

The world does not conform to Fisher's assumptions.

Fisher's models do not explain the diversity of the world

Why Wright is right, and Fisher is Wrong

Closer to the "real world"

Provides an aesthetically pleasing view of evolution.

The Fisher-Wright Debate Continues Today

Coyne, Barton, and Turrelli 1997

A Critique of Sewall Wright's Shifting Balance Theory of Evolution

"In view of these problems, it seems unreasonable to consider the shifting balance process as an important explanation for the evolution of adaptations."

Wade and Goodnight 1998

Perspective: The theories of Fisher and Wright in the context of metapopulations: When nature does many small experiments

"for the reasons discussed above, accepting [Fishers theory] over [Wright's theory] on the grounds of parsimony does not seem warranted to us."

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Bringing the Fisher/Wright controversy into the 21st century

Wright's Shifting Balance Theory
Lacks a formal theoretical Underpinning

This is not surprising:

Theory was developed in the 1930's

Today we would call his model a "complex system"

The theoretical and experimental methods for studying complex systems are only now being developed.

Wade and Goodnight (1998 Goodnight and Wade 2000)

Our goal was to make a first effort to bring Fisher's and especially Wright's models up to date.

A revised model must

Explain why Fisher’s model works

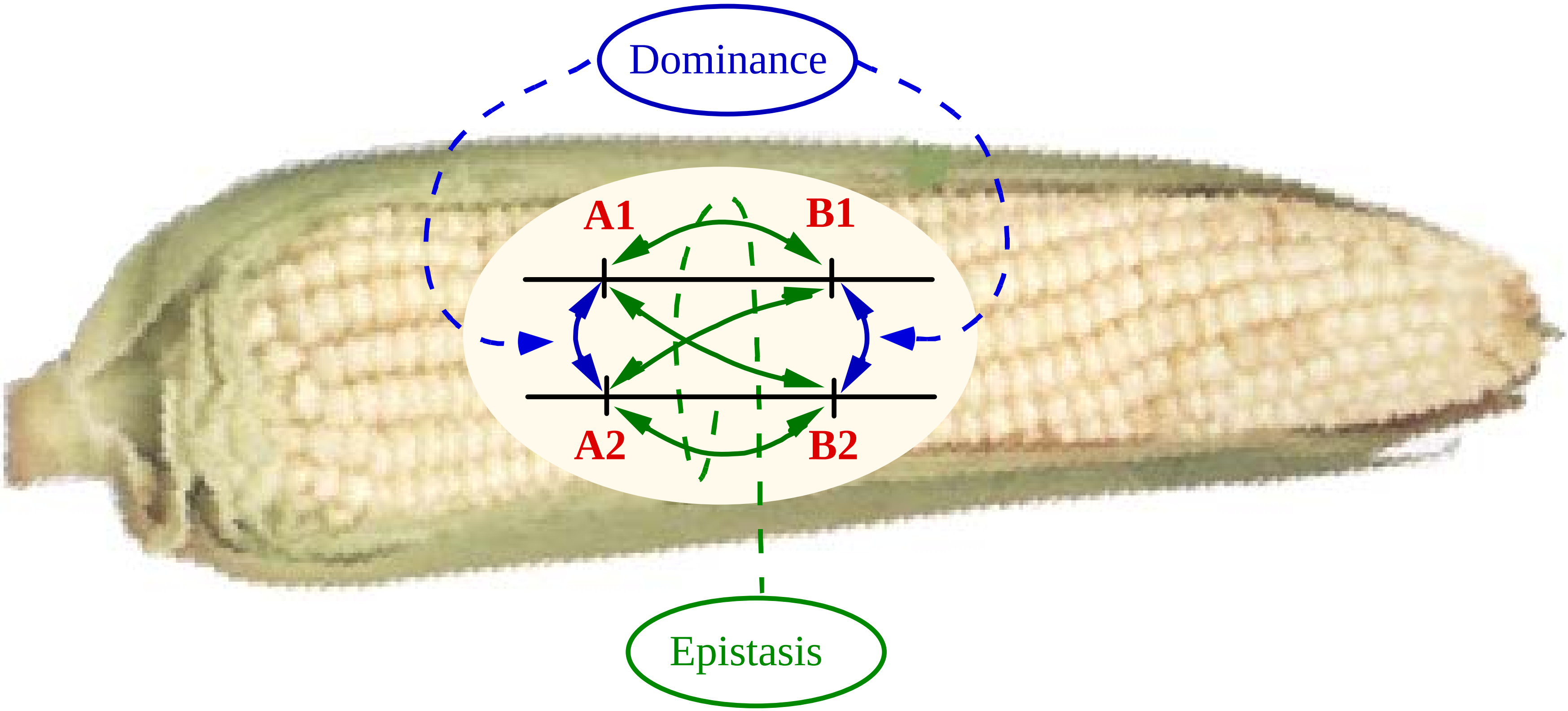
Provide for the evolution of novelty

Be consistent with current data

Wade/Goodnight perspective:

As with most historical controversies, both and neither are “right”. Both see a portion of a larger picture.

Additive VS a NonAdditive World



Additive World

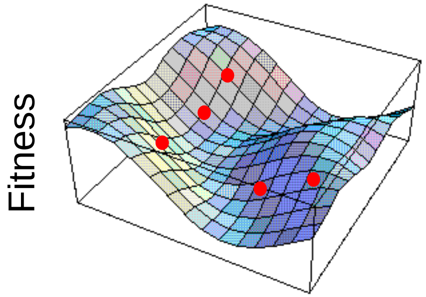
Only main effects of alleles (A1, A2, B1, B2)

NonAdditive World

Main effects of alleles
Plus Dominance
Plus Epistasis

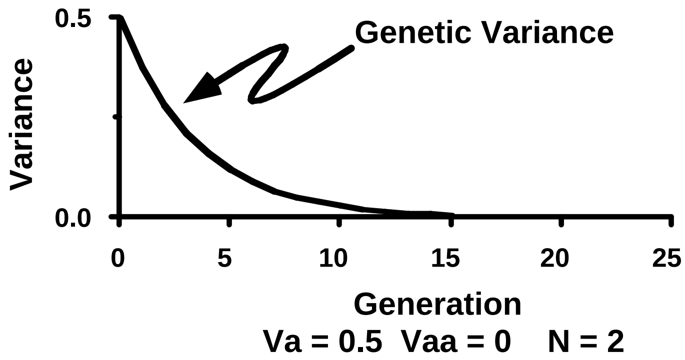
Wright was correct that Genetic Drift is Important in Evolution

Wright's Shifting Balance Theory
Phase 1, phase of Random Drift

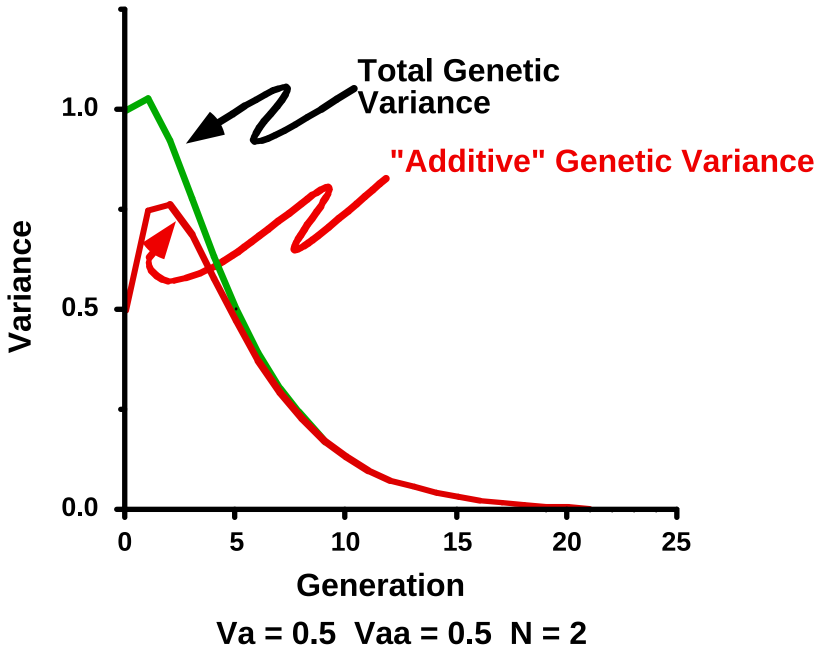


Adaptive Topography

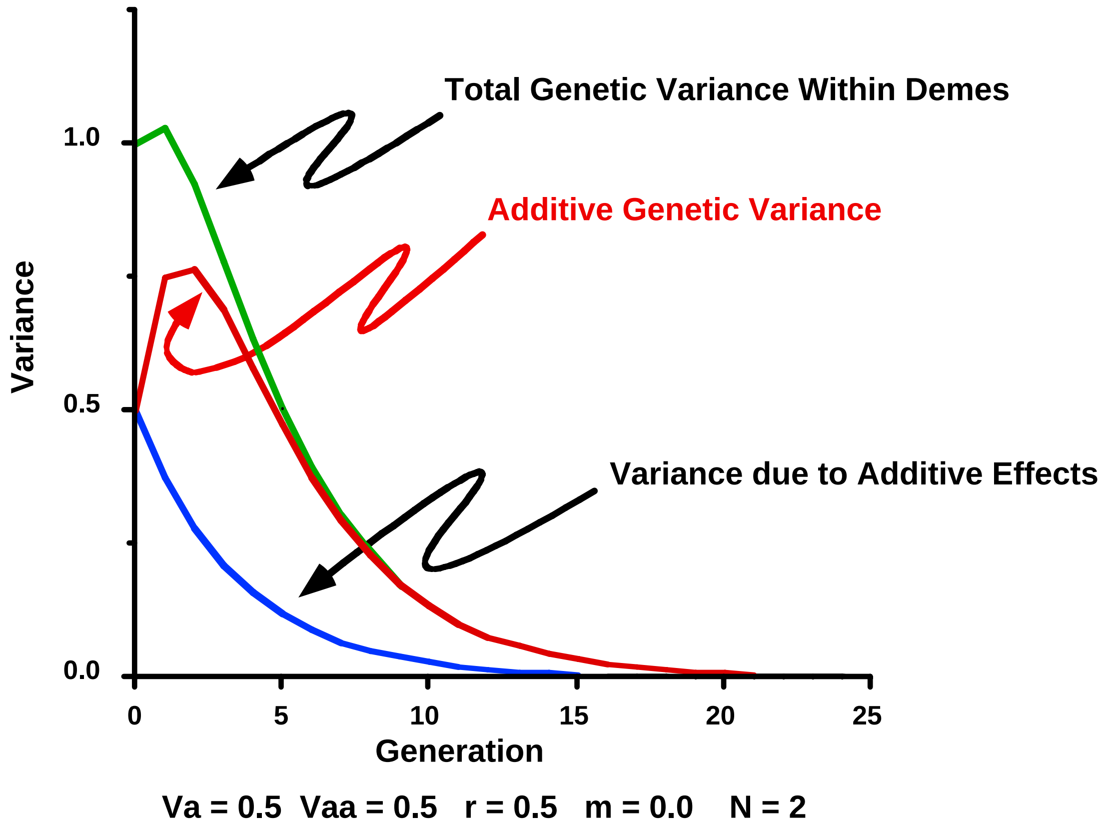
Additive World



NonAdditive World



Additive Genetic Variance = the Ability to Adapt



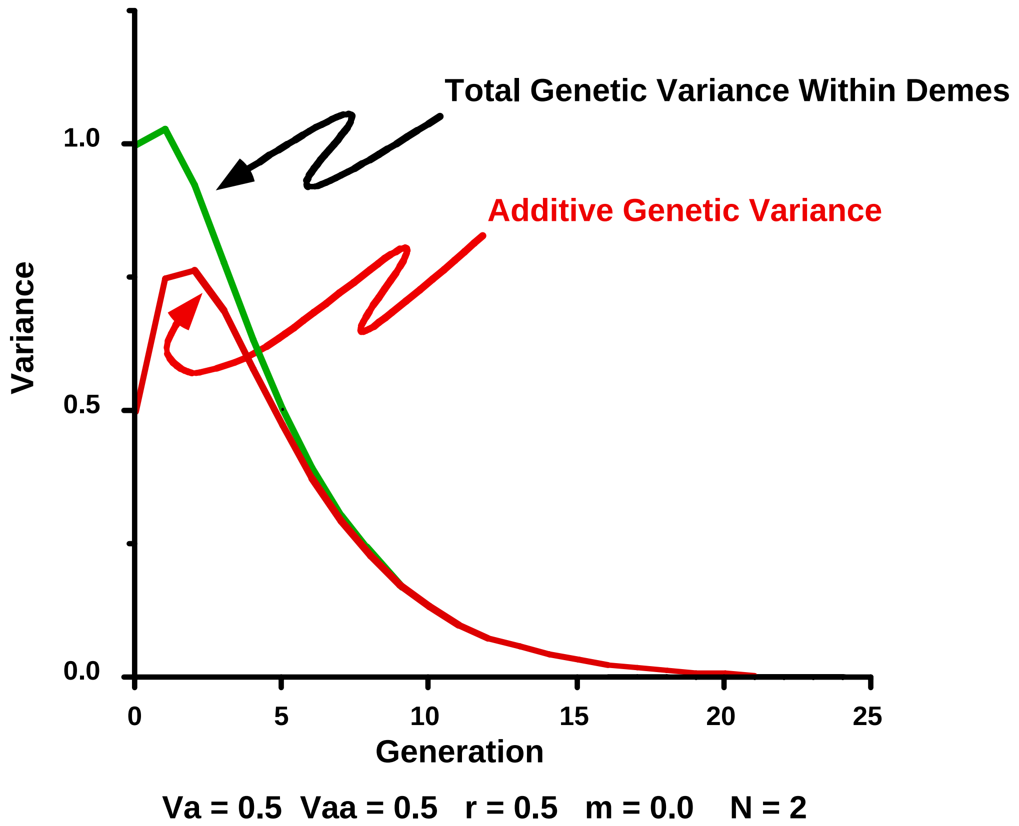
Additive World

Ability to adapt declines with small population size

Nonadditive World

Ability to adapt may increase with small population size

Genetic Drift Makes Nonadditivity Go Away!



Notice that after a few generations of small population size the nonadditive variance (green line minus red line) becomes very small.

Fisher was right! **Within** populations we can ignore gene interaction.

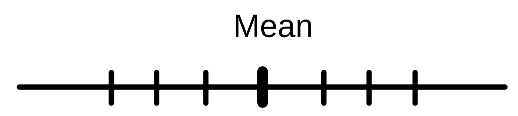
The question:
Where does this new evolutionary potential come from?

There are two ways to increase
the additive genetic variance:

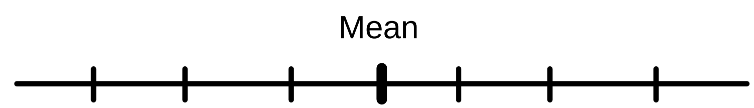
Increase the number of alleles — This is NOT happening

Spreading the alleles — This is what MUST be happening

Before Genetic Drift

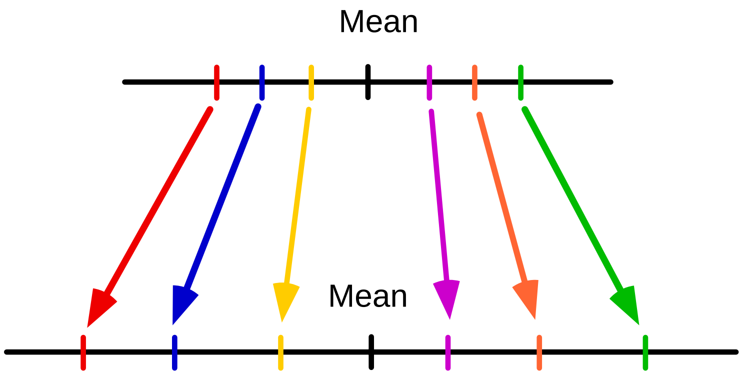


After Genetic Drift

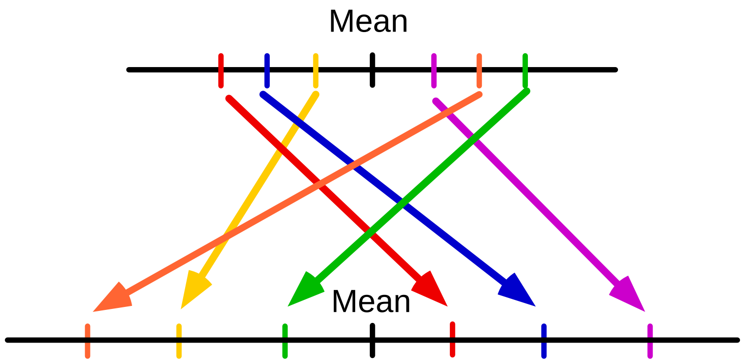


The “spreading” of alleles also changes the rank order of the allelic values!

This "spreading" is not a simple change in scale . . .



Rather it is a change in the rank order of Alleles?

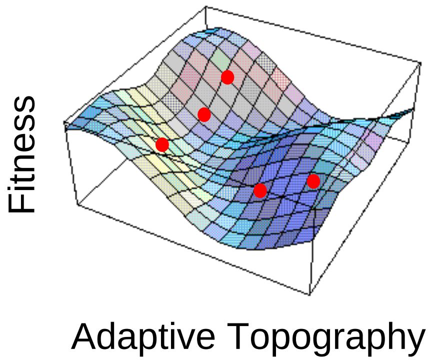


Wright is right!

Genetic drift changes evolutionary trajectories!

Wright was correct that Genetic Drift is Important in Evolution

Wright's Shifting Balance Theory
Phase 1, phase of Random Drift

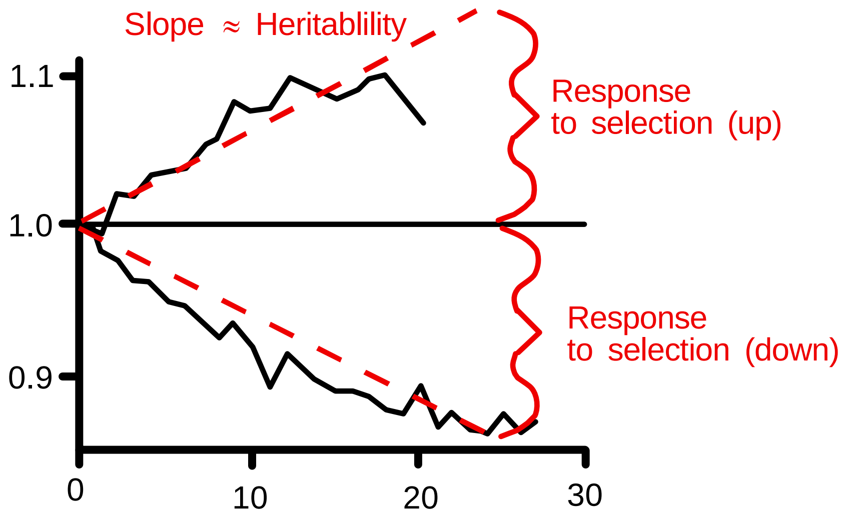


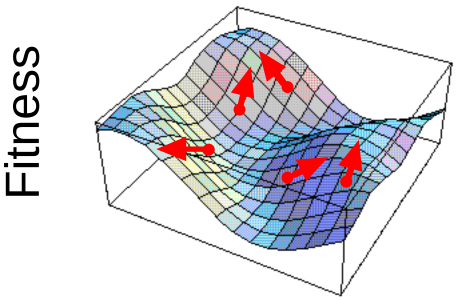
Additive World: Drift reduces genetic variation,
effects of alleles do not change

NonAdditive World: Drift can increase genetic variation
effects of alleles may shift unpredictably

Fisher was correct that selection refines adaptations

Wright's Shifting Balance Theory
Phase 2, phase of mass selection





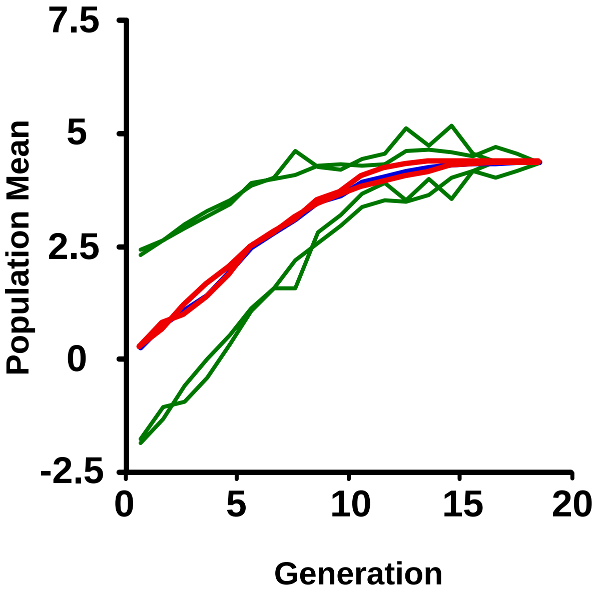
Adaptive Topography

Robertson's 1955
selection on thorax length in Drosophila

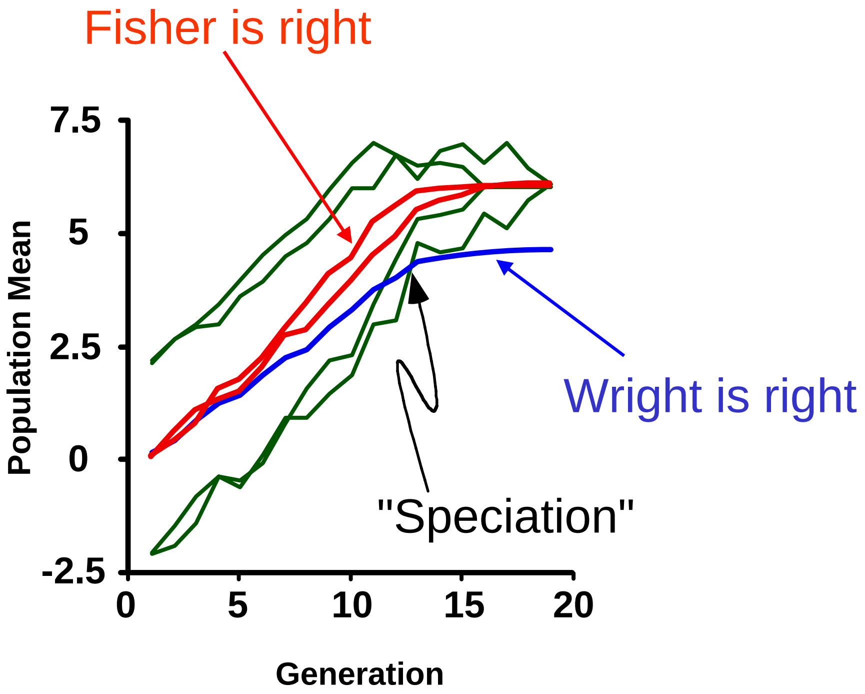
BUT: That may be limited to a within population view!

Simulation:
The Response to Selection in two isolated populations

Additive World



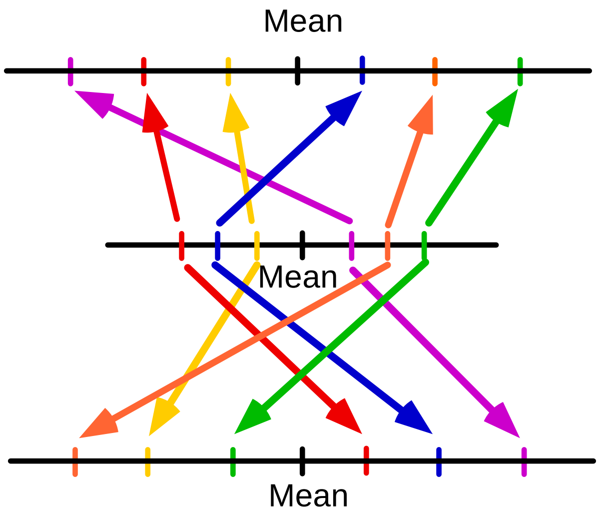
NonAdditive World



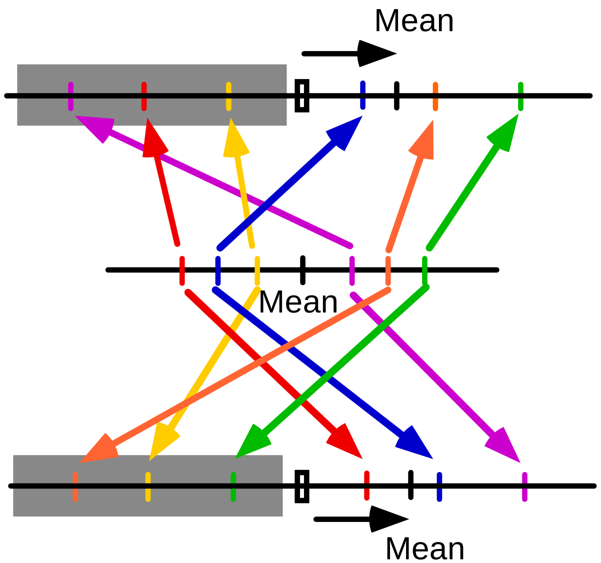
Parental populations
Hybrid population
2 genetic standard devations

Differentiation due to Selection is caused by the Spreading and Shifting of Allelic Values.

Before Selection

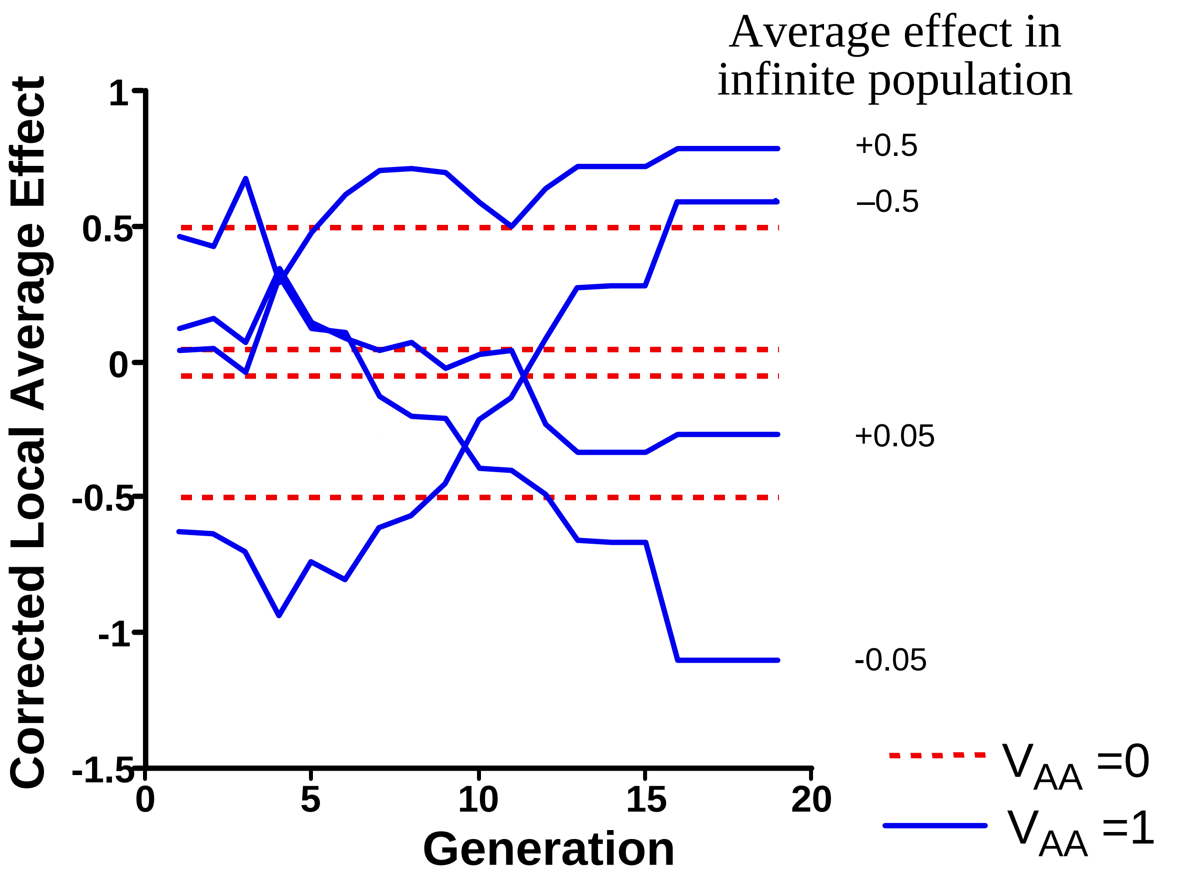


After Selection



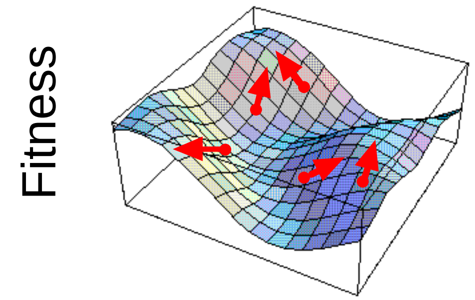
Offspring of migrants will be of low fitness!

Simulation:
The shift in Allelic Values in a selected population



On Selection:
Correct view combines Fisher and Wright

Wright's Shifting Balance Theory
Phase 2, phase of mass selection



Adaptive Topography

Fisher: Selection refines adaptations

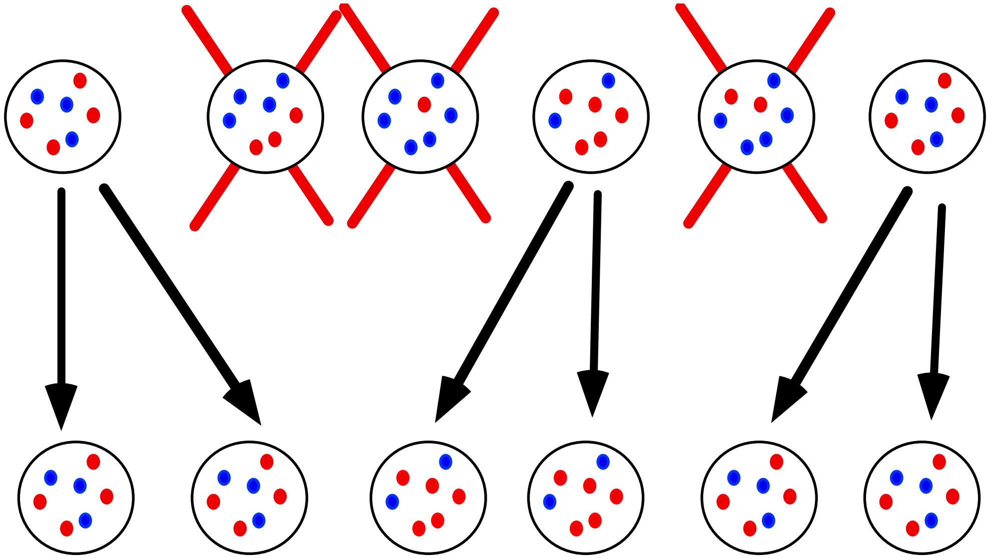
Wright: Selection leads to differentiation of populations

Wade/Goodnight view: Selection refines adaptations within populations, but leads to differentiation between populations.

Wright's Interdeme Selection = Group Selection

Wright's Shifting Balance Theory
Phase 3, phase of Interdeme Selection

Group selection: The differential survival and/or reproduction of groups



19 red
23 blue

26 red
16 blue

Interdeme or Group selection
How important is this?

Conventional Wisdom:

“Is there anything in evolution that can't be answered by Individual selection, that needs to be explained by selection acting on groups? . . . I can’t think of any.”

Jerry Coyne

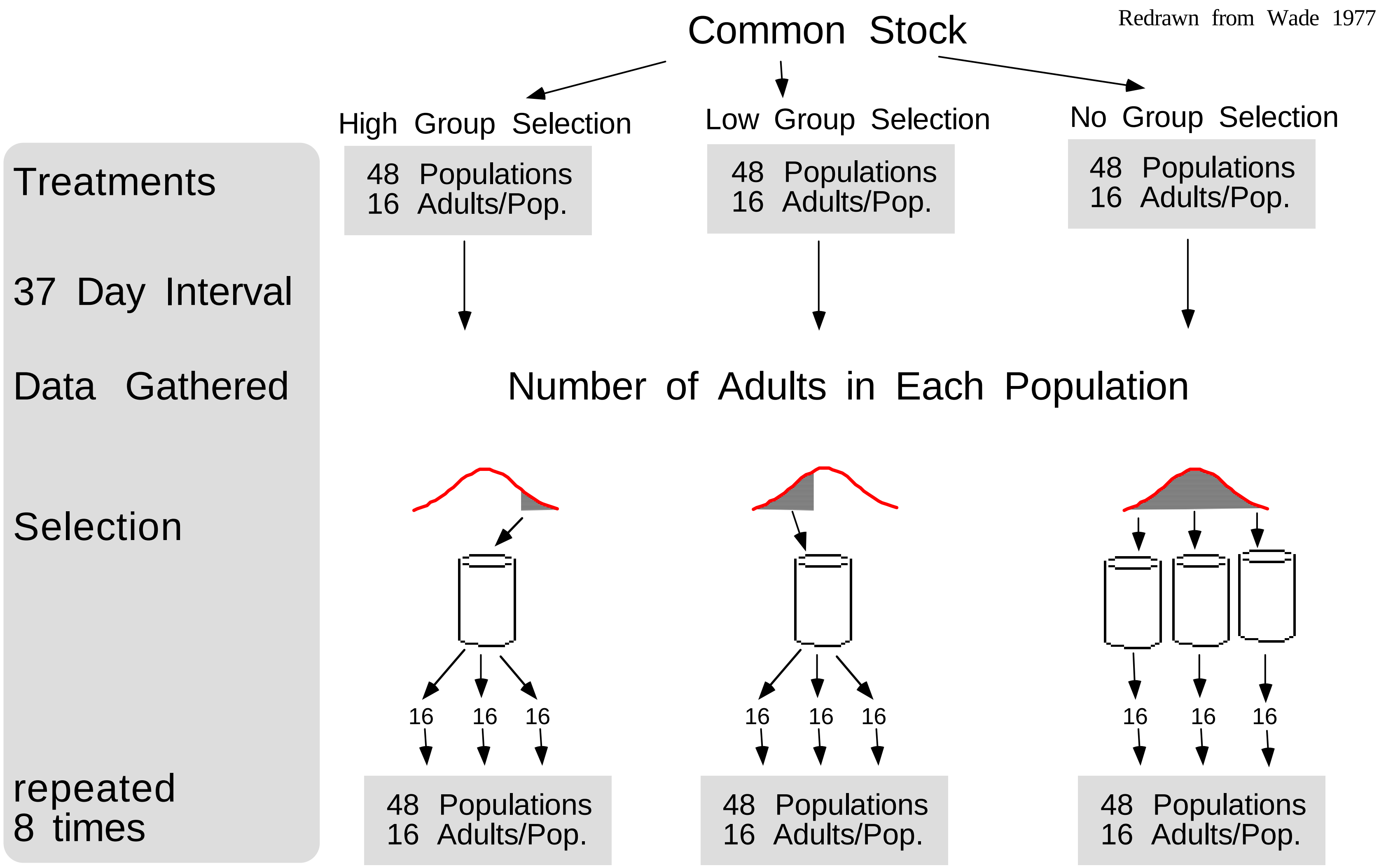
Quoted in Science August 9, 1996

“ . . . extinction and recolonization have only a limited potential to create, or coexist with, strong genetic differentiation . . .. This implies that adaptive evolution is unlikely to occur by classic interdemic selection, a conclusion that has often been reached.”

Harrison and Hastings 1996

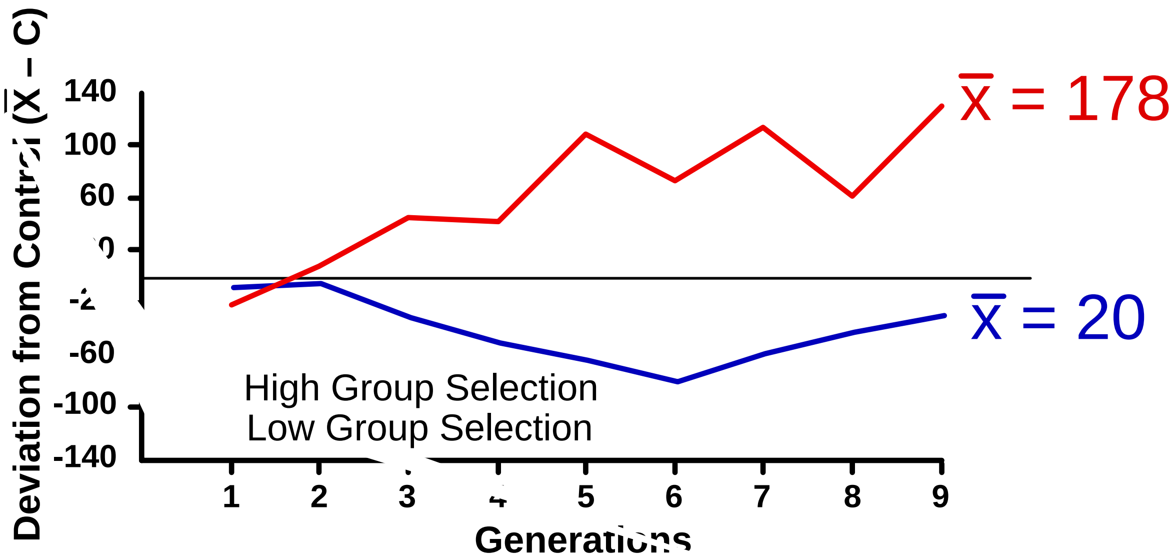
An Example:

The first manipulative study of group selection: Wade 1977



Wade Experiment Results

There was a rapid response to group selection!



Tribolium castaneum

Other Studies of Group Selection

Craig 1982 Evolution 36:271	Replicated group selection treatments, group & individual selection treatments
Goodnight 1985 Evolution 39:545	Group selection in plants, factorially combined group and individual selection treatments
Goodnight 1990 a&b Evolution 44:1614	Group selection on two species communities, analysis of the response to selection
Wade & Goodnight 1991 Science 253:1015	Group selection by differential migration rather than group extinction
Muir 1996 Poultry Science 75:447	Group selection in a vertebrate (Chickens), first commercial use of group selection in animals.

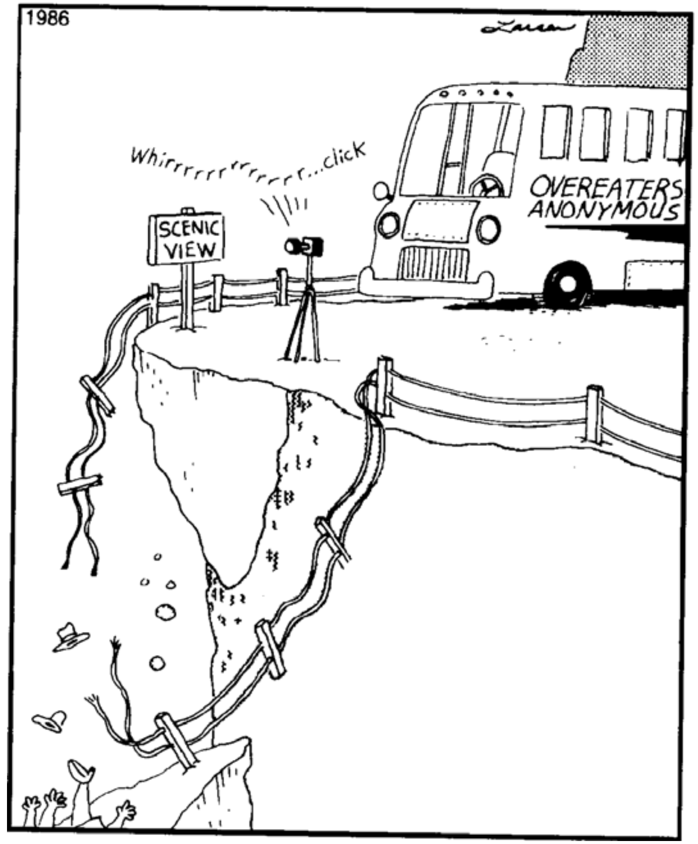
The Effectiveness of Group Selection Surprises even Group Selection Researchers!

Variables examined:
- Population Structure
  - Differential proliferation and extinction of groups
  - Differential migration
- Low levels of population differentiation

Taxa
- Plants (*Arabidopsis thaliana*)
- Insects (*Tribolium castaneum, T. confusum*)
- Vertebrates (Chickens)

Individual selection is always ineffective in these experiments.
(Goodnight 1985 -- **negative** response to individual selection)

Why is Group Selection So Effective?



The simple answer:

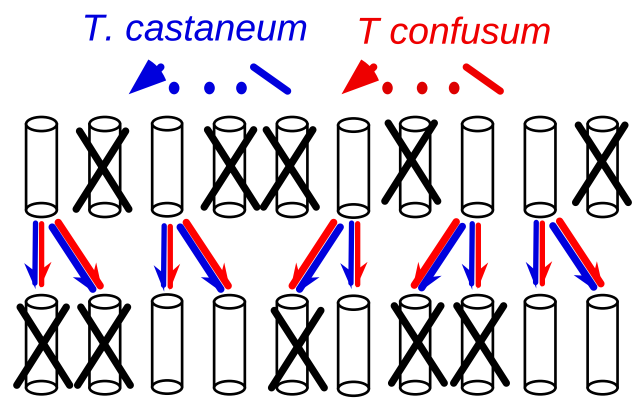
Gene interaction.

Actually, the important type of interaction appears to be genetically based interactions among individuals

Evidence for the role of Genetically Based Interactions Among Individuals

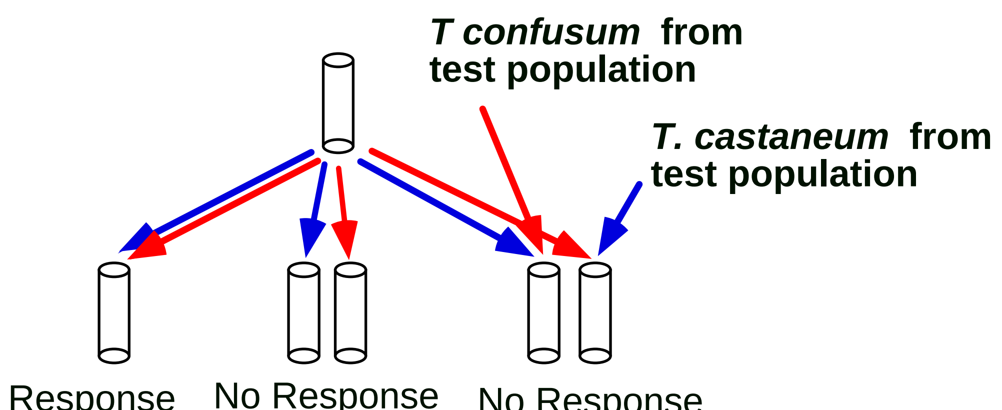
Responses to community selection in two species *Tribolium* communities are dependent on the genetical identity of both strains (Goodnight 1991)

Selection Protocol



Repeated for 9 generations of selection

Assays performed on each community



4 traits measured:

- **Population size in *T. castaneum***
- **Population size in *T. confusum***
- **Emigration Rate in *T. castaneum***
- **Emigration Rate in *T. confusum***

Group Selection:
Additive Vs Nonadditive World

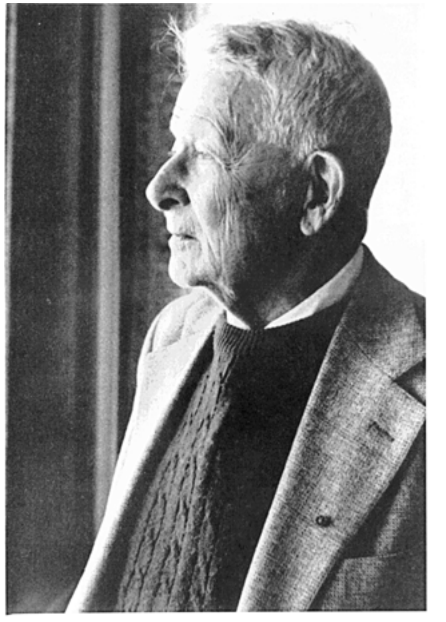
Additive World:

Group selection is much less effective than individual selection. Acts on the same genetic effects as individual selection, but averaging makes it less effective

Nonadditive world

Group selection is very effective, often more effective than individual selection. Group selection acts on variation that is not available to individual selection (genetically based interactions among individuals).

The Fisher-Wright Debate



Drift has little effect other than causing loss of genetic variation.

(1) Phase of Random Drift

Drift changes the effects of alleles on the phenotype

Individual selection refines adaptations by finding the best **genes** for the environment

(2) Phase of Mass (Individual) Selection

Individual selection finds best **genotypes** for the environment. Causes populations to differentiate

Group selection is less effective than individual selection. Of little importance in evolution.

(3) Phase of Interdeme Selection

Group selection is highly effective. Acts directly on gene interactions.

A Modern View of Evolution

Gene interaction is important, and must be acknowledged

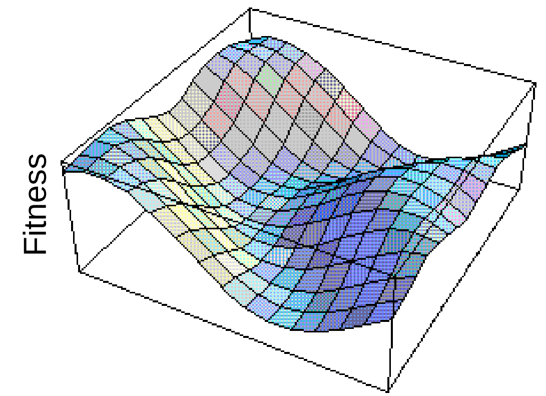
- It often will not be detectable within populations
- The main impact of gene interaction will be felt among populations

Genetic drift is probably insufficient by itself to generate major evolutionary effects.

The major effect of genetic drift is to change the effect of alleles on the phenotype.

Natural selection acts to amplify the effects of drift on allelic effects. What is a minor random force becomes a major force for differentiation when coupled with selection.

A Modern View of Evolution Continued



Wright's three phase process is worth retaining:

(1) Phase of Random Drift:

In a metapopulation drift causes a differentiation of allelic values.

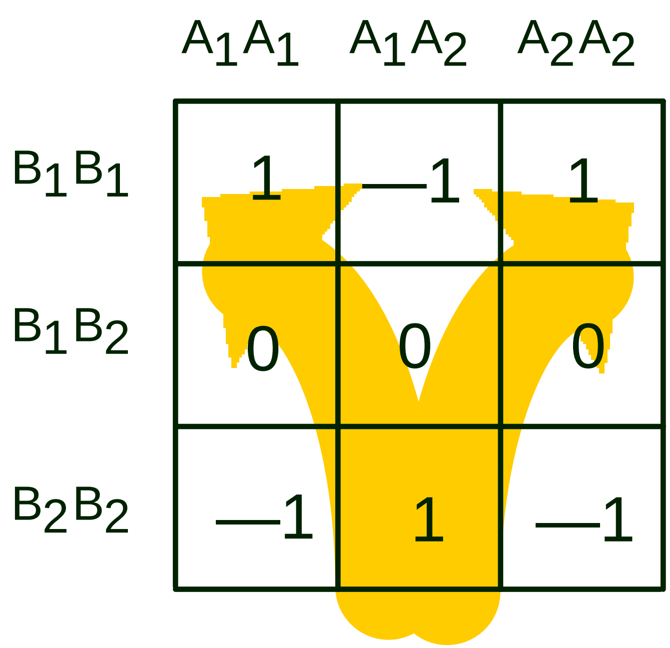
(2) Phase of Mass Selection:

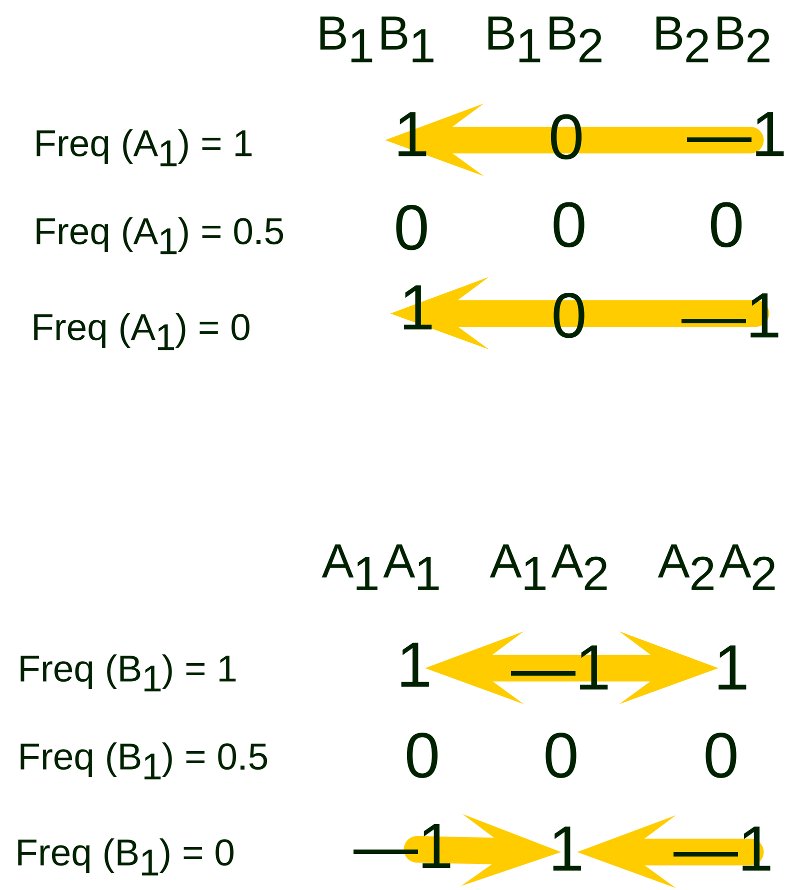
Selection acts to refine adaptations in the context of the specific genetic background.

(3) Phase of Interdeme Selection:

Group Selection acts (1) to spread genetic combinations, but (2) serves as an adaptive force in its' own right.

Gene Interaction and Speciation: Dominance by Additive Epistasis





In a Metapopulation fixed for the B_2 allele the introduction of a B_1 allele (by mutation or migration) can lead to speciation due to underdominance at the A locus