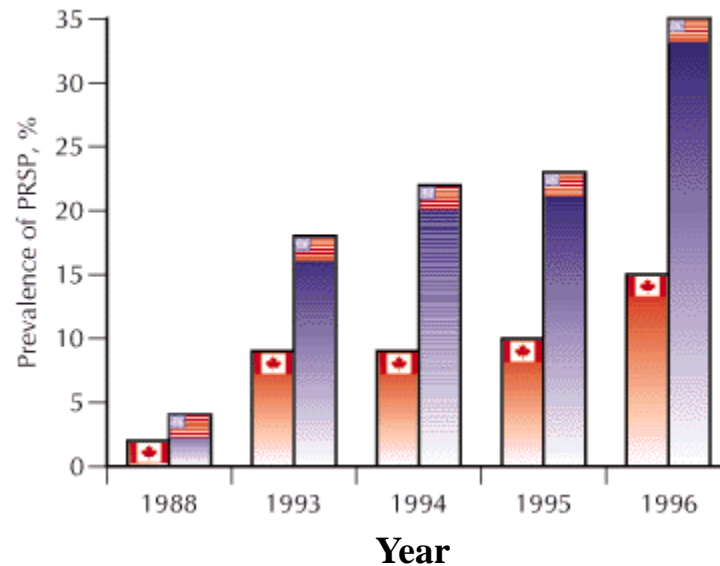# Natural Selection and Adaptation

The evolution of penicillin resistance in
***Streptococcus pneumoniae* infection in Canada and the US.**

Examples of Adaptation

Chiloglottis formicifera

- **Mimics female wasps**

Examples of Adaptation

A reed warbler feeds a common cuckoo chick

Host eggs   **Cuckoo eggs**
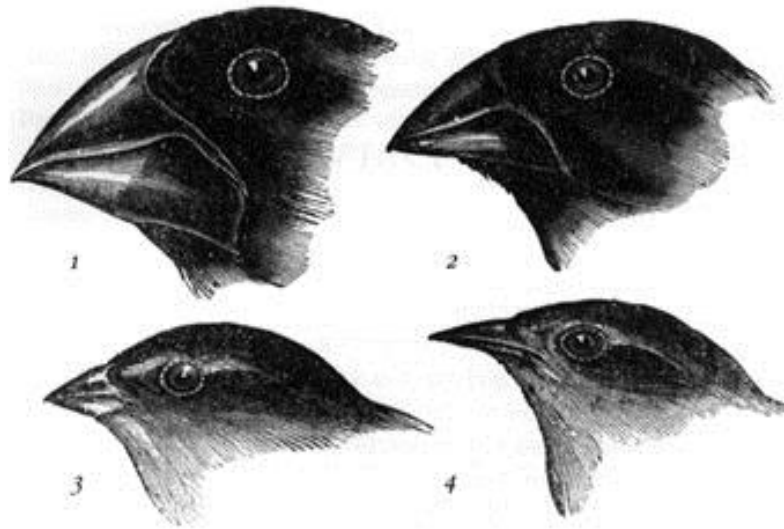
Examples of Adaptation


Monarch

Viceroy

Adaptation is a consequence of natural selection

Adaptation – A feature is an adaptation for some function if it has become prevalent or is maintained in a population because of natural selection for that function
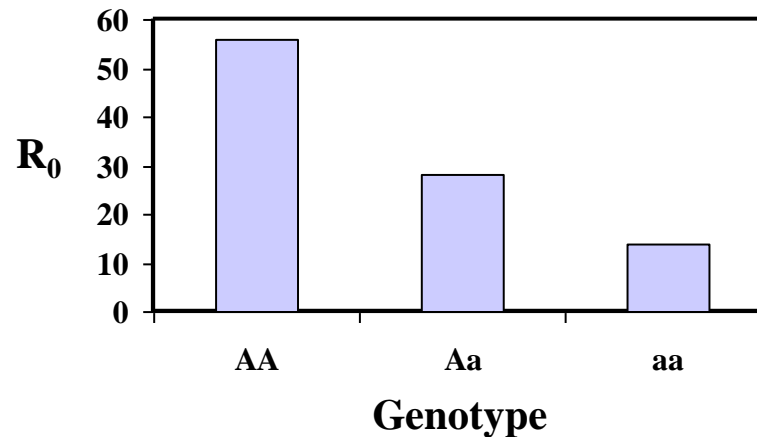
What is natural selection?

Natural selection – Any consistent difference in **FITNESS** (i.e., survival and reproduction) among phenotypically different individuals.
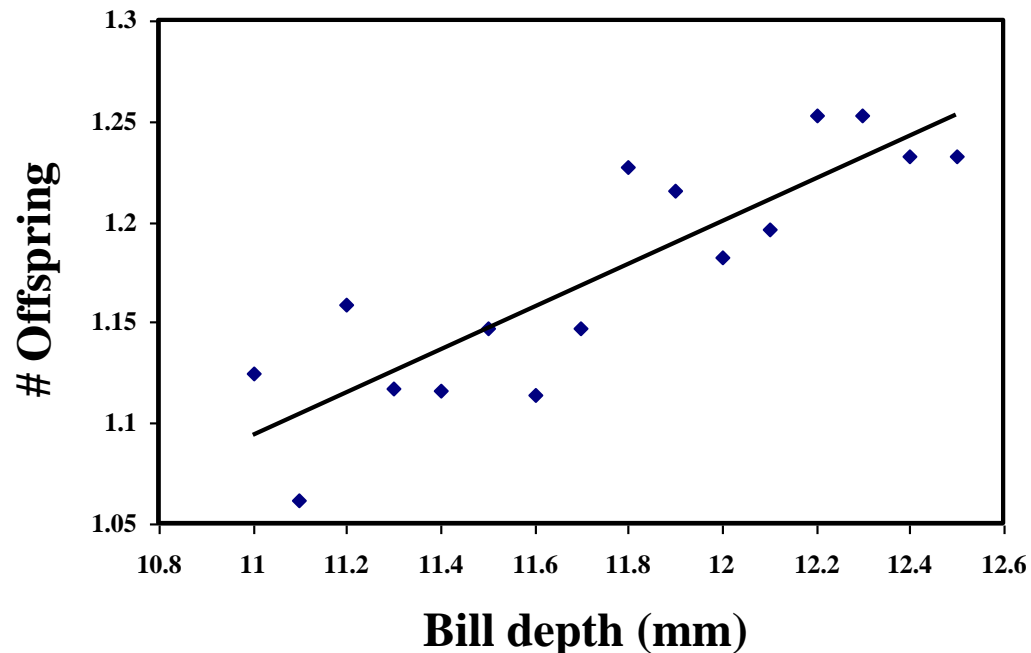
What is fitness?

Fitness – The fitness of a genotype is the average per capita lifetime contribution of individuals of that genotype to the population after one or more generations*

* Note that R_0 is a good measure of an organisms fitness only in a population with a stable size. Things are more complicated in growing populations!

Calculating fitness using life tables

Genotype AA

x	l_x	m_x	$l_x m_x$
1	1	0	0
2	1	1	1
3	.75	1	.75
4	.25	1	.25

$$W_{AA} = R_{0,AA} = 2.0$$

Genotype Aa

x	l_x	m_x	$l_x m_x$
1	1	0	0
2	.75	1	.75
3	.5	1	.50
4	.25	1	.25

$$W_{Aa} = R_{0,Aa} = 1.5$$

Genotype aa
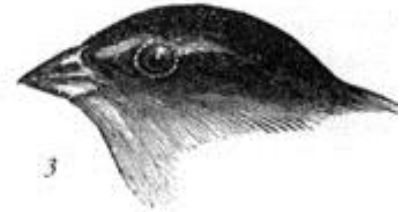
x	l_x	m_x	$l_x m_x$
1	1	0	0
2	.5	1	.5
3	.25	1	.25
4	.1	1	.1

$$W_{aa} = R_{0,aa} = .85$$

The three genotypes have different absolute fitnesses

Absolute vs. relative fitness

Genotype AA	Genotype Aa	Genotype aa
$W_{AA} = R_{0,AA} = 2.0$	$W_{Aa} = R_{0,Aa} = 1.5$	$W_{aa} = R_{0,aa} = .85$

- **The rate of genetic change under selection depends on *relative*, not *absolute*, fitness**

- **Relative fitness defines the fitness of genotypes relative to the best genotype and the selection coefficient *s***

$w_{AA} = \dfrac{W_{AA}}{W_{Max}} = \dfrac{2.0}{2.0} = 1$	$w_{Aa} = \dfrac{W_{Aa}}{W_{Max}} = \dfrac{1.5}{2.0} = .75$	$w_{aa} = \dfrac{W_{aa}}{W_{Max}} = \dfrac{.85}{2.0} = .425$
$s_{AA} = 0$	$s_{Aa} = .25$	$s_{aa} = .575$

Calculating the average fitness of a population using *w*

If a population is in Hardy-Weinberg proportions, the mean fitness of the population can be easily calculated:

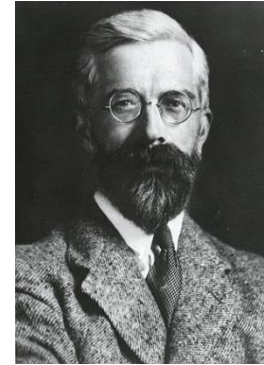$$\overline{w} = p^2 w_{AA} + 2pq w_{Aa} + q^2 w_{aa}$$

We now have the information we need to predict evolution

Predicting evolution at a single locus

Sewall Wright

$$\Delta_s\, p = \frac{pq}{\overline{w}}\,\frac{d\overline{w}}{dp}$$

R.A. Fisher

The slope of population mean fitness as a function of allele frequency

Fisher's fundamental theorem of natural selection

• The allele frequency always changes in such a way that the mean fitness of the population increases

• The rate of increase in population mean fitness is proportional to *pq*, the genetic variance of the population

Modes of selection on single genes

$s_{AA} < s_{Aa} < s_{aa}$ or $s_{aa} < s_{Aa} < s_{AA}$

- **Directional – One homozygote has the largest fitness, the other homozygote the smallest fitness**

$s_{Aa} < s_{aa}$ & s_{AA}

- **Overdominance – Heterozygote has the largest fitness**

$s_{Aa} > s_{aa}$ & s_{AA}

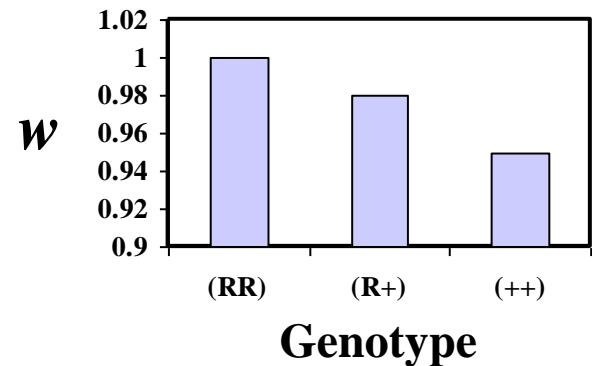- **Underdominance – Heterozygote has the smallest fitness**
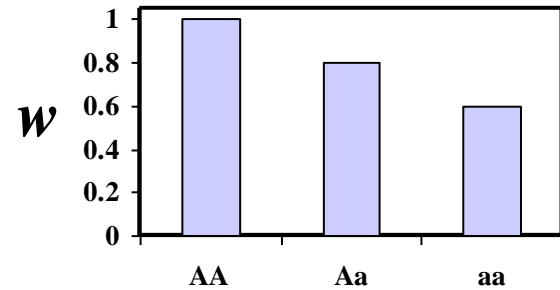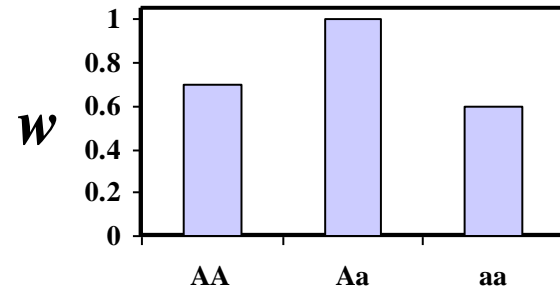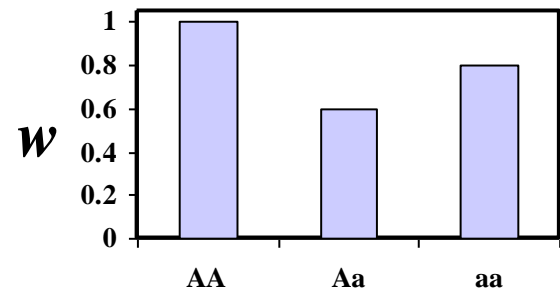
Directional selection
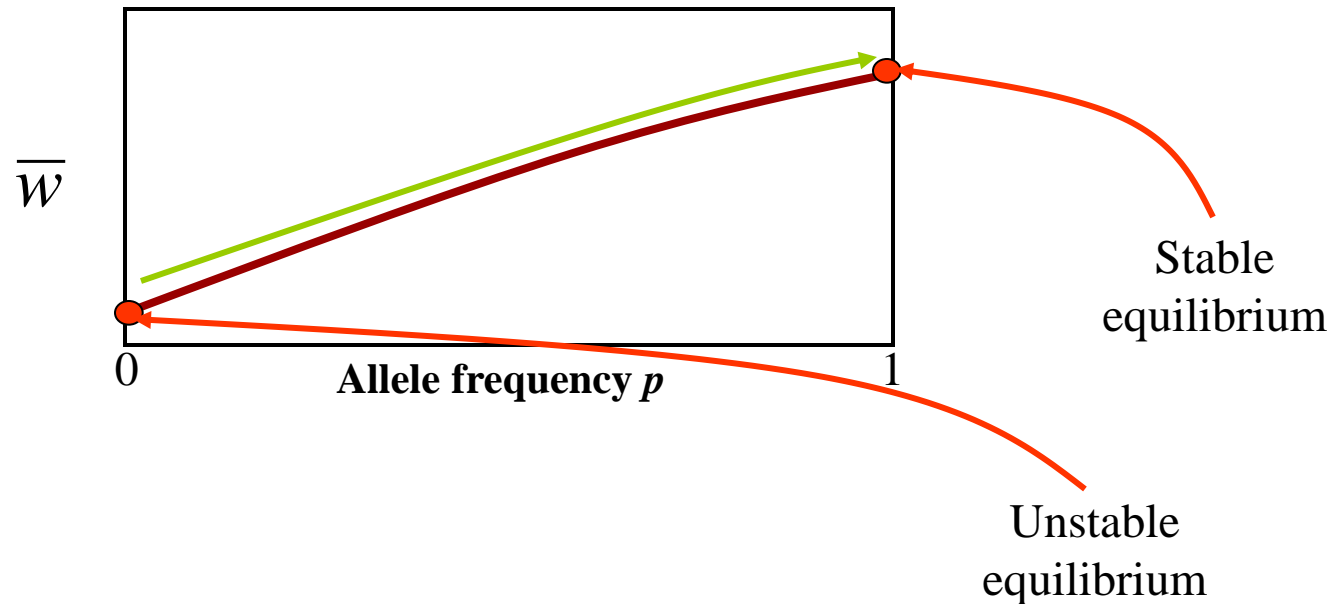
An Example: DDT resistance in Aedes aegypti

$(s_{RR} \approx 0; s_{R+} \approx .02; s_{++} \approx .05)$

- **Transmits Dengue Fever**

- **Target of extensive control efforts using DDT through 1968.**

- **Resistance to DDT is controlled by a single locus**

- **The R allele is resistant and the normal allele + is susceptible**

Predicting the outcome of directional selection

$$\Delta_s p = \frac{pq}{\overline{w}} \frac{d\overline{w}}{dp}$$

$\overline{w}$

Allele frequency p
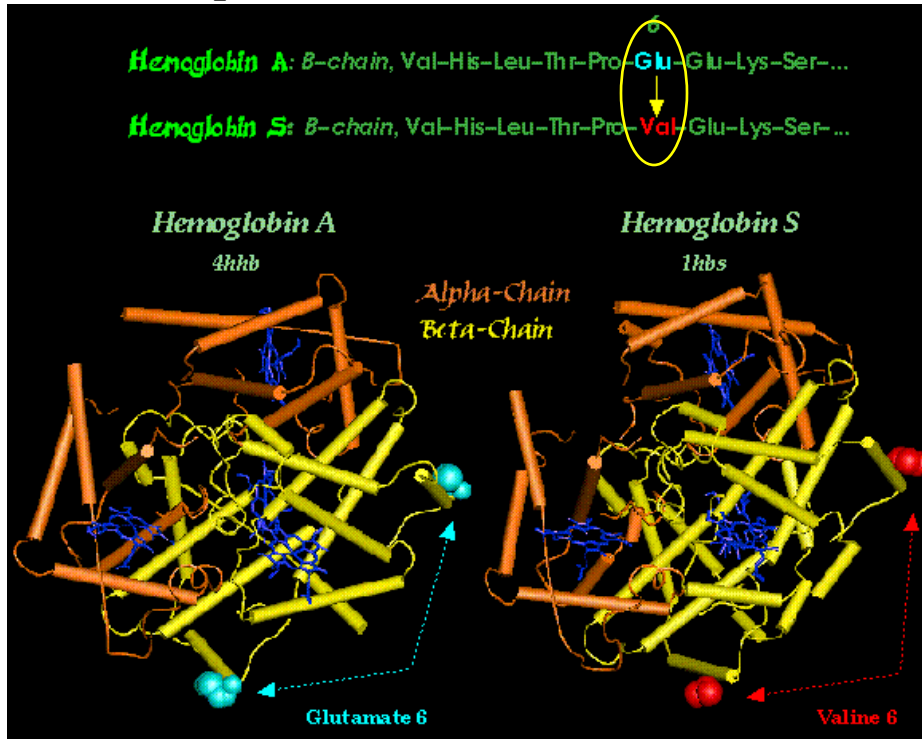
0   1

Stable
equilibrium

Unstable
equilibrium

• Population evolves until genetic variance is exhausted

• Population evolves to a global fitness maximum

• No genetic polymorphism/variance is maintained
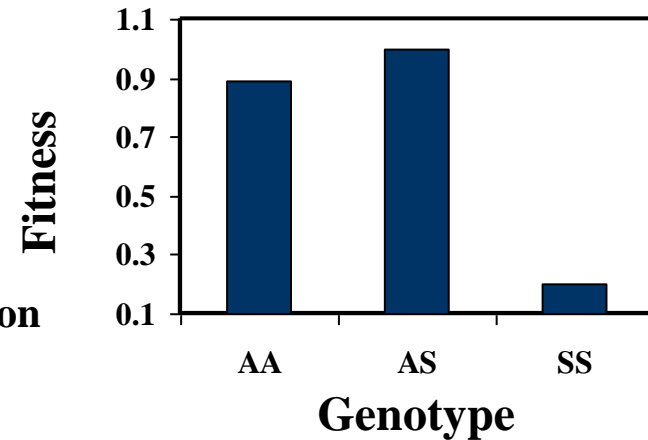
Directional selection on single loci

- **Directional selection ultimately leads to the fixation of the selectively favored allele.**

- **Polymorphism is not maintained.**

- **The empirical observation that polymorphism is prevalent suggests that other evolutionary forces (e.g., mutation, gene flow) must counteract selection, or that selection fluctuates over time so that different alleles are favored at different times.**

Stabilizing/Overdominant selection on single loci

An Example: Sickle cell and Malaria resistance.

Hemoglobin A: B-chain, Val-His-Leu-Thr-Pro-Glu-Glu-Lys-Ser-...

Hemoglobin S: B-chain, Val-His-Leu-Thr-Pro-Val-Glu-Lys-Ser-...

Hemoglobin A — 4hhb
Hemoglobin S — 1hbs
Alpha-Chain
Beta-Chain
Glutamate 6 — Valine 6

$(s_{AA} = .11, s_{SS} = .8)$
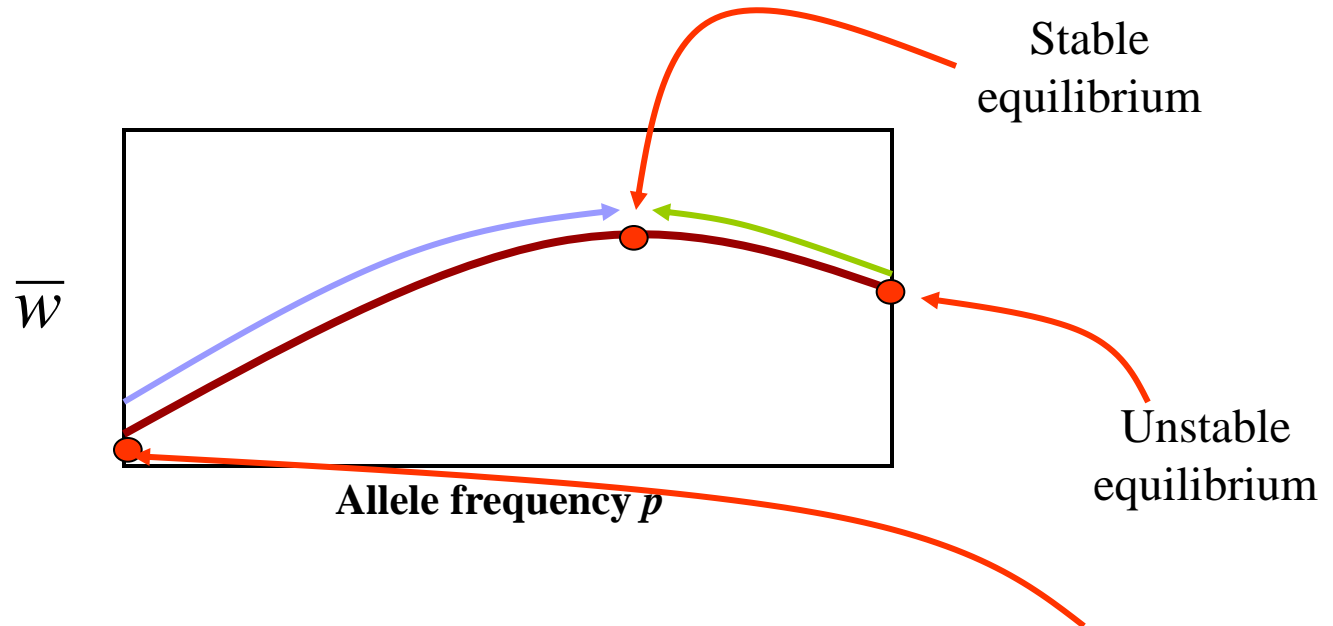

Fitness — Genotype — AA — AS — SS

• **Two alleles, A and S that differ at only a single amino acid position**

• **AA Individuals are susceptible to Malaria**

• **AS Individuals are resistant to Malaria and have only mild anemia**

• **SS Individuals have severe anemia.**

Predicting the outcome of overdominant selection

$$\Delta_s p = \frac{pq}{\overline{w}} \frac{d\overline{w}}{dp}$$

$\overline{w}$

Allele frequency *p*

Stable equilibrium

Unstable equilibrium

Unstable equilibrium

- Population evolves until $\dfrac{d\overline{w}}{dp} = 0$

- Population evolves to a global fitness maximum

- Genetic polymorphism is maintained

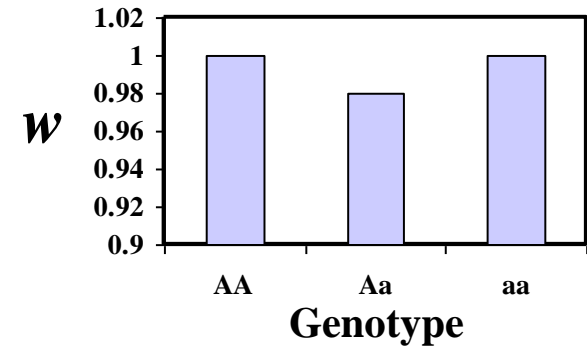# Overdominant selection on single loci

- **Overdominant selection leads to a stable polymorphism because heterozygotes, which carry both alleles, have the highest fitness**

- **This is compatible with the empirical observation that genetic polymorphism is abundant. However, overdominant selection may be quite rare.**

Underdominant selection on single loci
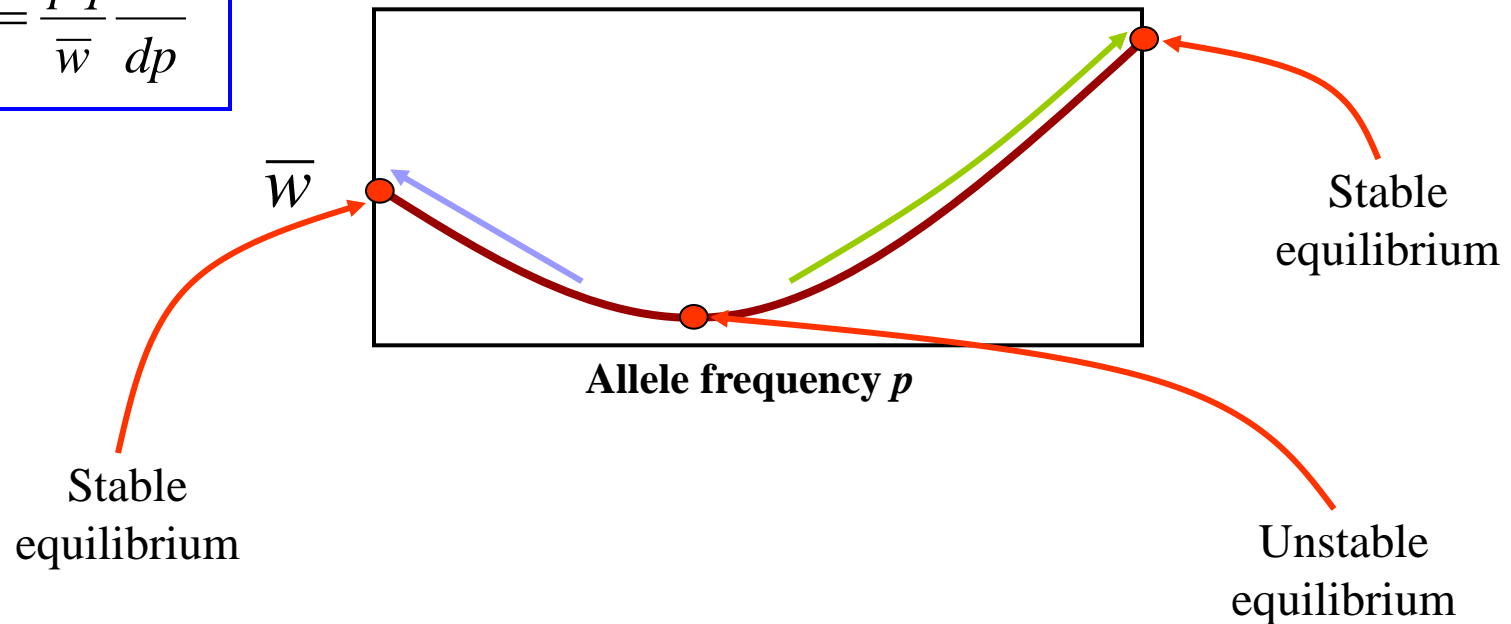
A hypothetical example: Bimodal resources

AA   Aa   aa
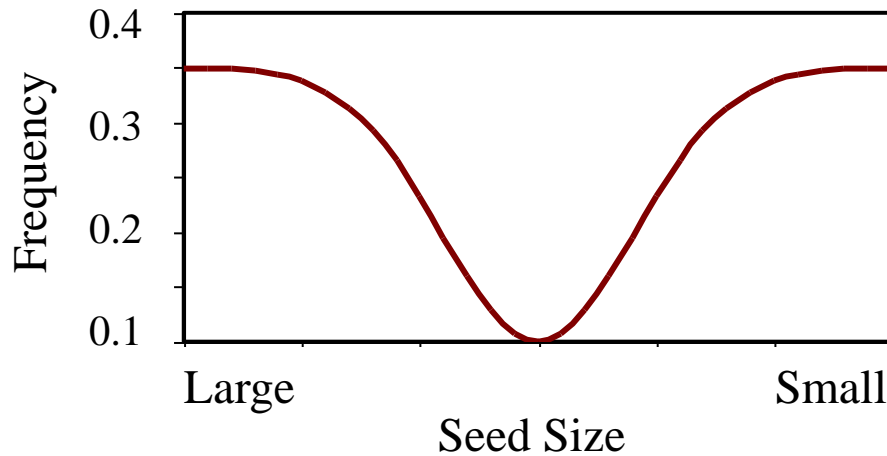
$(s_{AA} = 0; s_{Aa} = .02; s_{aa} = 0)$

Predicting the outcome of underdominant selection

$$\Delta_s p = \frac{pq}{\overline{w}} \frac{d\overline{w}}{dp}$$

$\overline{w}$

Allele frequency *p*

Stable
equilibrium

Stable
equilibrium

Unstable
equilibrium

- Population evolves to a **local** fitness maximum

- No genetic polymorphism/variance is maintained

- Sensitive to the 'starting point' of evolution

Underdominant selection on single loci

• **With underdominant selection initial allele frequency matters!**

• **As a consequence, polymorphism is not maintained and all genetic variance is lost**

Practice Problem

You are studying a population of Steelhead Trout and would like to know to what extent body mass is heritable. To this end, you measured the body mass of male and female Steelhead as well as the body mass of their offspring. Use the data from this experiment (below) to estimate the heritability of body mass in this population of Steelhead.

Maternal Body Mass (Kg)	Paternal Body Mass (Kg)	Average Offspring Body Mass (Kg)
2.1	2.6	2.3
2.5	2.9	2.5
1.9	3.1	2.7
2.2	2.8	2.4
1.8	2.7	2.3
2.4	2.4	2.2
2.3	2.9	2.7

From single loci to quantitative traits

Frequency — Plant height

Frequency — Plant height
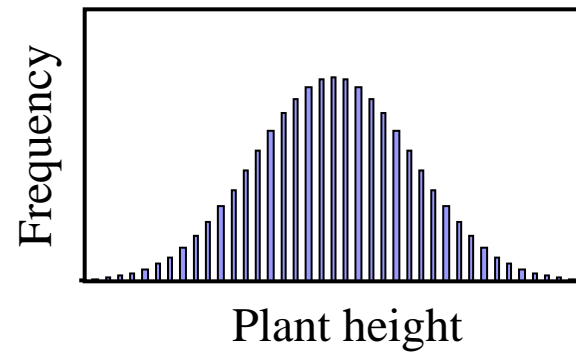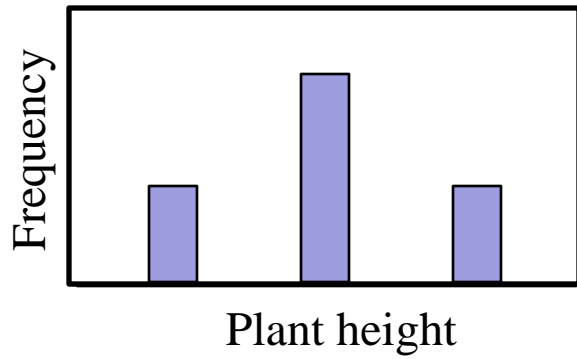
Predicting the evolution of quantitative traits

• **Quantitative traits are controlled by many genetic loci**

• **It is generally impossible to predict the fate of alleles at all the loci**

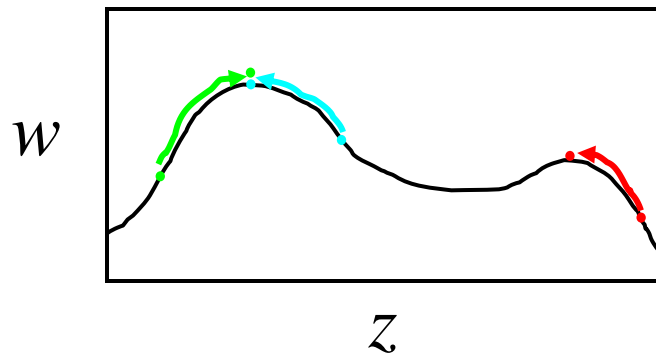• **Consequently, predictions are generally restricted to the mean and the variance (a statistical approach)**

Is there a general rule that applies in all cases?

As long as **additive genetic variance remains constant** the following holds true:

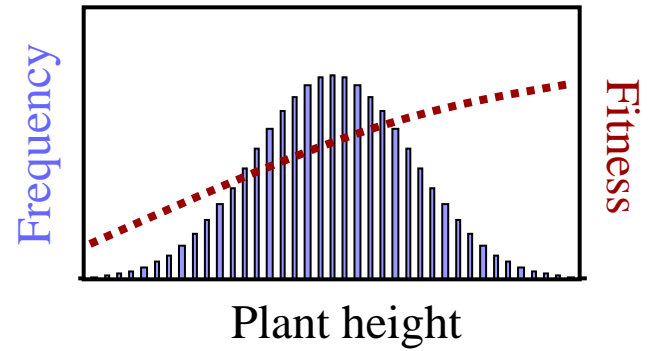$$\Delta \bar{z} = h_N^2 \boxed{\text{cov}[z, w]}$$
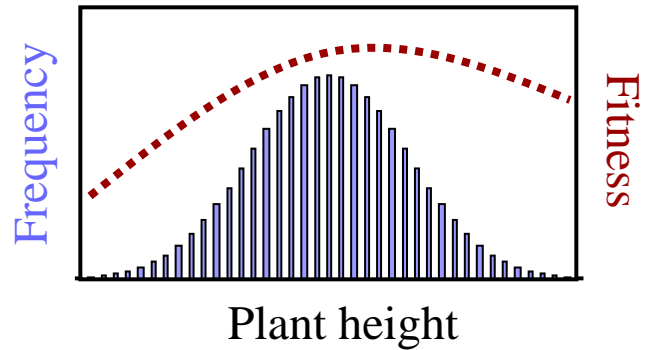
Covariance again!

- A population always evolves to increase its mean fitness locally (no valley crossing)

- The rate of evolution is proportional to the additive genetic variance

- Strong parallels to single locus results
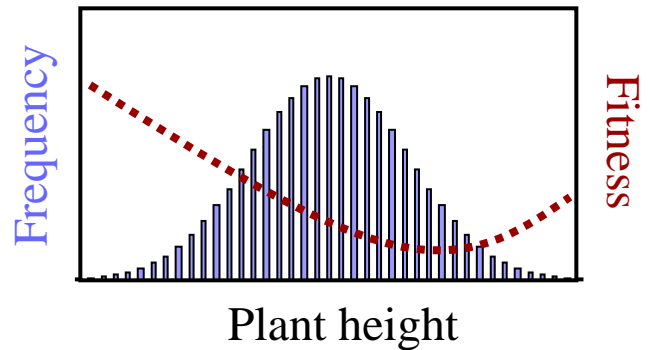
Modes of selection on quantitative traits
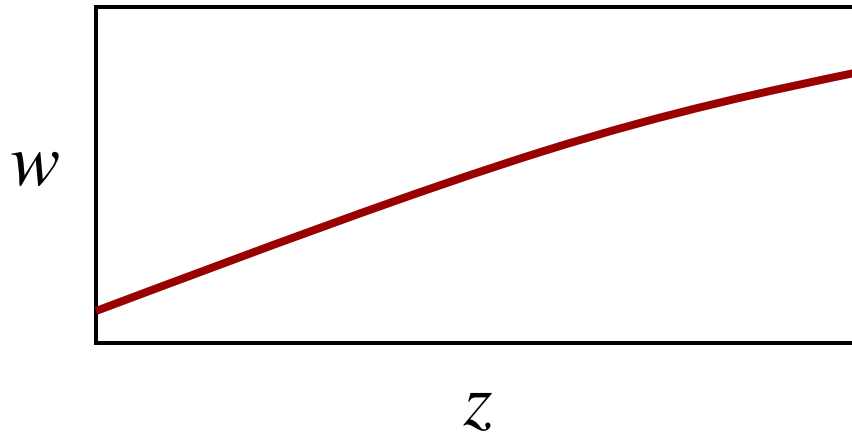
• Directional
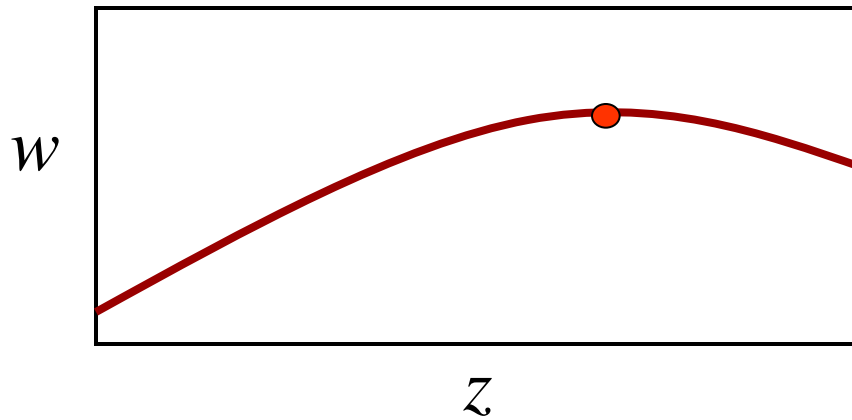

• Stabilizing

• Disruptive

Each type of selection has a different evolutionary outcome and consequence for adaptation
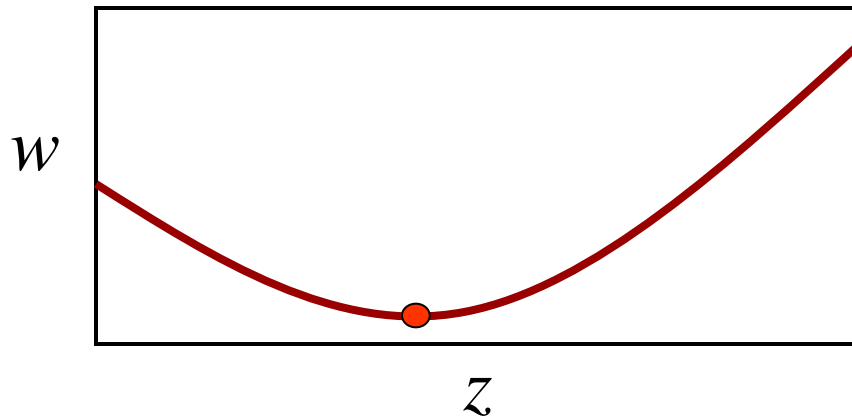
What is the outcome of directional selection?

What is the outcome of stabilizing selection?

What is the outcome of disruptive selection?

What data do we need to predict the evolution of quantitative traits?

$$\Delta \bar{z} = R = h_N^2 \, \text{cov}[z, w] = h_N^2 S$$

• **We can predict the change in the mean of a quantitative trait (also known as the response to selection and denoted R) if we can measure:**
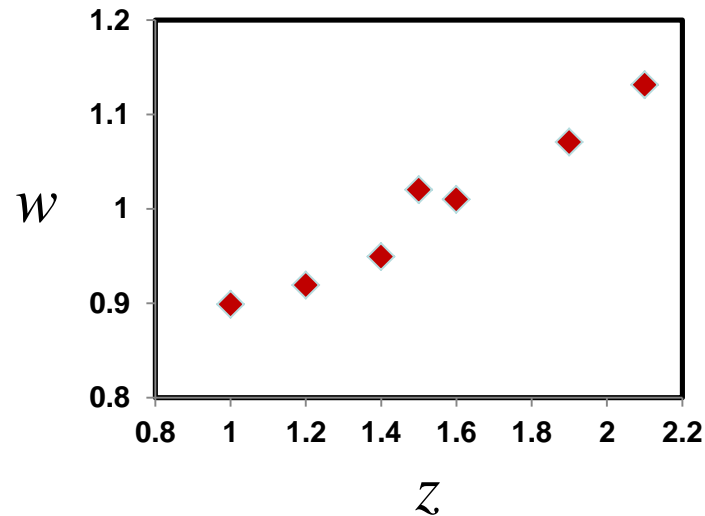
1. The narrow sense heritability

and

2. The *Selection differential*

Estimating the selection differential I:
Fitness is continuous

If fitness is continuous, the selection differential S can be estimated by calculating the covariance between phenotype and _relative_* fitness

z	w
1	0.899
1.2	0.919
1.4	0.949
1.5	1.02
1.6	1.01
1.9	1.071
2.1	1.131

$$\text{cov}[z, w] = \frac{\displaystyle\sum_{i=1}^{n}(z_i - \bar{z})(w_i - \bar{w})}{n} = \frac{\displaystyle\sum_{i=1}^{n}(z_i - 1.528)(w_i - 1.0)}{7} = .02684$$

Estimating the selection differential II: Truncating selection

If fitness has only two possible values ($W = 0$ or $W = 1$), the selection differential S, can be estimated as the difference between the mean phenotypic value of the individuals selected as parents ($W = 1$) and the mean phenotypic value of all individuals in the population before selection
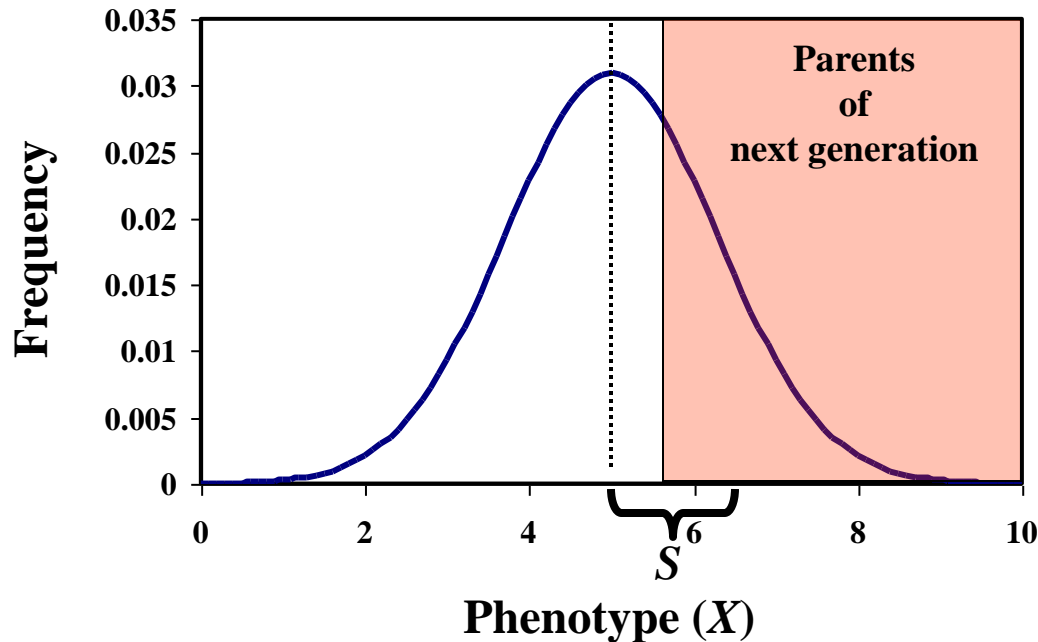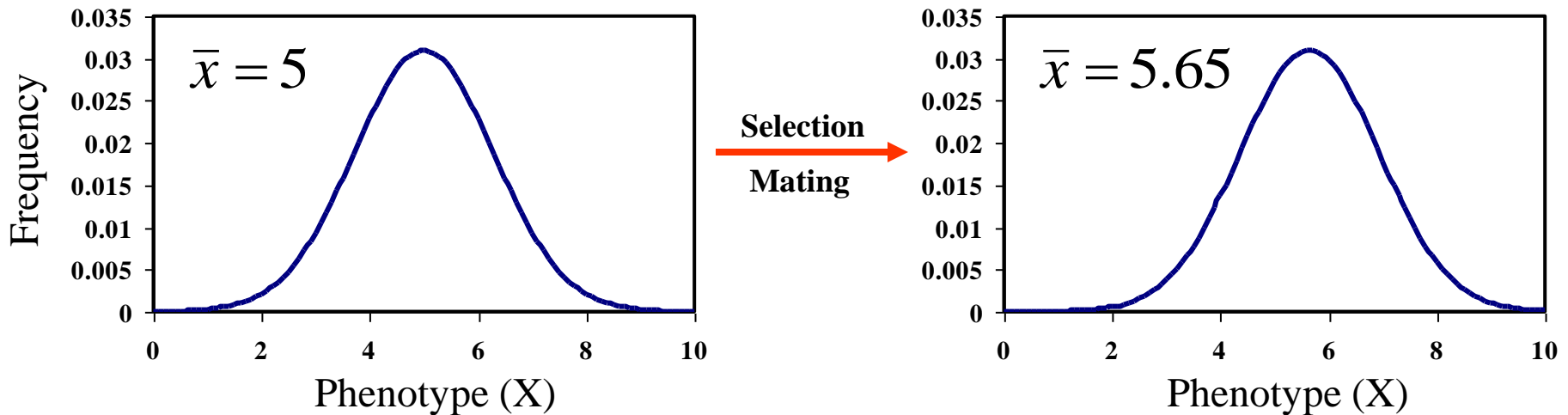

$$S = \bar{x}_{selected} - \bar{x}_{beforereselection} = 6.3 - 5 = 1.3$$

Predicting the response to selection, *R*

$$\Delta \bar{z} = R = h_N^2 \, \text{cov}[z, w] = h_N^2 S$$

• If in addition to the selection differential we have estimated the heritability as, for example, 0.5, we can predict the response to selection using the equation:

$$R = .5(1.3) = .65$$

An example of selection on quantitative traits

Trophy hunting and evolution in the bighorn sheep
Ovis canadensis

An example of selection on quantitative traits

- A game reserve offered a unique opportunity to study the evolution of quantitative traits

- Measured the heritability of two phenotypic traits: horn size and ram weight using an established pedigree

- Measured the difference in trait values of harvested vs non-harvested rams, from which information the selection differential could be estimated

- Followed the population mean of these traits over 30 years

An example of selection on quantitative traits

Heritabilities: $h^2_{horn} = .69\,; h^2_{weight} = .41$
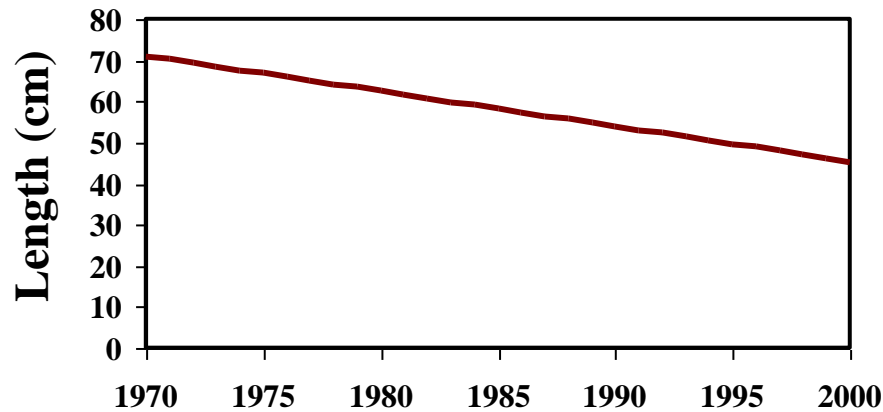
Selection differentials: $S_{horn} \approx -1.24\,; \; S_{weight} \approx -.89$

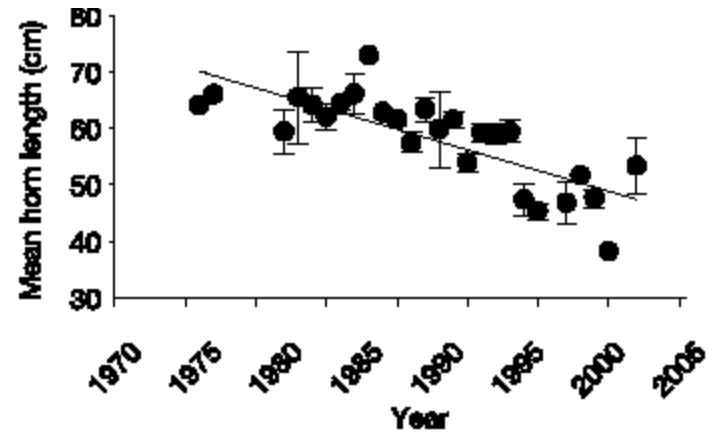**Making some simplifying assumptions, we predict the following responses to selection:**

$$R_{horn} = .69(-1.24) = -.856 \qquad R_{weight} = .41(-.89) = -.364$$

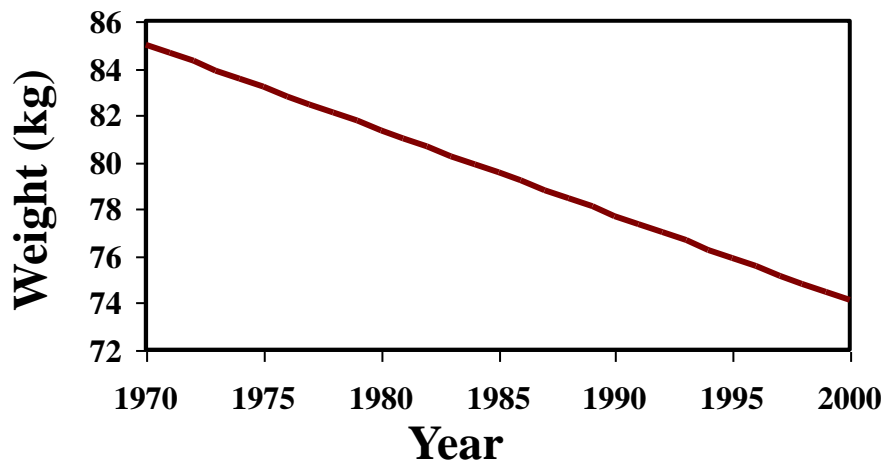# An example of selection on quantitative traits
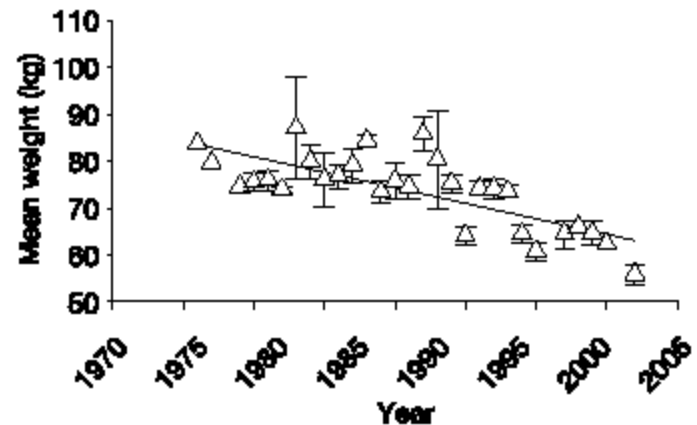
Prediction for horn length

Observed horn length

Prediction for ram weight

Observed ram weight

Coltman et. al. 2003. Nature

What are the implications?

- **Traditional wildlife management has focused on Ecology (population sizes)**

- **This study shows that over only 30 years, evolution has occurred**

- **Suggests that, in some cases, management strategies must also consider evolution**

Practice Problem

A team of scientists working on a species of marine crab was interested in determining whether natural selection was favoring increased shell thickness as a defense against predators. The same team was also interested in predicting whether increased shell thickness would evolve as a result. To this end, the scientists measured the average shell thickness of all crabs in the population at the beginning of the year and found it to be $\bar{x}_T = 10mm$. At the end of the year, before the crabs mated and produced the next years offspring, the scientists measured the average shell thickness of the surviving crabs (those that were not killed by predators), estimating the mean shell thickness of these selected parents as $\bar{x}_S = 12mm$. In a previous study, the same group of scientists had estimated that the slope of a regression of mid-parent shell thickness on offspring shell thickness was 0.50. Use this information to answer the following questions.

A. What is the heritability (narrow sense) of shell thickness?

B. What is the selection differential acting on shell thickness?

C. What will the response to selection exerted by predators be?

D. What do you estimate the shell thickness of the crabs will be in the next generation?

Practice Problem

As you have seen in lecture, the evolution of a quantitative trait in response to natural selection is described by the following equation:

$$\Delta \bar{z} = h_N^2 \, \mathrm{cov}[z, w] = h_N^2 S$$

Explain what each piece of the equation above means, how each might be measured, and why each is important for evolution by natural selection. Ten points for a full explanation of each term.