Week 9-10 Highlights

(https://evolution.berkeley.edu/evolibrary/home.php)

Evolution

Definition: Descent with modification.

This definition encompasses-

(1) small-scale evolution- commonly referred to as “Micro Evolution”

(a) changes in allele frequency in a population from one generation to the next

(b) heritable changes in frequency of phenotypes in a population

(2) large-scale evolution- commonly referred to as “Macro Evolution” such as the descent of different species from a common ancestor over many generations.

We've defined evolution as descent with modification from a common ancestor, but exactly what has been modified?

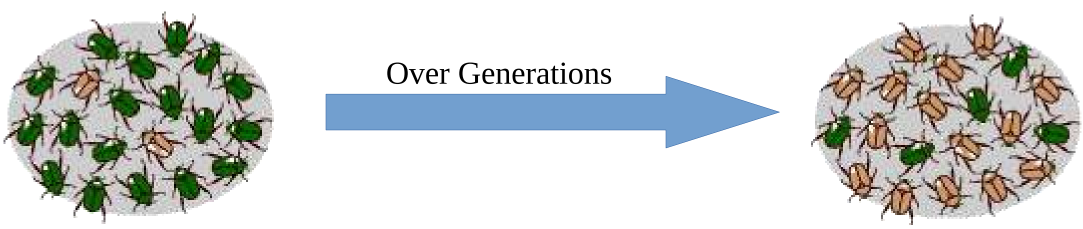
We refer to a heritable modification of phenotypic or allelic frequency in a population over generations.

Example 1: Consider a beetle population. Consider two characters

(1) Body colour: Individuals are of two colours- green and brown.

(2) Body size: Individuals are of different sizes.

Let us say that both these characters are heritable (ie have a genetic basis)



(Generation t) (Generation t+n)

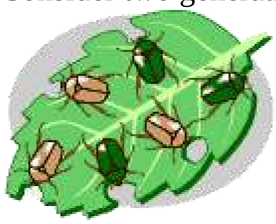
The frequency of the two body colour phenotypes within the beetle population has changed over generations. Additionally, we can show that this is a heritable change (ie, green and brown body coloured beetles from generation t+n will give rise to green and brown body coloured beetles respectively).

Therefore, by definition, the beetle population has evolved with respect to body colour.

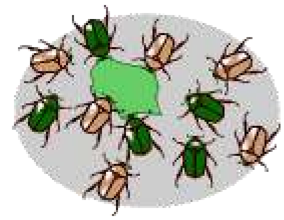
Note that the distribution of beetle body size has not changed over generations. Therefore, the same population has not evolved with respect to body size.

Example 2: Consider a different beetle population. Consider a character- Body size.

Consider two generations of beetles.



(Generation t)



(Generation t+1)

Beetles in generation t had access to lot of food as larvae. Therefore they became large sized adults. Beetles in generation t+1 got very little food as larvae. Therefore, they became small sized.
Can we say that body size has evolved in this population? No.
Why? Suppose that we took beetles from gen t+1 and gave their progeny ample food. The progeny will develop large body size. That is to say the change in body size was not "heritable" (or not "Genetic").

Evolution only occurs when there is a change in allele frequency within a population over time. That is, the changes are heritable and can be passed on to the next generation.

What can cause a change in frequency distributions within populations over generations?
The most important mechanism that can cause change in frequency distribution in populations over time (ie Evolution) is **Natural Selection.**

Selection:
definition: Heritable differential reproductive success.

Darwin's idea

1. There is phenotypic variation within breeding groups (*populations*).
2. Part of the observed variation is *heritable*.
3. Some individuals are more successful in survival & reproduction (*Darwinian fitness*) than others.
4. Survival and reproduction are non-random. That is, certain phenotypes have better fitness than other phenotypes. Variation influences fitness: those with the most favourable *phenotypes* are *naturally selected.*

Therefore, phenotypes with higher Darwinian fitness will increase in frequency within a population over generations.

If you have heritable variation AND differential reproduction you will have evolution by natural selection as an outcome. It is as simple as that.

What causes heritable variation in phenotypes?
Mutation is the ultimate source of variation. For asexual organisms, mutation is the only way to create new heritable variations. In Sexually reproducing organisms, recombination can also create new phenotypes.

What causes differential reproduction?
There could be many reasons-
(a) Internal to the organism: for example some organisms in a population carry a lethal form of an allele- this will reduce the chances that an organism will get to reproduce.
(b) Environment: Environment is here defined as anything that is non-self with respect to the organism. That is, all biotic and abiotic factors that are not the organism itself. The environment can interact with the phenotype of the organism to affect the reproduction of the organism. For example, consider a bacteral population that have heritable variation in resisting a particular antibiotic. If that antibiotic is now added to the environment of the bacterial population, some bacteria will survive better than others and therefore will be better able to reproduce than others.
The agent in the environment that is majorly responsible for bringing about differential reproduction is called **"Selective Agent"**. In the current example, Antibiotic would be the selective agent.

Darwinian Fitness:
Extremely crudely put, it is equivalent to the number of progeny an organism produces relative to the others in the population.
In other words, it is the number of copies of oneself that an organism contributes to the next generation, relative to others in the population.

Fitness is relative:
Fitness of an individual is expressed relative to another individual of the population ie, an individual has higher or lower fitness compared to another individual.

Fitness is context specific:
Fitness is defined with respect to an environment. Fitness relationships between individuals can change if the environment is changed ie, an individual with high fitness in a given environment can become an indivual with low fitness in a different environment.

Observe that Fitness and Selection are both related to differential reproduction.
A high fitness phenotype is favoured by selection (or is "selected for").
A low fitness phenotype is disfavoured by selection (or is "selected against").

What Evolution is NOT:

The term "evolution" is commonly misused, often accidentally but sometimes with purpose, so it is also necessary to clarify what evolution is not.

Most importantly, **evolution does not progress toward an ultimate or proximate goal** (Gould 1989). Evolution is not "going somewhere"; it just describes changes in inherited traits over time.

Selection does not plan ahead. It just happens. Therefore, **Evolution is local in time and space** ie, a given population evolves in response to selection at that point in time.

Evolution, Selection and Adaptation are NOT synonyms.
(a) Selection is the driving force and Evolution is the outcome.
(b) When populations evolve to be better suited to a given environment, we say that the populations have Adapted. The process is called Adaptive Evolution. All evolution may not be adaptive. Consider a population of beetles as in the exampe above. Say that a large number of green beetles *accidentally* got crushed by a falling tree and a large number of brown beetles survived- *purely by chance*. In the next generation, there will be more brown beetles in the population than green beetles. One can show that

this is a heritable change. Therefore the beetle population has *<u>Evolved</u>*. However, this accidental death of the green beetles does not make the beetle population better adapted to their environment. Therefore, this is NOT adaptive evolution.
In other words, all Adaptation is Evolution but not all Evolution is Adaptive.

Individuals DO NOT evolve. Individuals DO NOT adapt. Populations evolve and adapt.
Individuals can Acclimate. For example, if an individual moves to a high altitude place from the plains, the RBC count in his blood may go up with in a few days in response to the climate. If so, we say that the individual has acclimatised.
The term “adapt” has a very specific meaning within evolutionary biology.

Selection is NOT random. Therefore, Adaptation is NOT random.
Mutations are random. Selection *<u>sorts</u>* these random mutations. The variants that have higher fitness will increase in frequency over time.

Rate of Evolution:
Evolution can occur very rapidly – even over a single generation.
Selection can lead to large divergence between populations with in a short duration. The rapidity of evolution depends on the available variation and the selection pressure.

Evolutionary Trade-off:
Suppose that due to evolution certain organisms become better at a certain character (say trait 1) but this leads to a decline in certain other character (say trait 2). Then, these two characters are said to trade-off with each other. For example, organisms that are selected for high progeny production very early in life show reduced lifespan. Thus early life progeny production and lifespan are supposed to trade-off with each other.

Heritability:
Broadsense Heritability: Proportion of total phenotypic variance that is explained by genetic variance.

$V_P = V_G + V_E + 2Cov(GxE)$ (setting $2Cov(GxE) = 0$),

$V_P = V_G + V_E$

$H^2 = V_G / V_P$

$\mathbf{H^2 = V_G / (V_G + V_E)}$

Narrowsense Heritability: Proportion of total phenotypic variance that is explained by additive genetic variance

$V_G = V_A + V_D + V_I$ where A = Additive, D = Dominance, I = Epistatsis

$V_P = V_A + V_D + V_I + V_E$ (setting 2Cov(GxE) = 0),

h^2 = VA/VP

$$\mathbf{h^2 = V_A/(V_A + V_D + V_I + V_E)}$$

Approaches to measuring Heritability

1. Similarity between relatives: Parents and offspring; Siblings

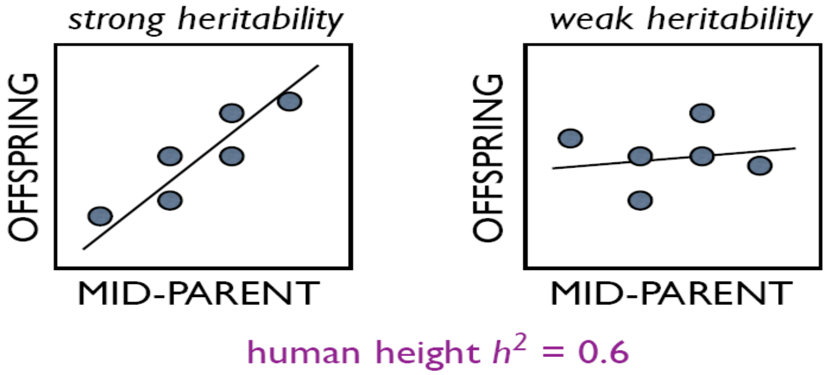
2. Response to selection: selection will only change the population mean if the variation is heritable.

Mid Parent- Offspring Regression:

Consider a large number of families where each family consists of a set of parents and their progeny. From each member of a family, collect data for the character of interest (say height, weight, beak length etc).
For each family, do the following-
Calculate the average value of the parents- call it Mid-Parent value.
Calculate the average value of the offspring of that family.

You will now have a matched set of mid-parent and average offspring values.
Plot mid parent value on X axis and average offspring value on Y axis.
Plot a linear regression line (best fit line).
The slope of the line is a measue of the heritability of the trait in that population.

Note that Heritability of a trait is specific to a population. Think about it- it is defined in terms of variance in a population; it is estimated as the slope of a regression line using values from teh population. This means that heritability values for a given trait can change across populations or over time.



Problems with estimating heritability using parent-offspring regression:

1. Maternal effects: Offspring share the same mother. Mother can pass on non-genetic effects that can cause similarities. These effects cannot be further inherited in the next generations.
2. Parents and offspring share the same environments that can lead to similarities in their phenotype but these similarities are not then inherited by future generations.
3. Since in a large number of species females (and males) mate with multiple partners, it is difficult to assign paternity (ie identify the father). Therefore, calculating mid-parent value is difficult.

Some estimates of heritability:

Morphological traits = 0.51

Behavioural traits = 0.37

Physiological traits = 0.31

Life-history traits = 0.27

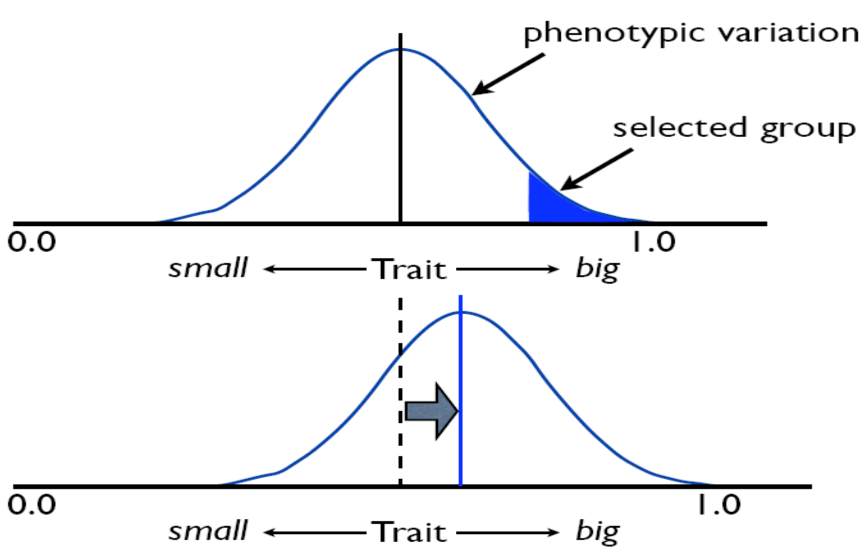
Consider a population that has been in the same environment for a large number of generations and therefore has adapted to that environment. In this environment, some traits will be more important for fitness than others.

The closer a trait is related to fitness, the lower the V_G we expect (think why?).

Life-history traits (fertility, survival etc.) are closely linked to fitness. Therefore, in populations well adapted to their environment, such traits will have very low heritability.

Note: Think what is the meaning of a trait having zero heritability.

Directional Selection:
When selection favours phenotypes from one extreme of a phenotypic distribution. That is, phenotypes from one extreme of a distribution have higher fitness compared to the phenotypes from the rest of the distribution.
With directional selection, the mean of the distribution is expected to shift in the direction of selection.



Limits to Directional Selection:
There are several reasons why traits might not evolve in a single direction over time. Consider the evolution of beak size in finches of Daphne Major. Bigger beak may not always be better because-

1. May be poorer at manipulating smaller objects. Can’t handle smaller seedss when they are abundant.

2. More energetically expensive to produce.

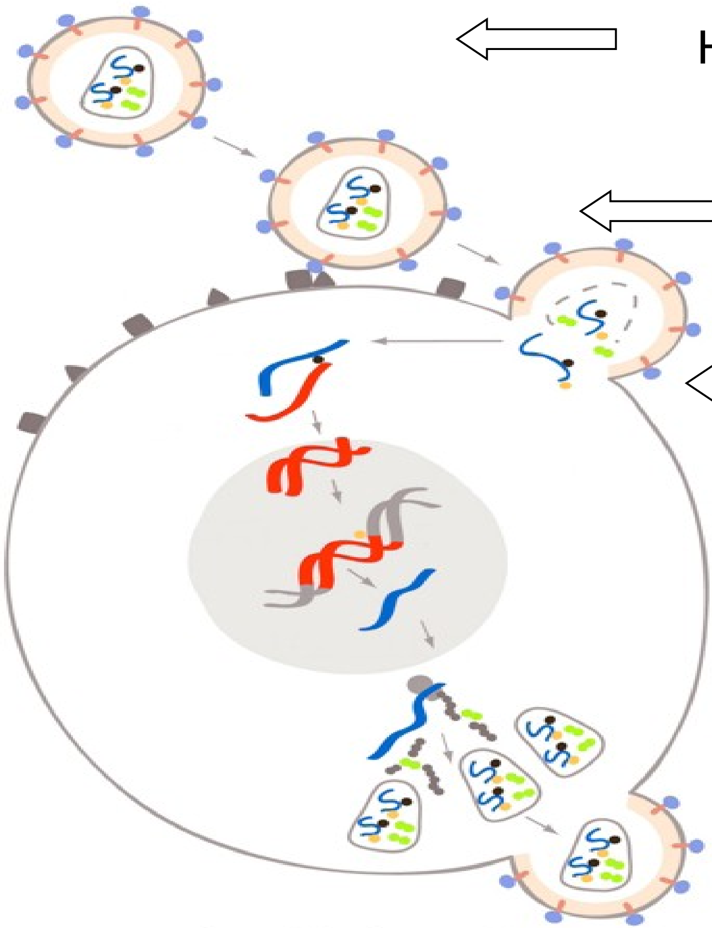
    This might lead to slower growth. May have less energy for other parts.

3. Affects vocal communication, other aspects of mate choice.

4. Genetically correlated with other traits also under selection- Larger beaks can crack seeds but are pooer at twisting action. Both actions are needed to open seeds.

Retro Viruses

- **HIV is an RNA based virus.**
- **Its genetic code needs to be translated into DNA before it can transcribe anything.**
- **It depends upon reverse transcription within the host cell to convert itself into DNA.**



HIV virion (Capsule+ RNA+ Enzymes)

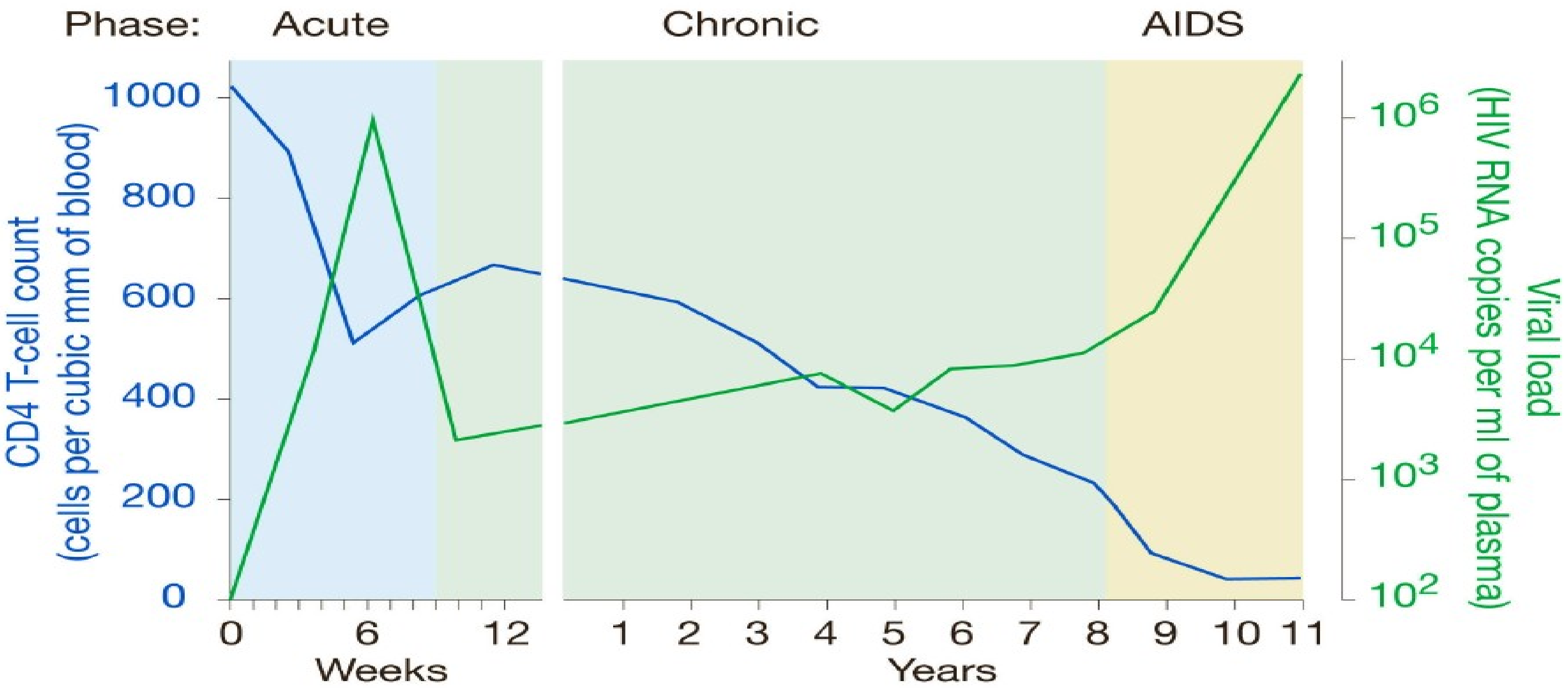
HIV virion binds to cell receptors
(CD4 and coreceptor)

Reverse transcriptase makes
DNA from viral RNA

Integrase splices HIV DNA
Into host cell DNA.
HIV mRNA is transcribed

New HIV proteins are made
By host cell and assembled
Into new virions

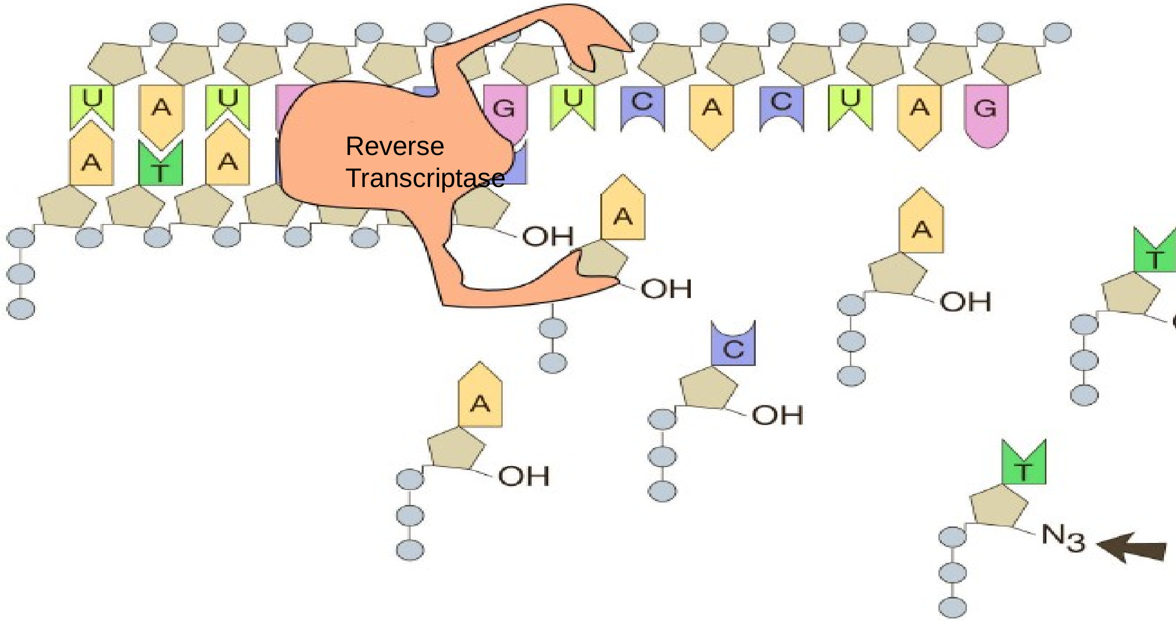
Progression of HIV infection



AZT

- A promising therapy based ontriking reverse transcriptase into inserting a terminating base.
- Instead of normal Thymidine the enzyme inserts Azide Thymidine
- AZT worked in initial trials. Stopped the decline of macrophages.

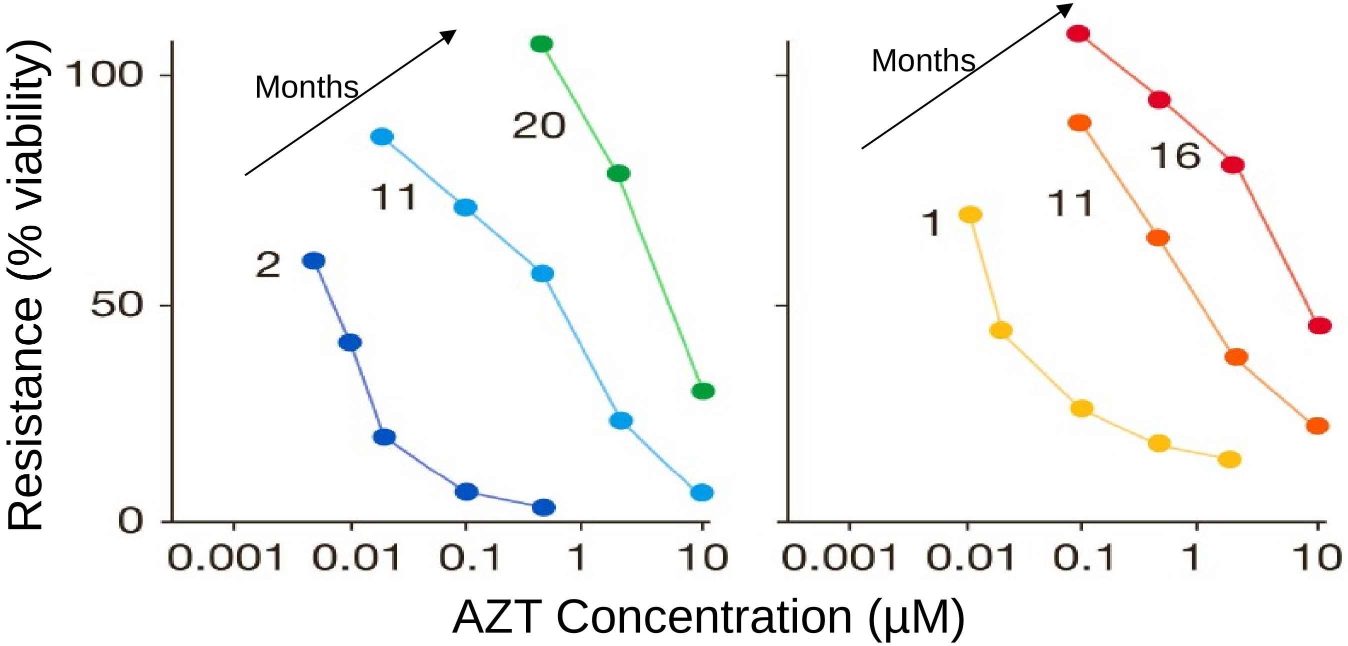
How AZT works



Azide Thymidine

AZT stops working quickly

(a)

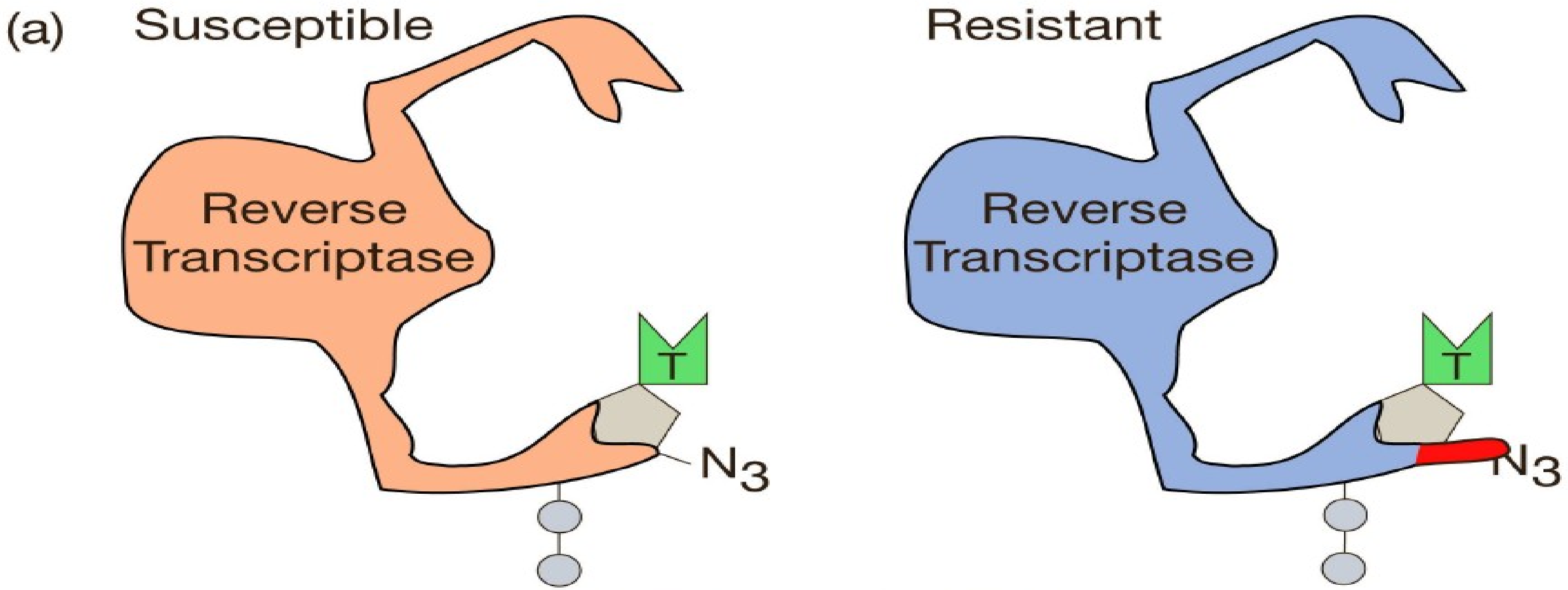


Why does resistance develop?

- Patient’s own cells may change to avoid AZT
  - May exclude it from the cell or fail to phosphorylate it.

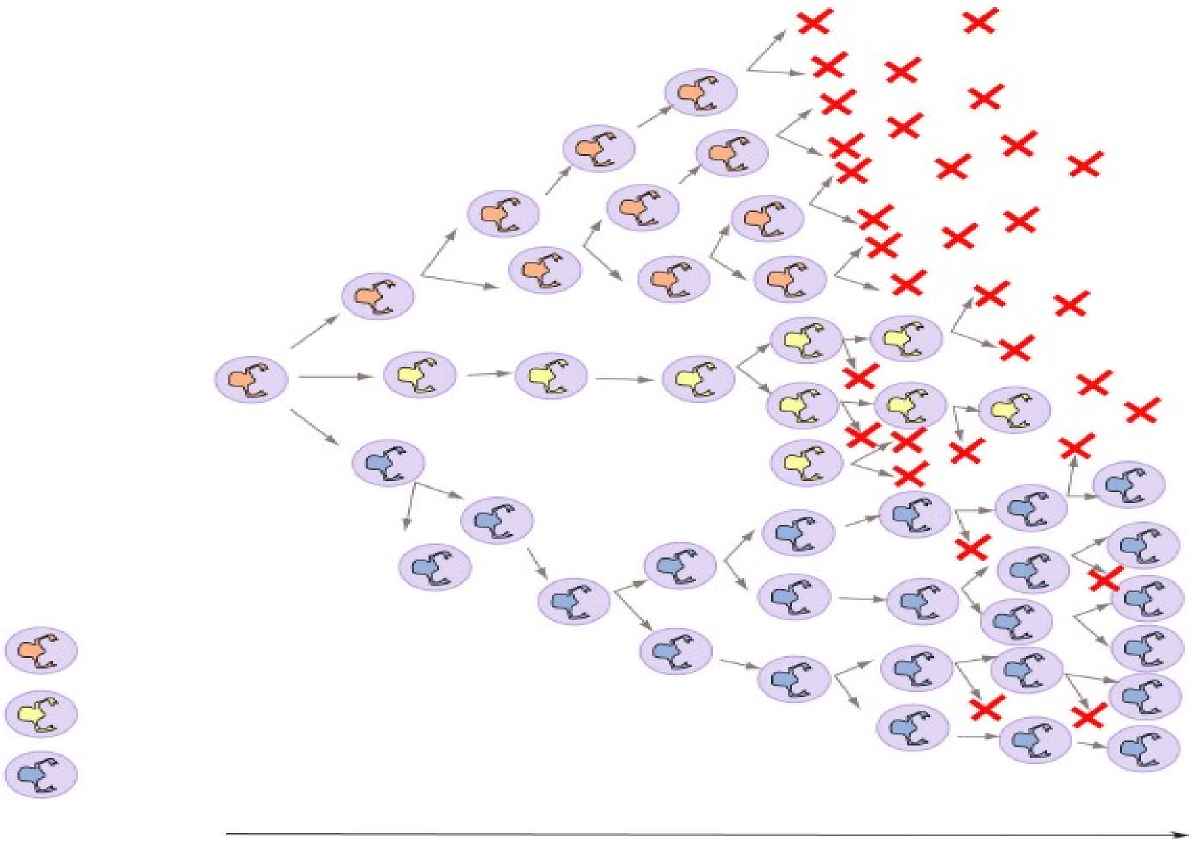
- The virus could evolve to avoid using AZT during reverse transcription.

Changes in the RT active site evolve very quickly



Bad copy makes good evolvability

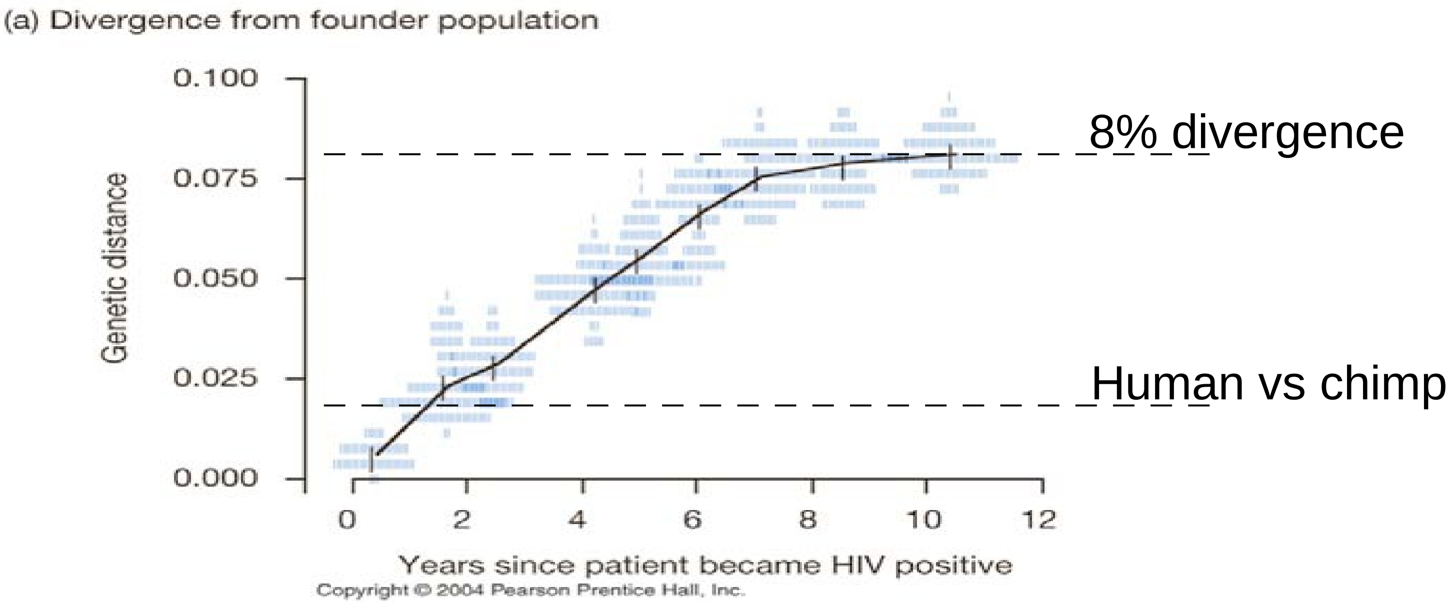
- RT highly error prone
  - No error correction mechanism
  - Highest rates of mutation
  - 50% of the DNA copies mutated
- Virion: Many thousands of generations with in a host (est generation time 1.2 days)

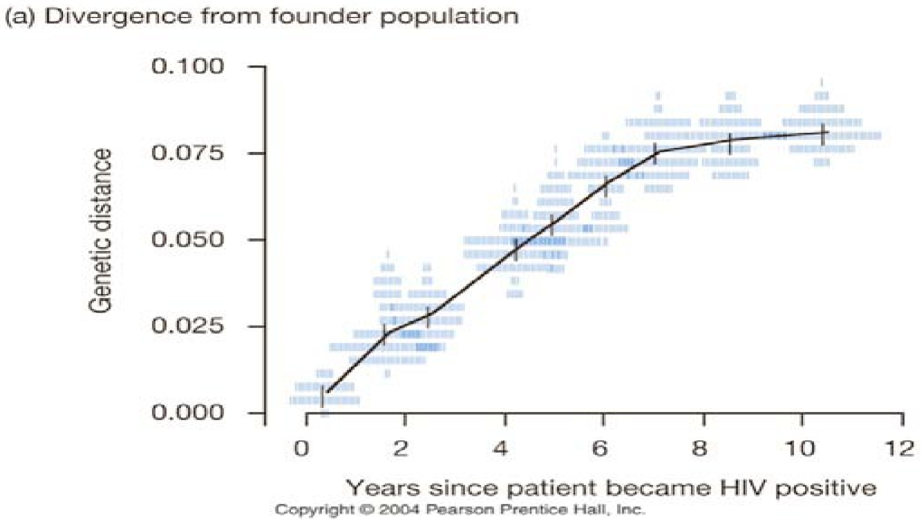


Lessons

- Variation
- Heritable
- Non random survival and reproduction
  - That is natural selection in operation!

Divergence at binding site genes





8% divergence

10 years ~ 3000 generations

- 4 × the divergence between humans and chimp
- Humans and chimps diverged ~5.4 mya

~ 500,000 generations
×2
=1,000,000 generations

1,300 times faster sequence divergence in HIV RT

Compensatory evolution

- AZT-resistant RT will copy more slowly than susceptible RT
  - This fitness trade-off indicates that removal of therapy should lead to a reversion to non-selective forms.
- Would pulsed treatment be better?
  - Body retains copies of old virions
  - Resistance re-evolves very quickly
  - Resistant forms become more efficient with prolonged exposure

Why kill the host?

- Death of the host means the death of all virions carried by the host
- No further possibility of transmission

- Evolution does not think ahead
- Virulence usually correlated with host availability/ease of transmission

Levels of selection

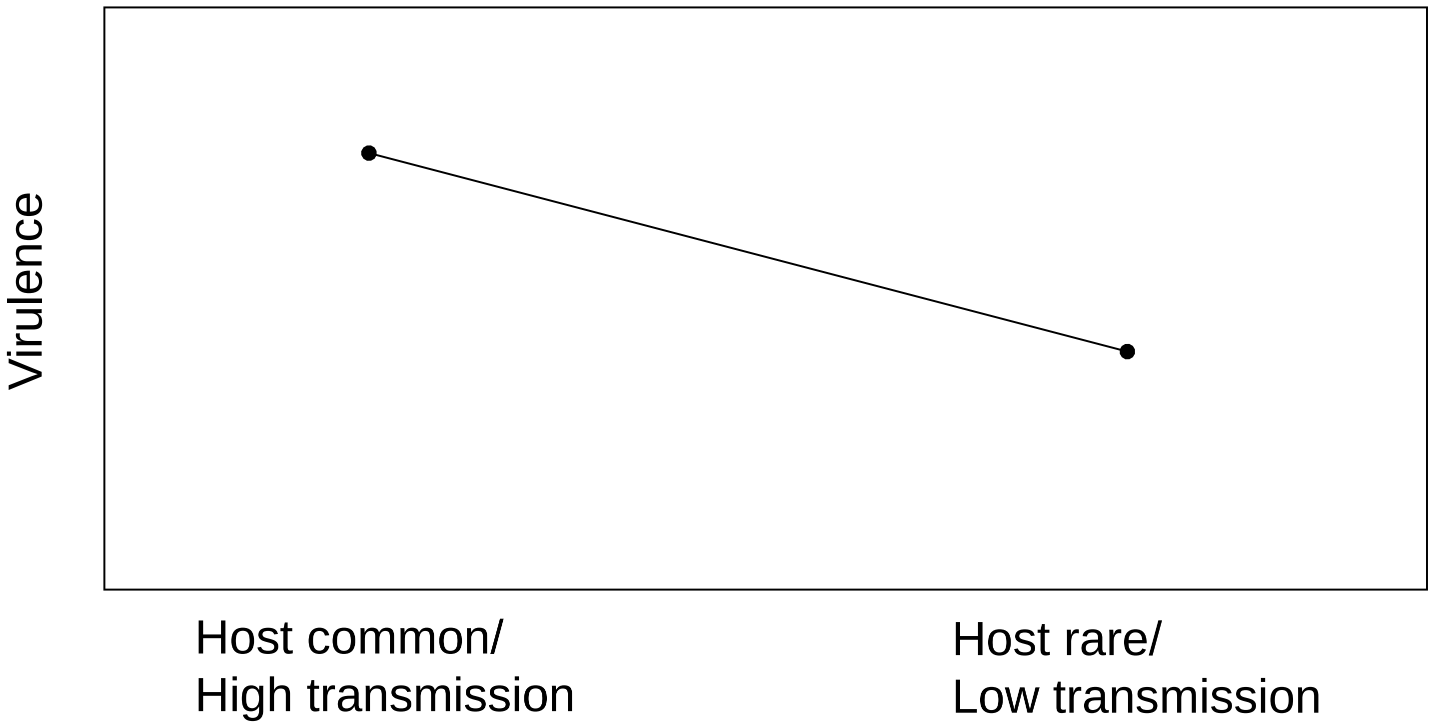
- Fitness of a virion
  - Intra host success[1] × inter host transmission[2]

1. Selection with in the infected host favours the viral particles that multiply most rapidly

   These successful viral particles may rapidly degrade host performance and the probability of transmission

2. Selection for transmission between hosts may favour lower virulence

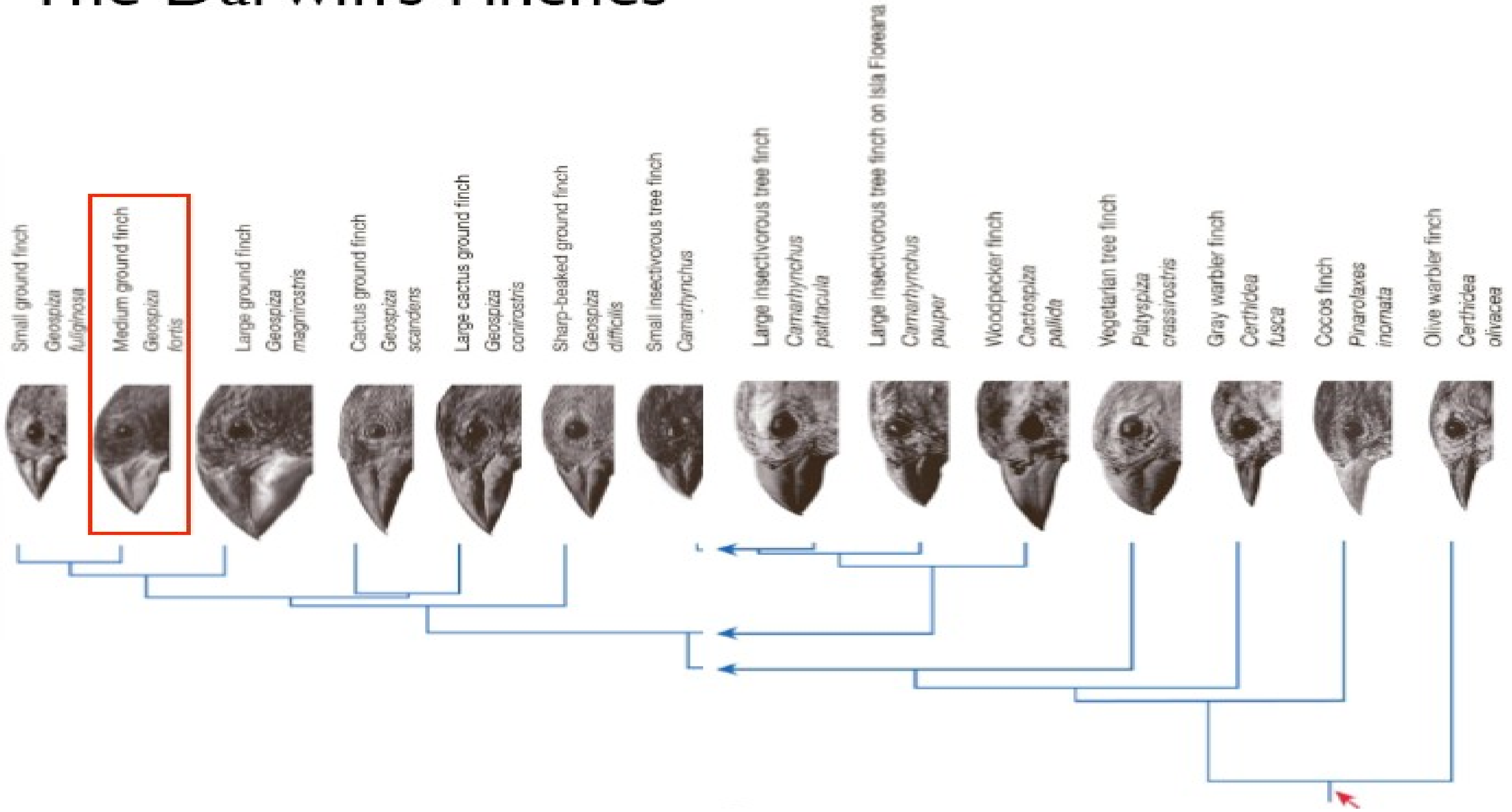
Transmission effects on virulence



The famous finches

- 3 decades of research by Peter and Rosemary Grant and colleagues
- Galapagos is a “natural laboratory”
  - Replica populations relatively isolated on different islands.
  - Smaller islands = easy to census.
  - Survival, reproductive success, morphology can be measured on site.

The Darwin's Finches



Prerequisites for selection

- Genetic variation in the population for a trait related to fitness.

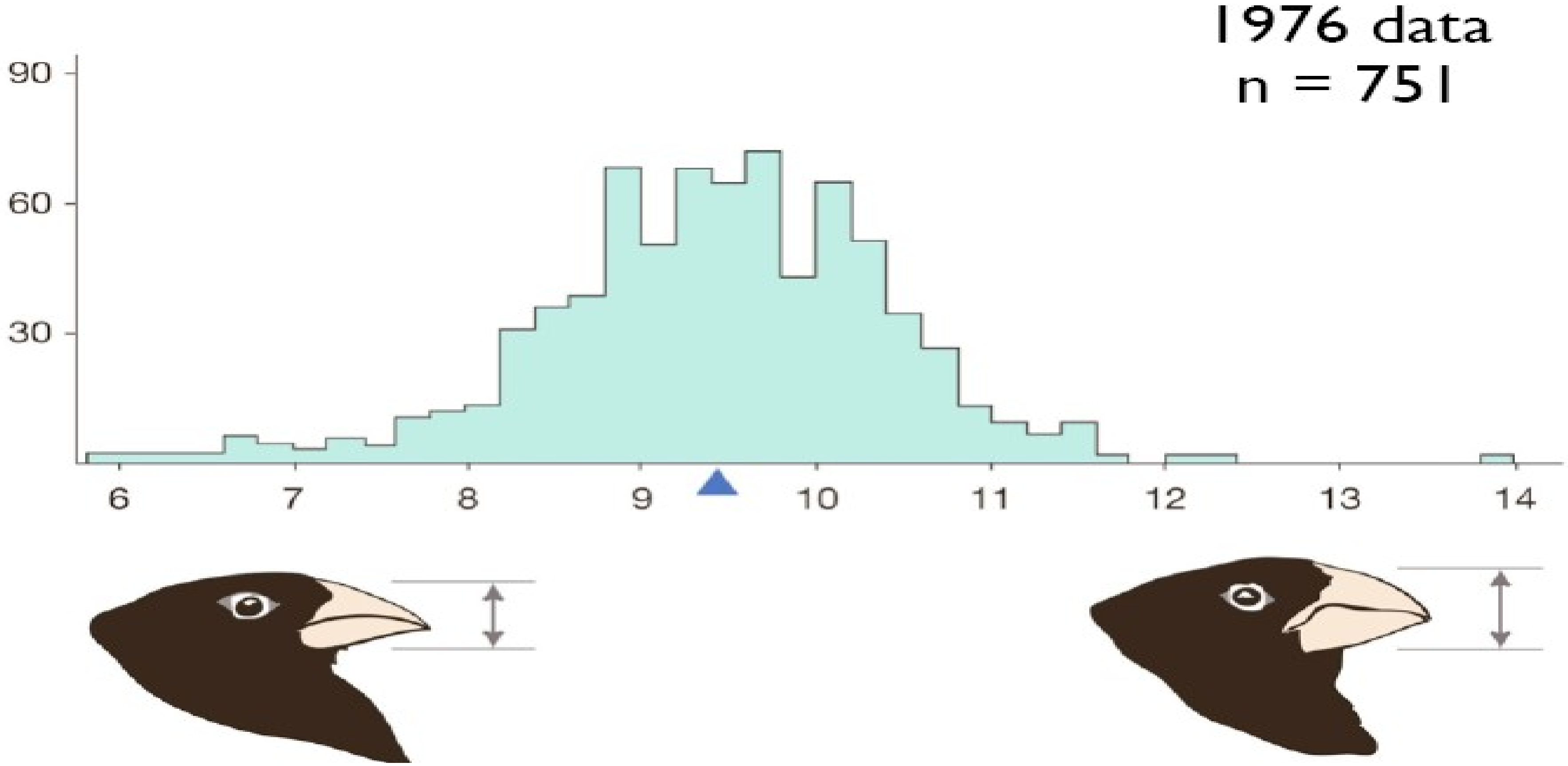
  Beak size important to finches in foraging

- Agent of selection

  seed abundance and type believed to select for beak morphology

  seeds available influenced by season, rainfall etc.

Phenotypic Variation: *G. fortis* beak depth



Is this variation heritable?

Approaches

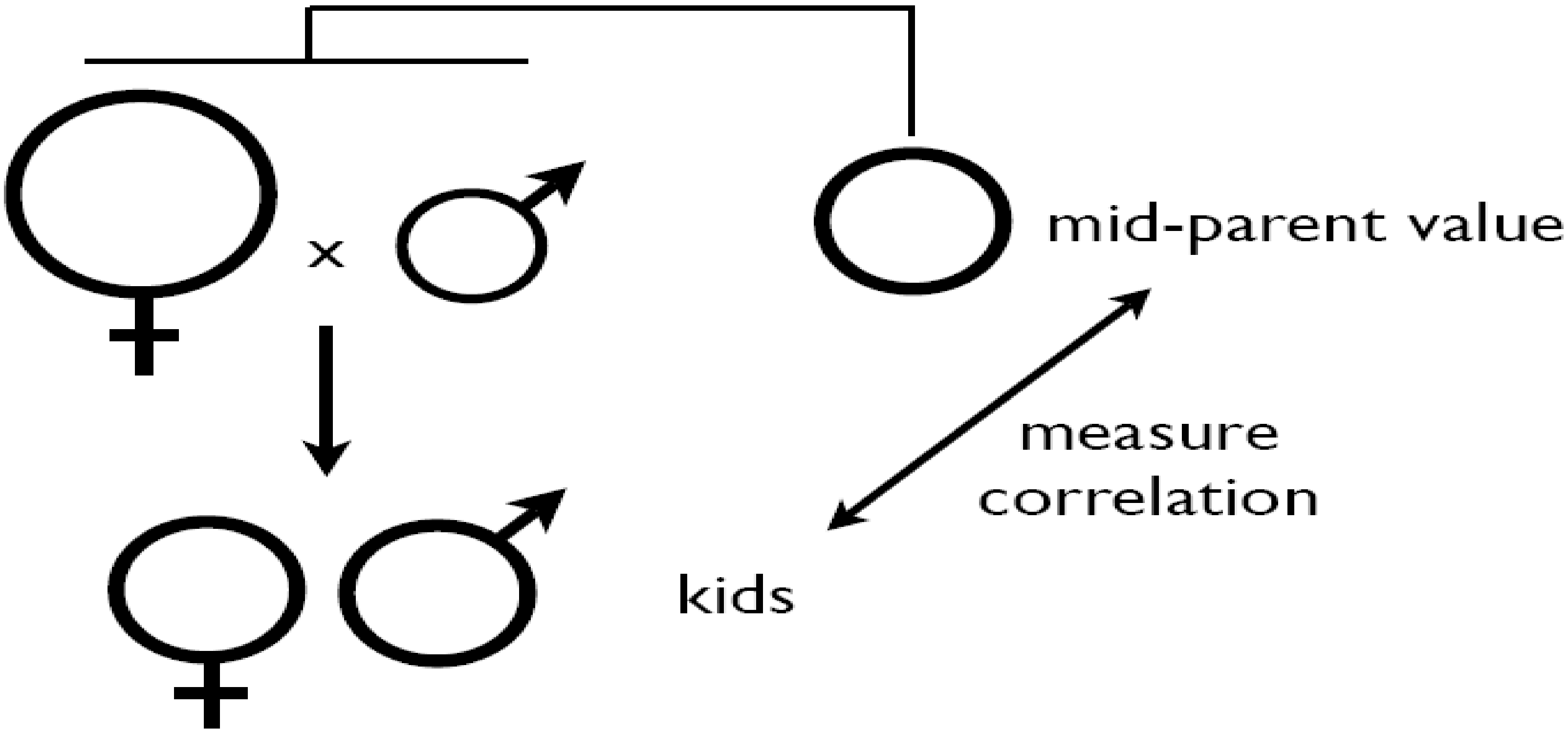
Similarity between relatives

- Parents and offspring
- Siblings

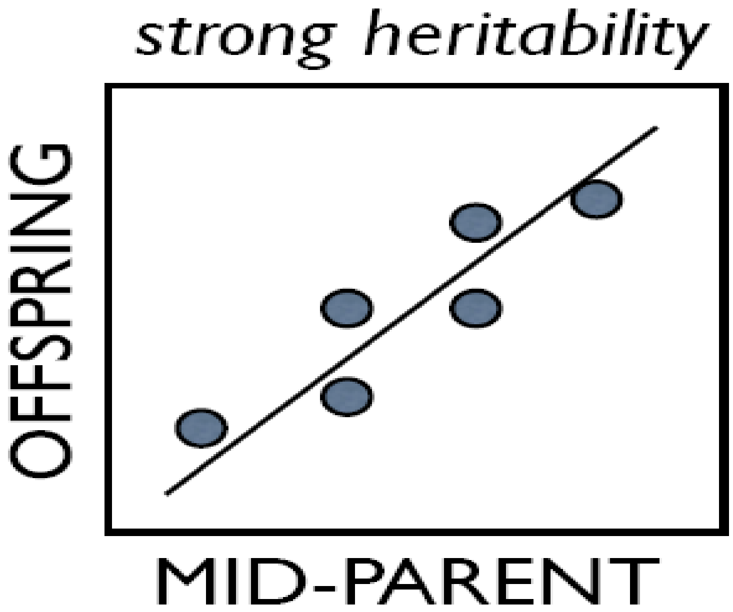
Response to selection

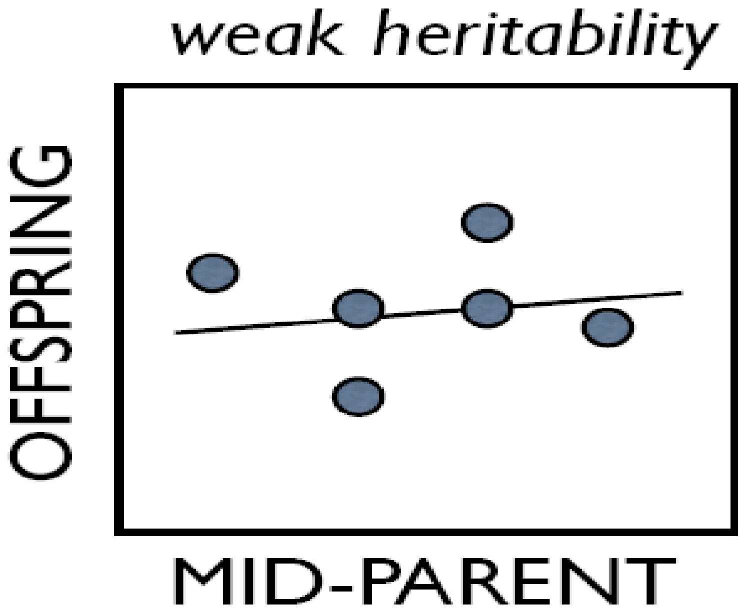
selection will only change the population mean if the variation is heritable

Basic QG



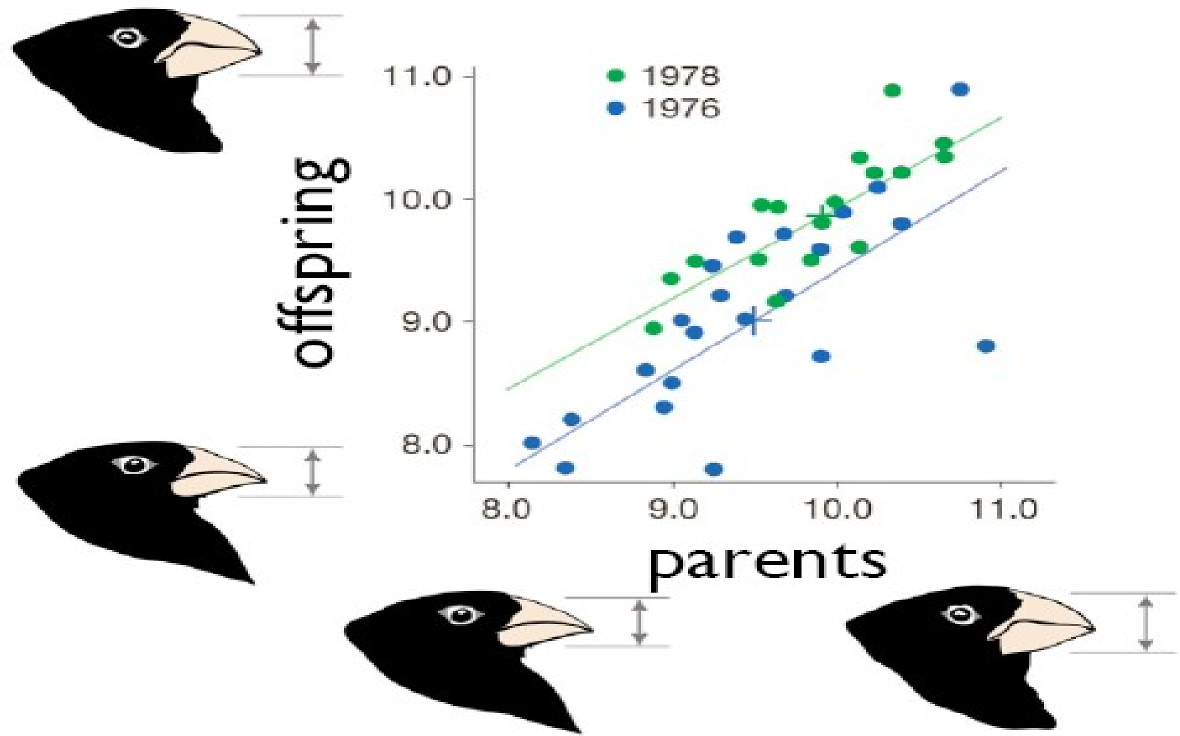
The correlation between parents and offspring is a measure of heritability





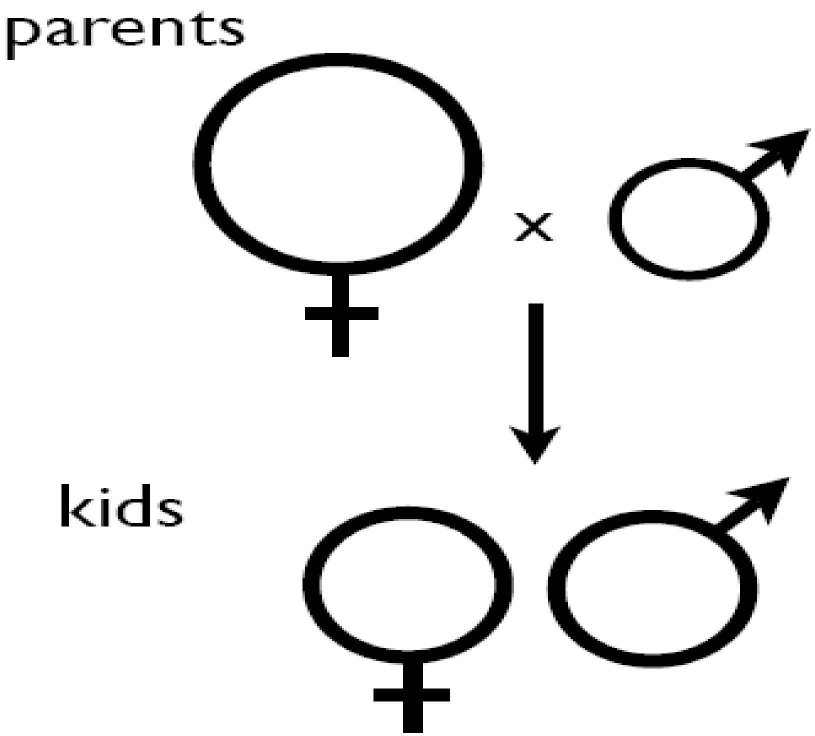
human height $h^2 = 0.6$

back to finches...



from Boag 1983

Problems with heritability



1) kids have same mother

- maternal effects conflated with heritability

2) parents & kids reared in same environment

- $V_{environmental}$ conflated with $V_{genetic}$

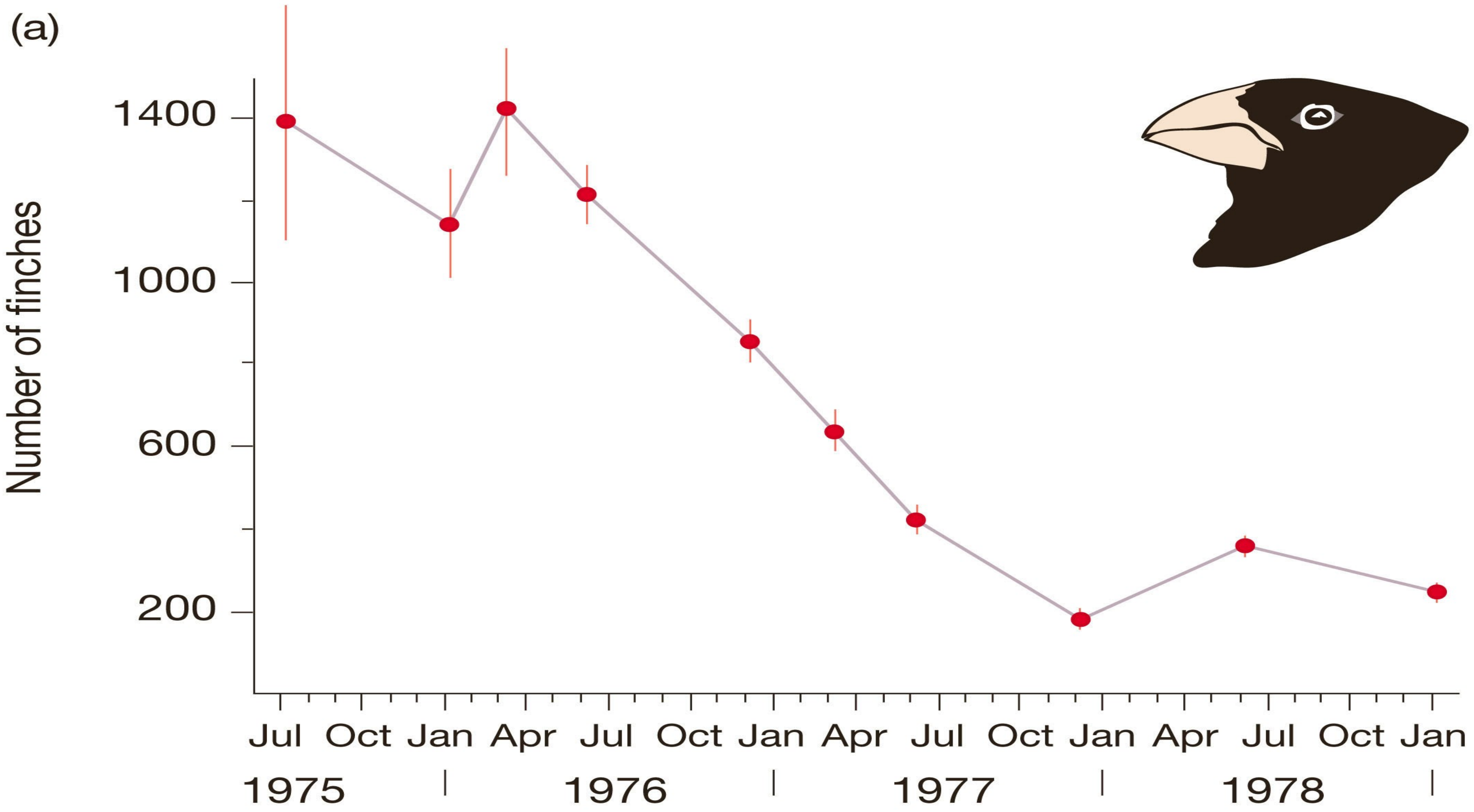
3) Paternity uncertain

- extra-pair copulation reduces estimate of heritability.

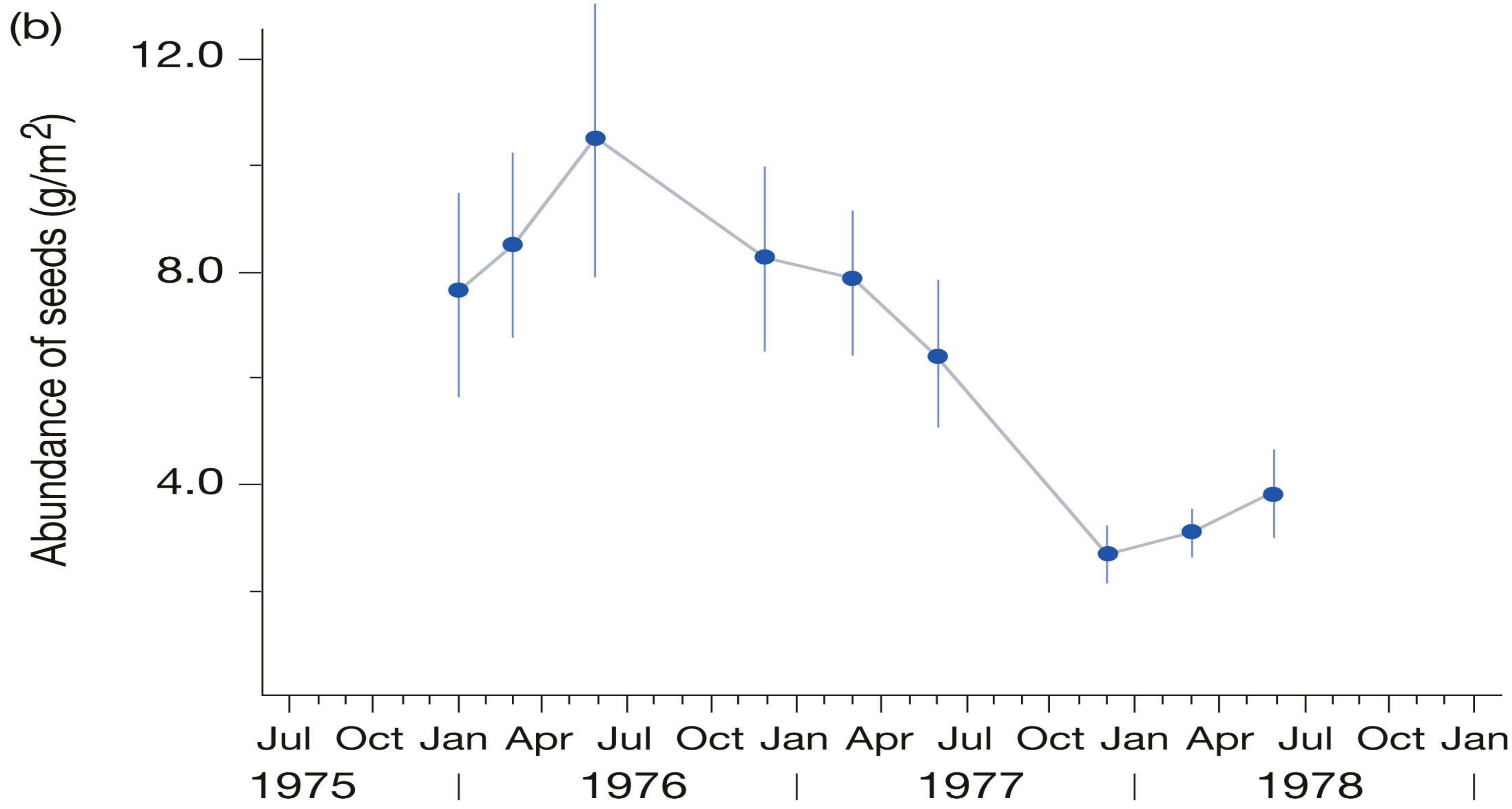
Postulate 3:

Do individuals vary in survivorship and reproduction?

- Study on Daphne Major in 1977
- It was a major year of drought
    - <1/5 normal rainfall
- Plants failed to flower
- Seed production declined
- Birds died *en masse*

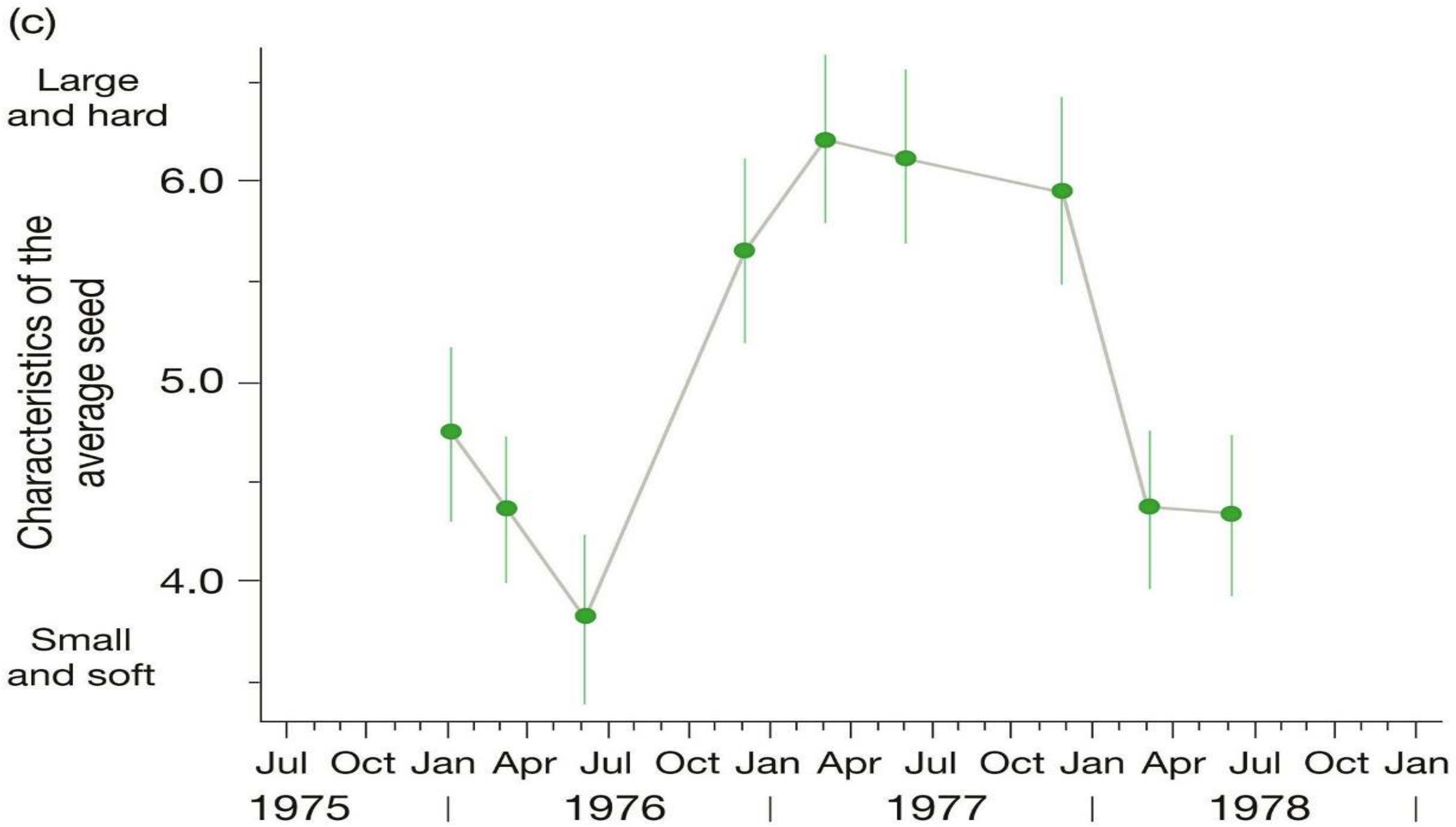


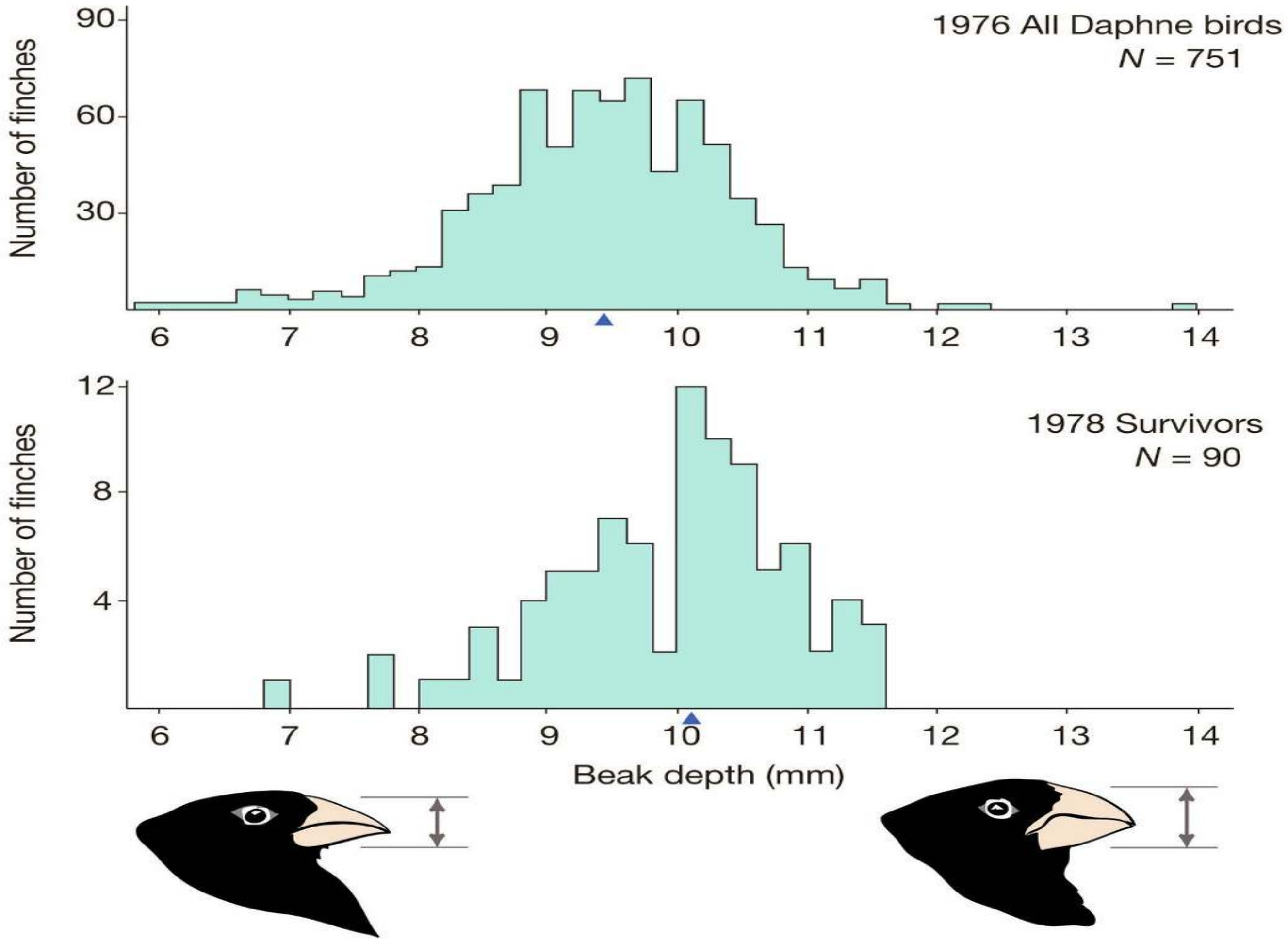
(a)
Number of finches
1400
1000
600
200
Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan
1975
1976
1977
1978


(b)
Abundance of seeds (g/m²)
12.0
8.0
4.0
Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan
1975
1976
1977
1978

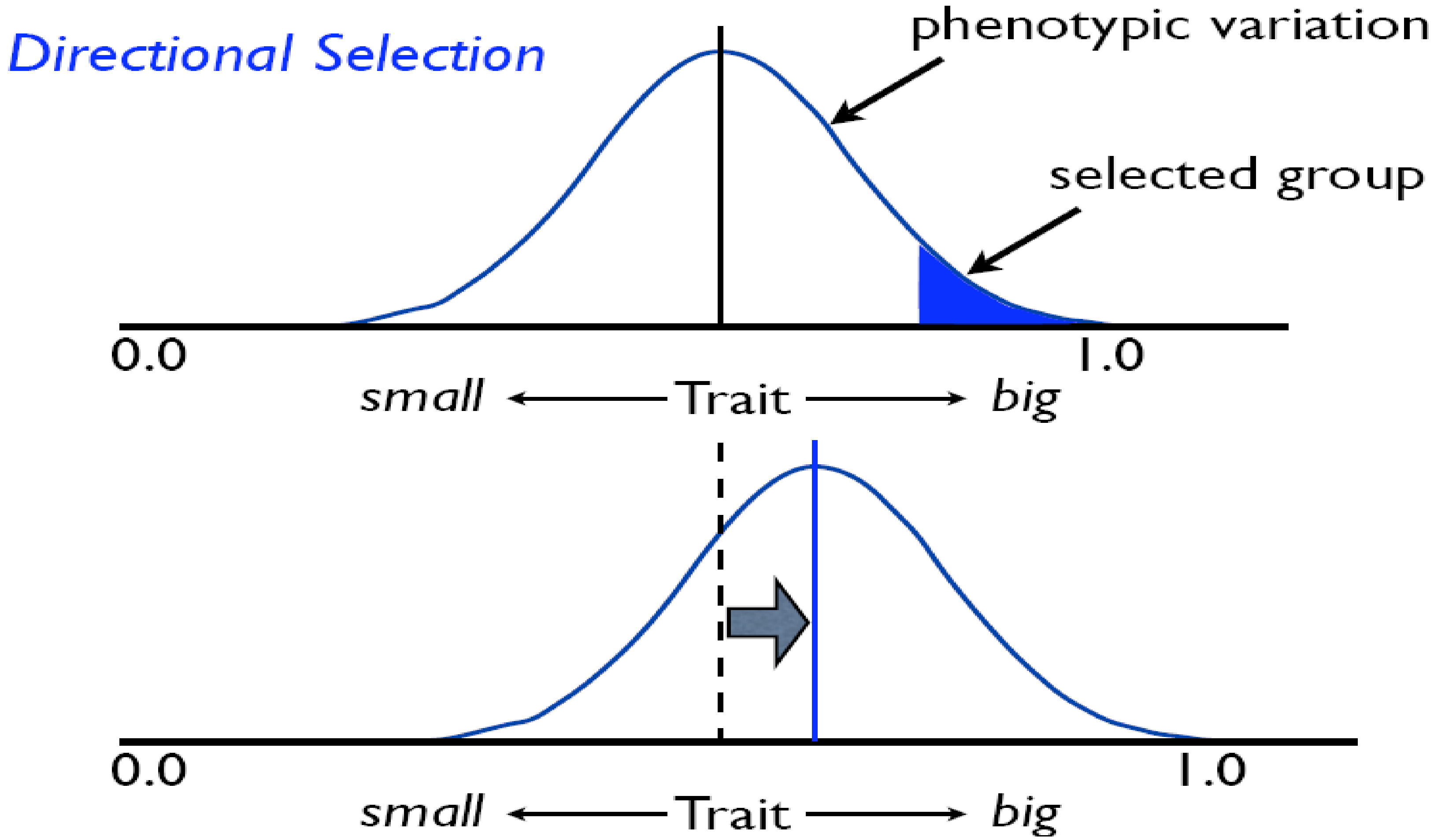
Postulate 4:

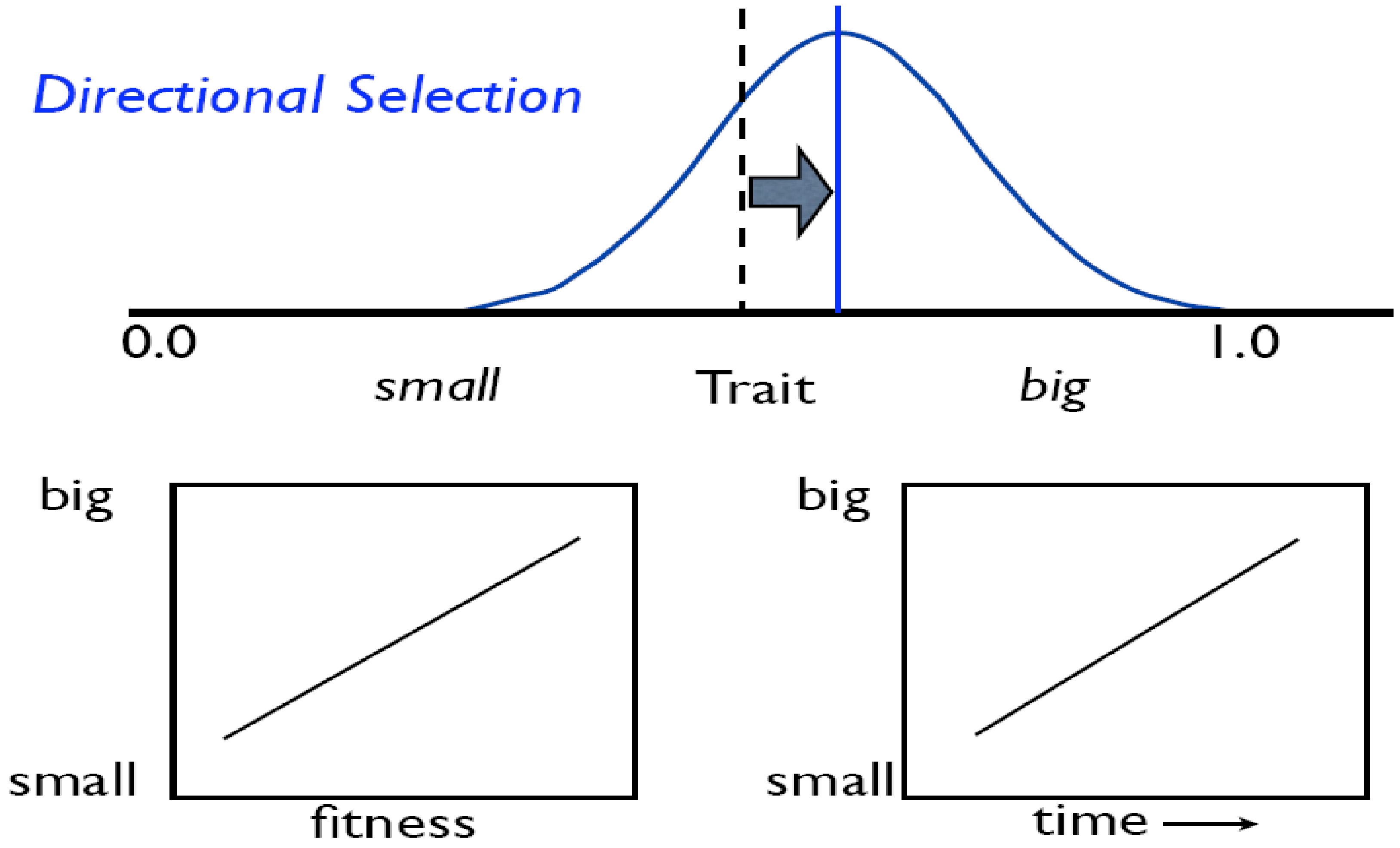
Is survivorship and reproduction non-random?


(c)
Large and hard
Small and soft
Characteristics of the average seed
6.0
5.0
4.0
Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan Apr Jul Oct Jan
1975
1976
1977
1978



90
60
30
Number of finches
1976 All Daphne birds
N = 751
6
7
8
9
10
11
12
13
14
12
8
4
Number of finches
1978 Survivors
N = 90
6
7
8
9
10
11
12
13
14
Beak depth (mm)

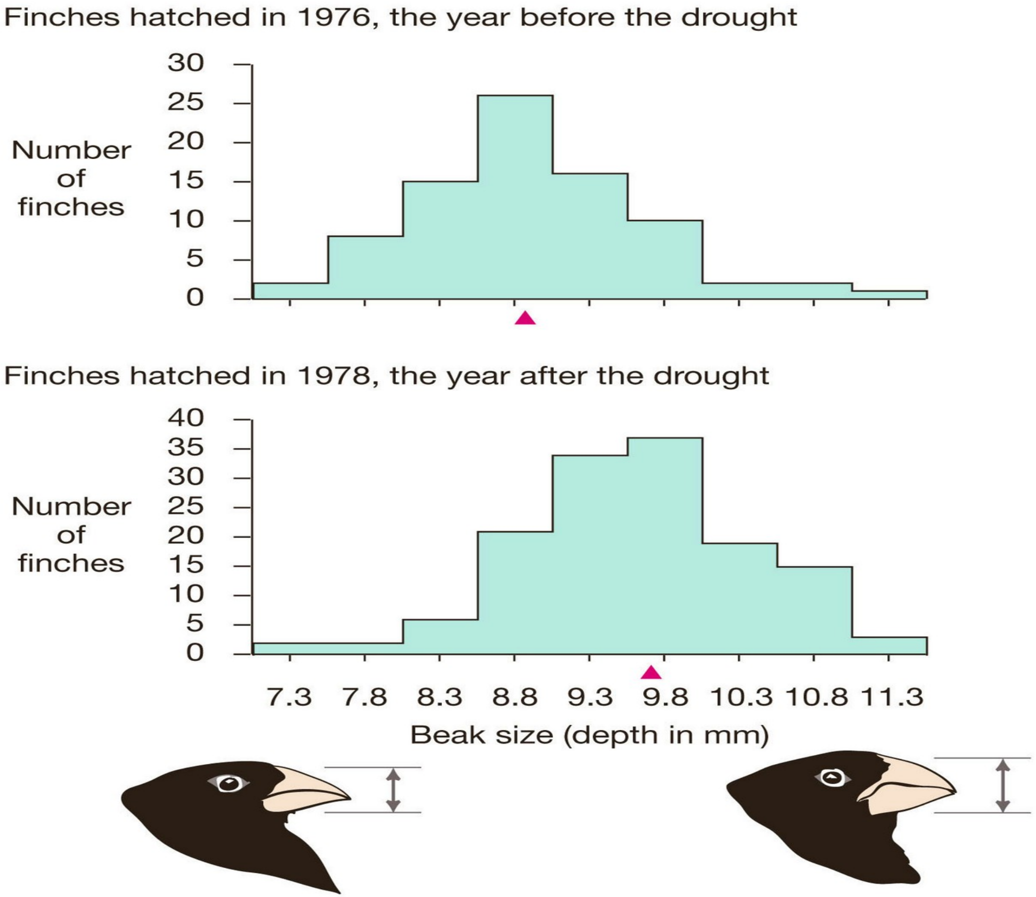

Directional Selection
phenotypic variation
selected group
0.0
1.0
small
Trait
big
0.0
1.0
small
Trait
big



Directional Selection
0.0
1.0
small
Trait
big
big
small
fitness
big
small
time

Therefore,

Did the finch population Evolve?



Finches hatched in 1976, the year before the drought
30
25
20
15
10
5
0
Number of finches
Finches hatched in 1978, the year after the drought
40
35
30
25
20
15
10
5
0
Number of finches
7.3 7.8 8.3 8.8 9.3 9.8 10.3 10.8 11.3
Beak size (depth in mm)