# The study of natural selection

## Topics

1) What is natural selection?
2) Direct observations of selection
3) How common is natural selection?
4) What are the causes of natural selection?
5) How variable is natural selection?
6) What are the forms of natural selection?
7) What is sexual selection?
8) The problem of correlated characters

# Natural selection (1858)

Darwin
1809-1882

Wallace
1823-1913

George Richmond https://en.wikipedia.org/wiki/Portraits_of_Charles_Darwin

English Heritage, http://wallacefund.info/content/paintings-and-sculptures

# 1) What is natural selection?

Natural selection is a process in which

# 1) What is natural selection?

Natural selection is a process in which

**If a population has**:

a. variation among individuals in some attribute or trait;

b. a consistent (nonrandom) relationship between that trait and mating ability, fertility, fecundity, or survivorship ('component of fitness')

c. inheritance of the trait

# 1) What is natural selection?

Natural selection is a process in which

**If a population has**:

a. variation among individuals in some attribute or trait;

b. a consistent (nonrandom) relationship between that trait and mating ability, fertility, fecundity, or survivorship ('component of fitness')

c. inheritance of the trait

**Then**:

1. the trait frequency will differ among age classes or life-history stages, beyond that expected from ontogeny;

2. the trait distribution of offspring in the population will be different from that of the parent population.

J. A. Endler, *Natural Selection in the wild* (1986)

# 1) What is natural selection?

Natural selection is a process in which

**If a population has**:

a. variation among individuals in some attribute or trait;

b. a consistent (nonrandom) relationship between that trait and mating ability, fertility, fecundity, or survivorship ('component of fitness')

c. inheritance of the trait

**Then**:

1. the trait frequency will differ among age classes or life-history stages, beyond that expected from ontogeny;

2. the trait distribution of offspring in the population will be different from that of the parent population.

But this is natural selection and evolution, whereas it is better to distinguish the two

# 1) What is natural selection?

Natural selection is a process in which

**If a population has**:

a. variation among individuals in some attribute or trait;

b. a consistent (nonrandom) relationship between that trait and mating ability, fertility, fecundity, or survivorship ('component of fitness')

c. inheritance of the trait

**Then**:

1. the trait frequency will differ among age classes or life-history stages, beyond that expected from ontogeny;

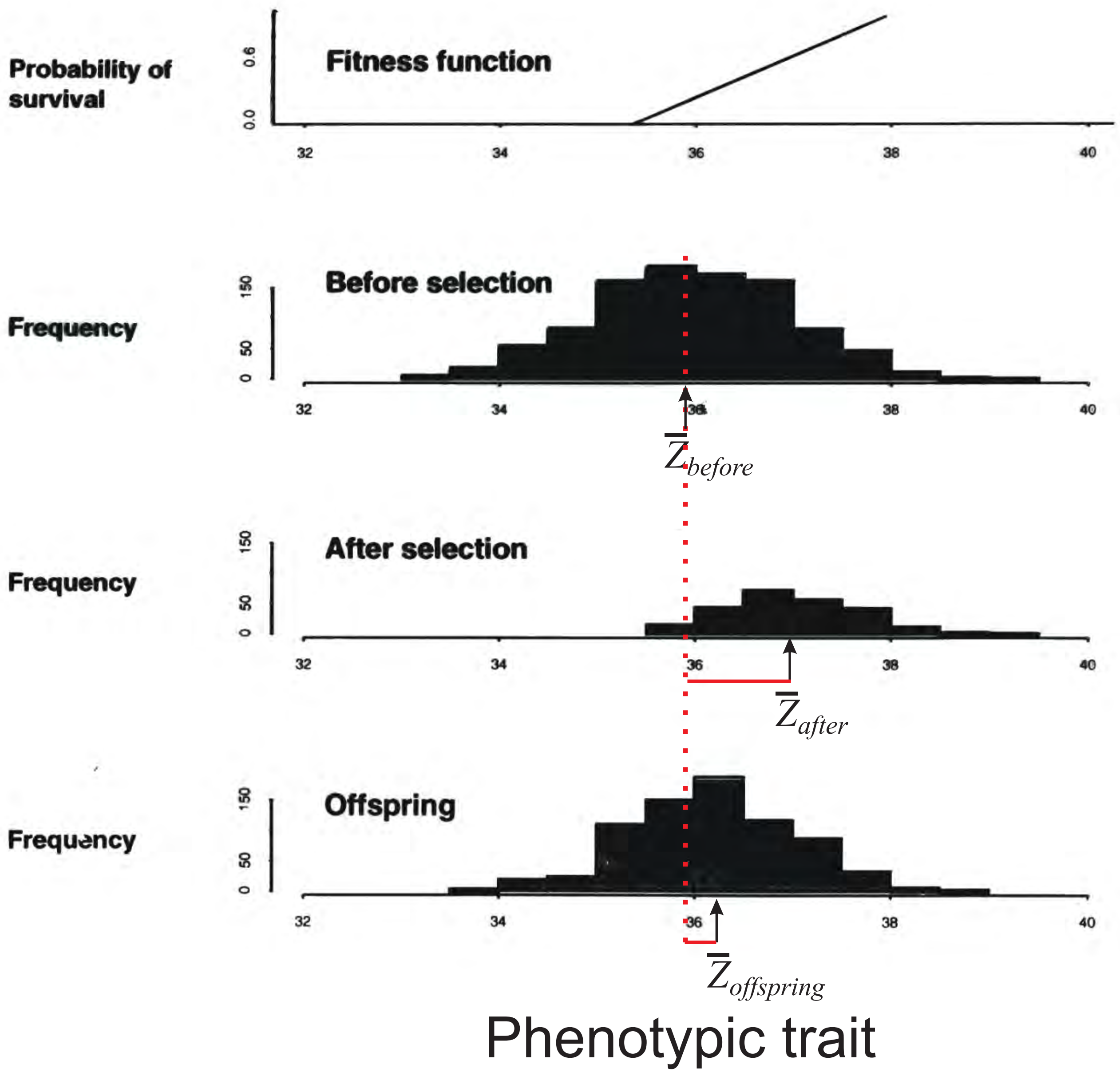
2. the trait distribution of offspring in the population will be different from that of the parent population.

# 1) What is natural selection?

*"Natural selection acts on <u>phenotypes.</u> It is ineffective unless it favours one genotype at the expense of another, but it may occur without doing so.*
*We (…) judge the intensity of Natural Selection (…) by a comparison of the actual parents of the next generation with the population of which they are a sample."*

J. B. S. Haldane (1954)

# Illustration of directional natural selection

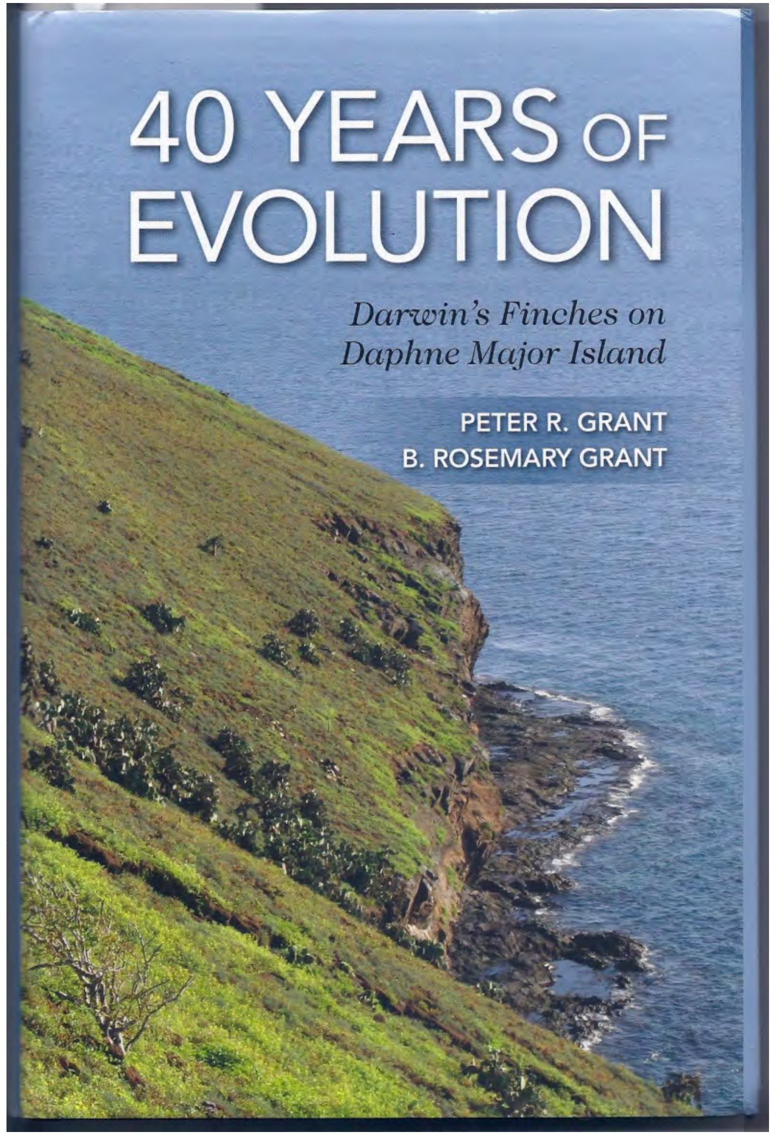



$$S = \bar{Z}_{after} - \bar{Z}_{before} = 1$$

$$\Delta\bar{Z}_{offspring} = h^2 S = 0.2$$

# 2) Direct observations of natural selection

Selection on medium ground finch on a Galapagos island

# Galapagos living

# 2) Direct observations of natural selection

40 years of changes in beak size in *Geospiza fortis*

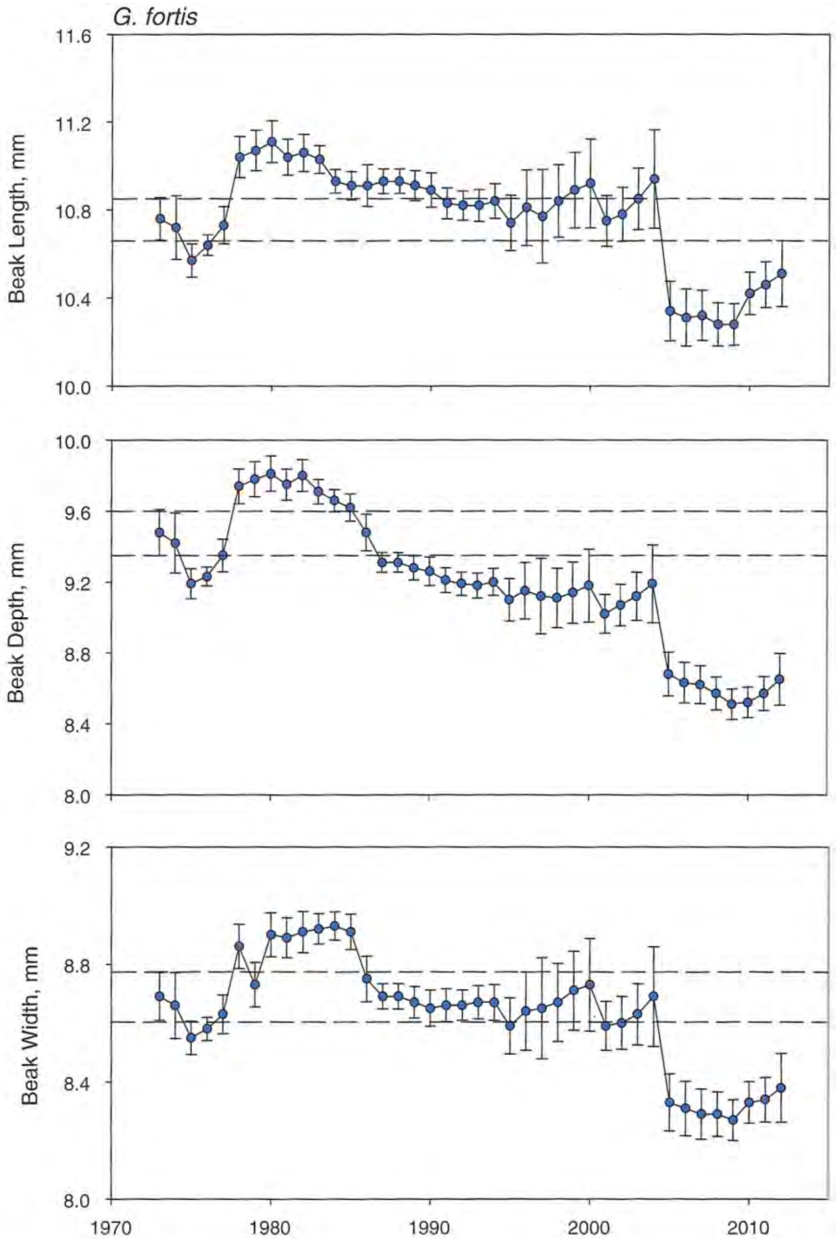
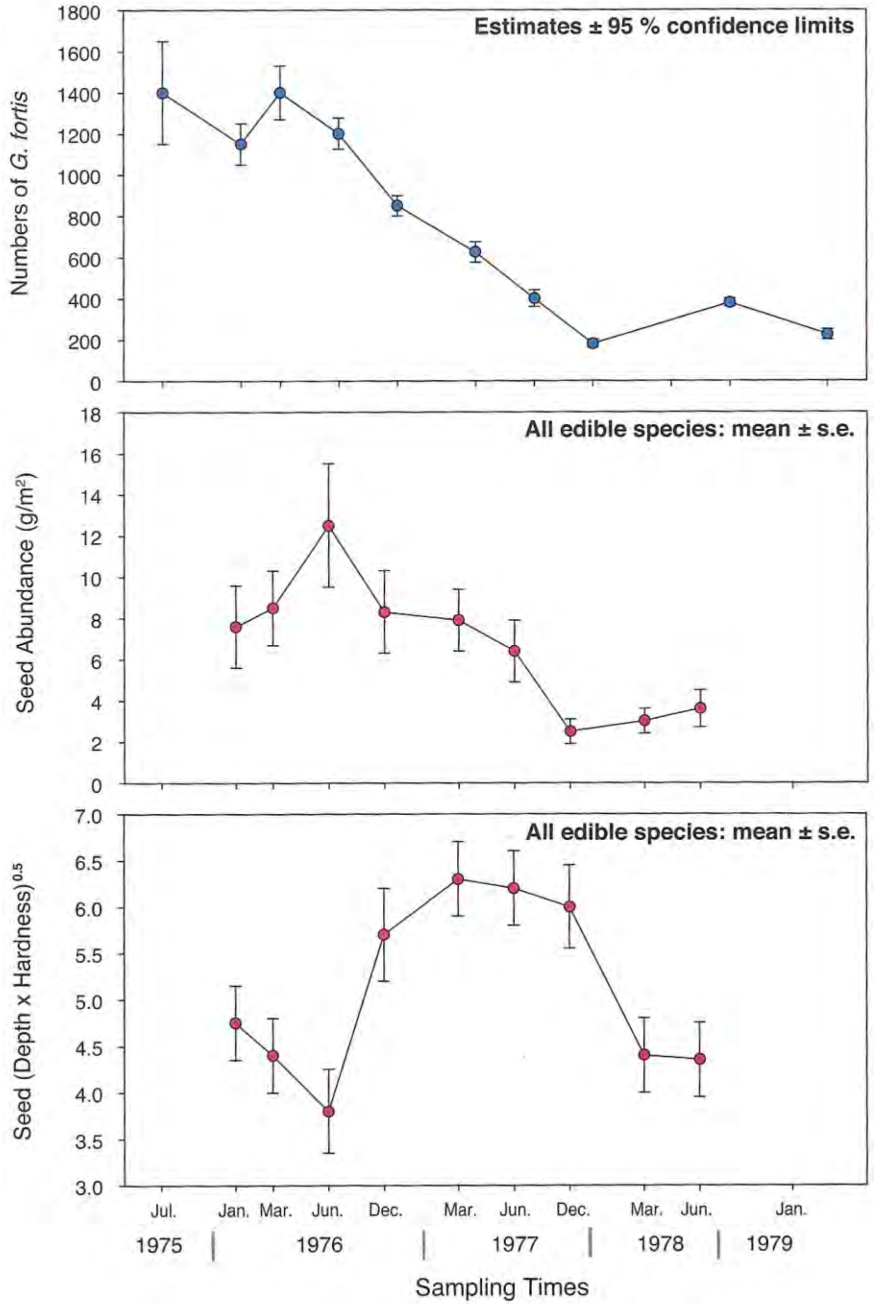
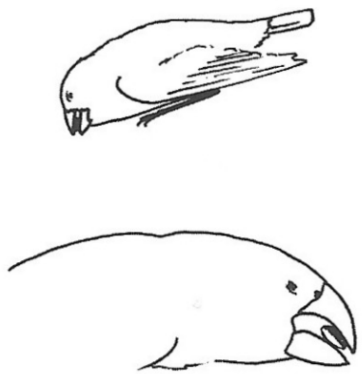



Fig. 11.4 Trends in *fortis* beak traits. Means and 95% confidence limits are shown for all birds alive in each year. Parallel horizontal lines mark the upper and lower 95% confidence limits on the first estimate of a mean based on a large sample size (in 1973). Sample sizes are in table A.11.2. Statistical tests of annual heterogeneity use measurements of each bird only once, and they were grouped in years of known or inferred hatching: for beak length $F_{23,\ 3843} = 12.6158$, $p < 0.0001$; for beak depth $F_{23,\ 3796} = 30.0389$, $p < 0.0001$; and for beak width $F_{23,\ 3843} = 16.3765$, $p < 0.0001$. Number of years = 24; in other years there was little or no breeding.

# 2) Direct observations of natural selection




## Focus on the drought of 1977



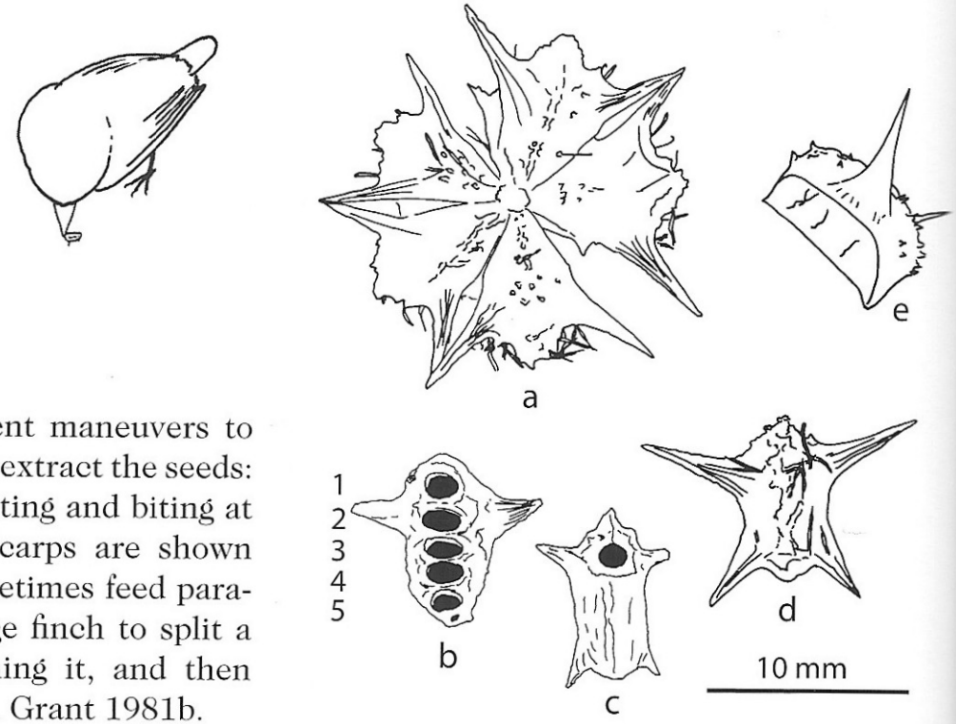



**Fig. 4.7** *G. fortis* use different maneuvers to open *Tribulus* mericarps and extract the seeds: either by crushing or by twisting and biting at the corners. Exploited mericarps are shown below. Small individuals sometimes feed parasitically by waiting for a large finch to split a mericarp into two by crushing it, and then seizing an ejected seed. From Grant 1981b.

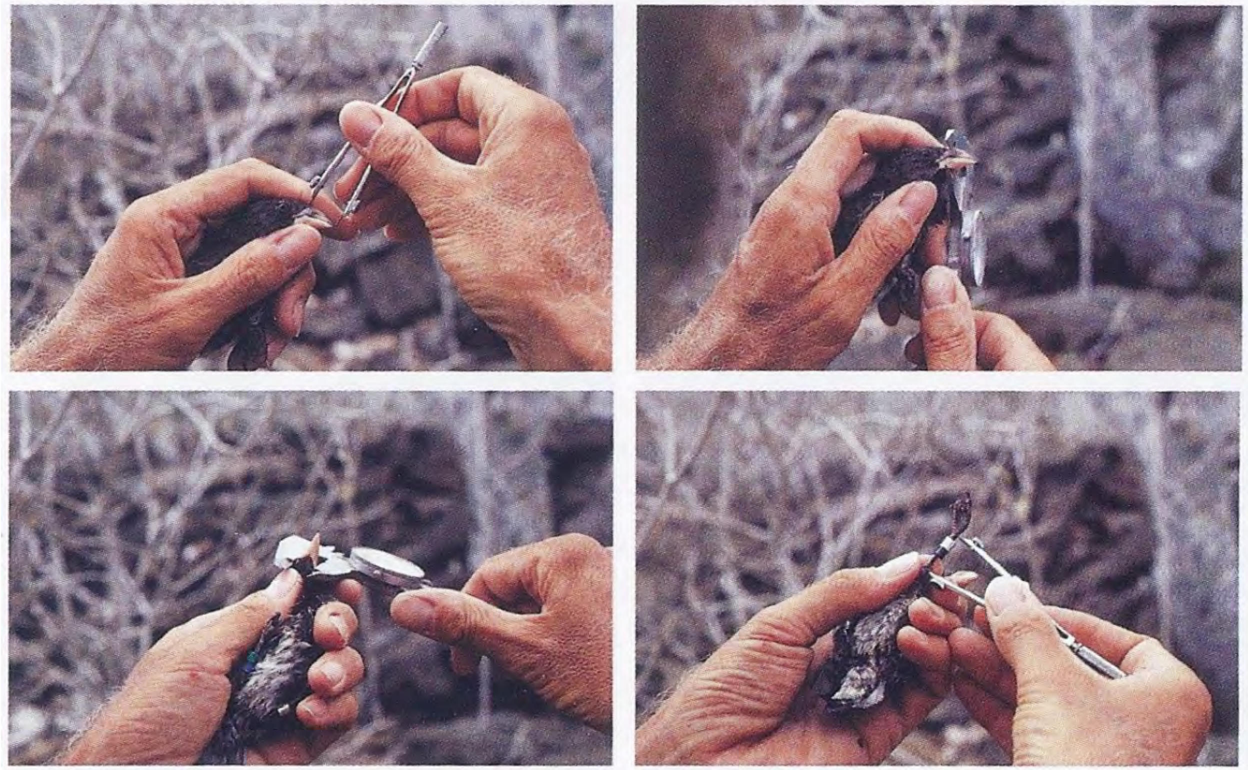
**Fig. 4.5** Temporal changes in *fortis* numbers and their principal dry-season food in the drought of 1977. **Upper**: Finch population estimates and 95% confidence limits derived from a Lincoln index based on regular visual censuses of marked

# 2) Direct observations of natural selection

## Focus on the drought of 1977

Fig. P.4 Phenotypic variation in the *G. fortis* population on Daphne.

Measuring birds



# 2) Direct observations of natural selection

Focus on the drought of 1977

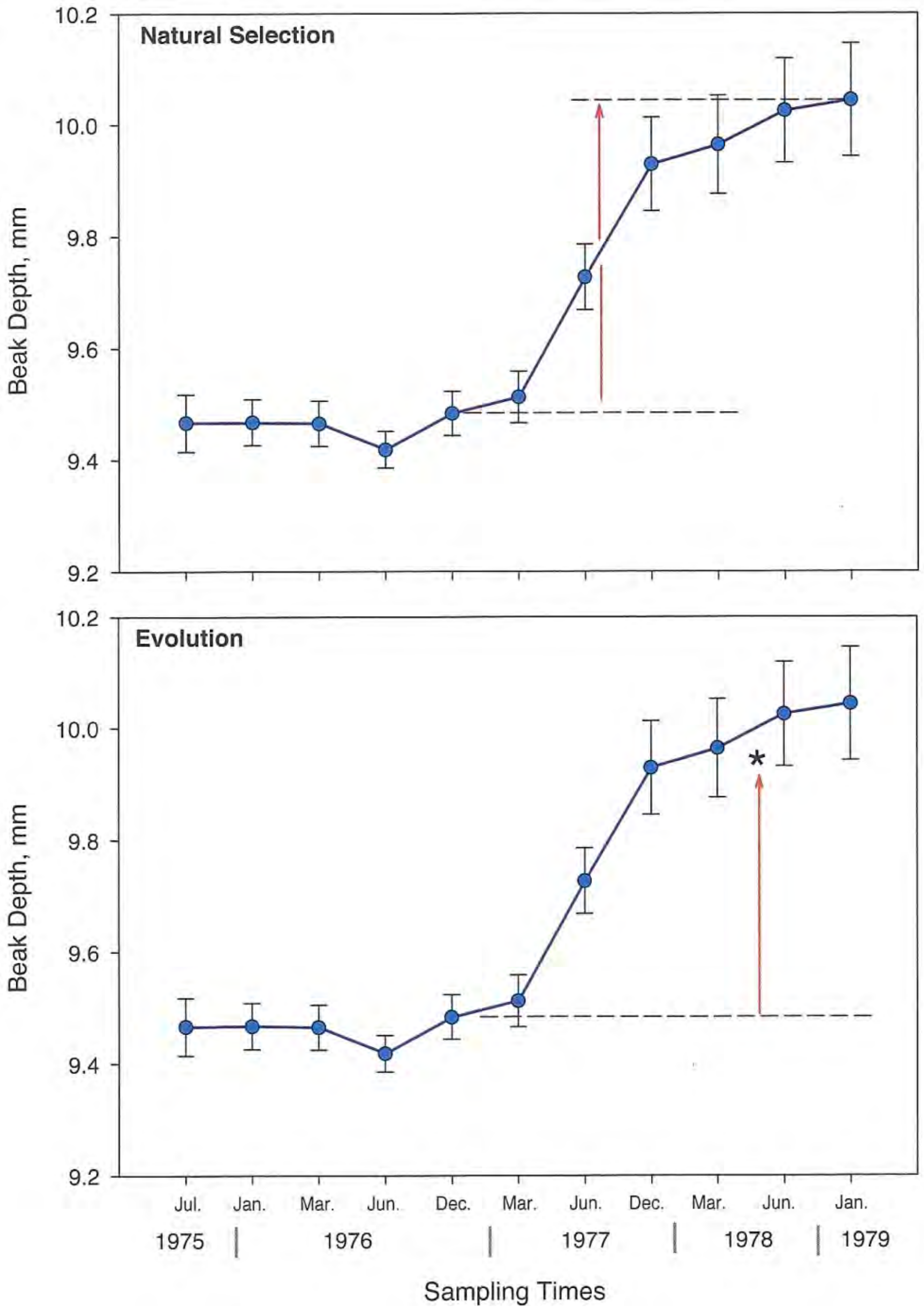



Fig. 4.6 Natural selection within one generation (above) followed by evolutionary change between generations (below). The asterisk (below) indicates the average beak depth of the next generation (9.94 mm), which is the observed evolutionary response to natural selection. It is well within sampling error of the predicted average (9.83 mm) (Grant and Grant 1995a). From Grant and Grant 2010a.

# 2) Direct observations of natural selection

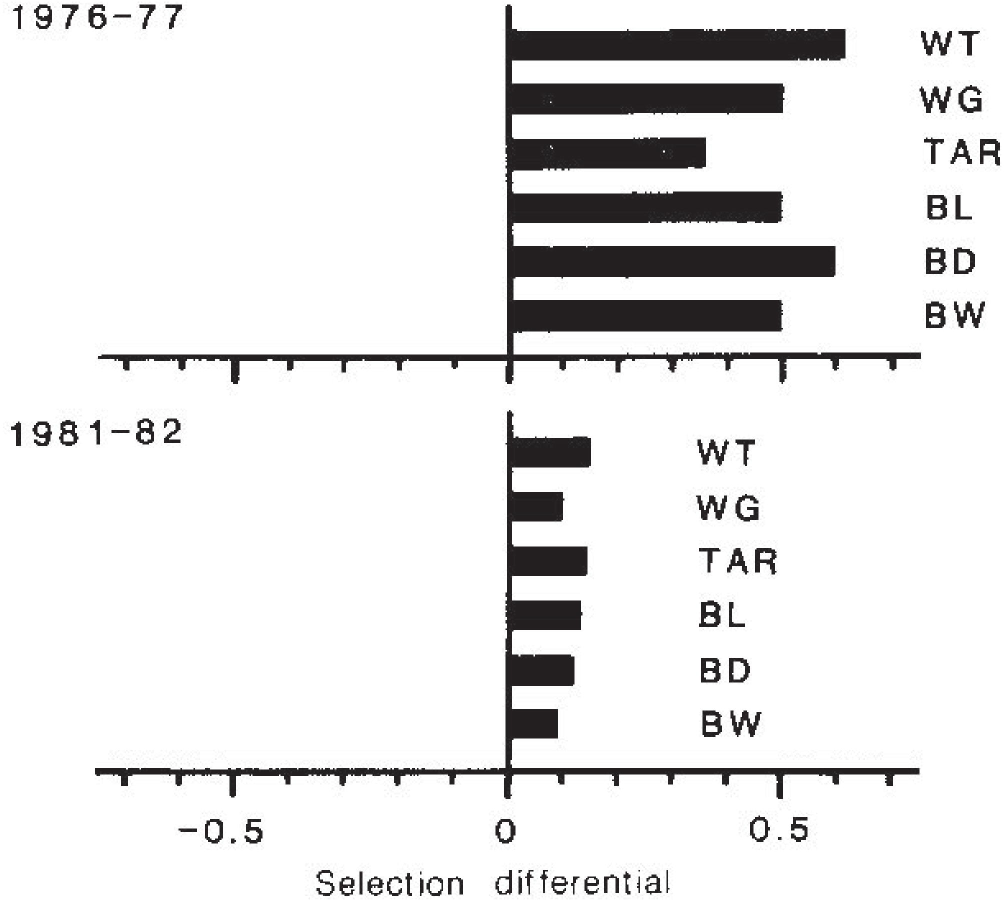



**Fig. 1** Selection differentials for traits of adult *G. fortis* during two years of drought and low food supply, 1976-77 and 1981-82

Traits measured are shown as follows. WT, weight; WG, wing length; TAR, tarsus size; BL, bill length; BD, bill depth; BW, bill width.

Directional selection differential

$$S = \bar{Z}_{after} - \bar{Z}_{before}$$

# 3) How common is natural selection?

## Endler (1986) survey

Direct demonstration of natural selection on heritable traits in wild populations

| Kind of traits | No. species | No. traits |
|---|---|---|
| Morphological (external dimensions) | 85 | 199 |
| Physiological (resistance; life history; tolerance) | 27 | 56 |
| Biochemical (allozymes) | 12 | 59 |
| Two or more kinds | 17 | |
| Total | 141 | 314 |

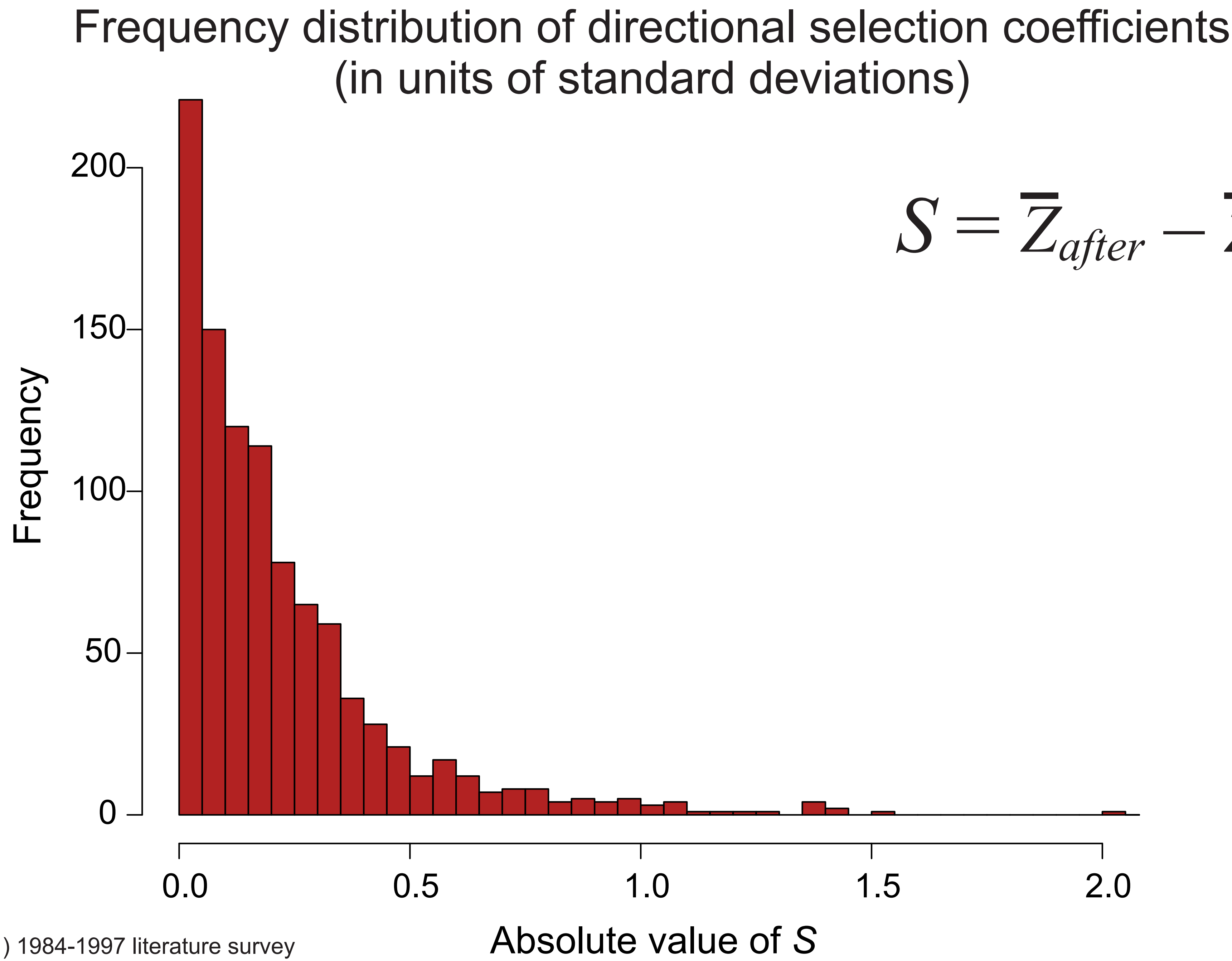
## Kingsolver et al (2001) 1984-1997 survey

**Table 3:** Number of estimates of linear selection in the database as a function of taxon, trait type, and fitness component

| Taxon | | Trait | | Fitness component | |
|---|---|---|---|---|---|
| Estimates of linear selection gradients[a] | | | | | |
| Invertebrates | 333 | Morphology | 815 | Mating success | 407 |
| Plants | 363 | Life history/phenology | 128 | Survival | 288 |
| Vertebrates | 297 | Principal component | 33 | Fecundity | 271 |
| … | … | Behavior | 14 | Total fitness | 19 |
| … | … | Interaction | NA | Net reproductive rate | 3 |
| … | … | Other | 3 | Other | 5 |
| Estimates of linear selection differentials[b] | | | | | |
| Invertebrates | 233 | Morphology | 594 | Mating success | 267 |
| Plants | 183 | Life history/phenology | 125 | Survival | 293 |
| Vertebrates | 337 | Principal component | 21 | Fecundity | 142 |
| … | … | Behavior | 10 | Total fitness | 34 |
| … | … | Interaction | NA | Net reproductive rate | 12 |
| … | … | Other | 3 | Other | 5 |

Note: NA = not applicable.
[a] $N$ = 993 total estimates.
[b] $N$ = 753 total estimates.

# 3) How common is natural selection?

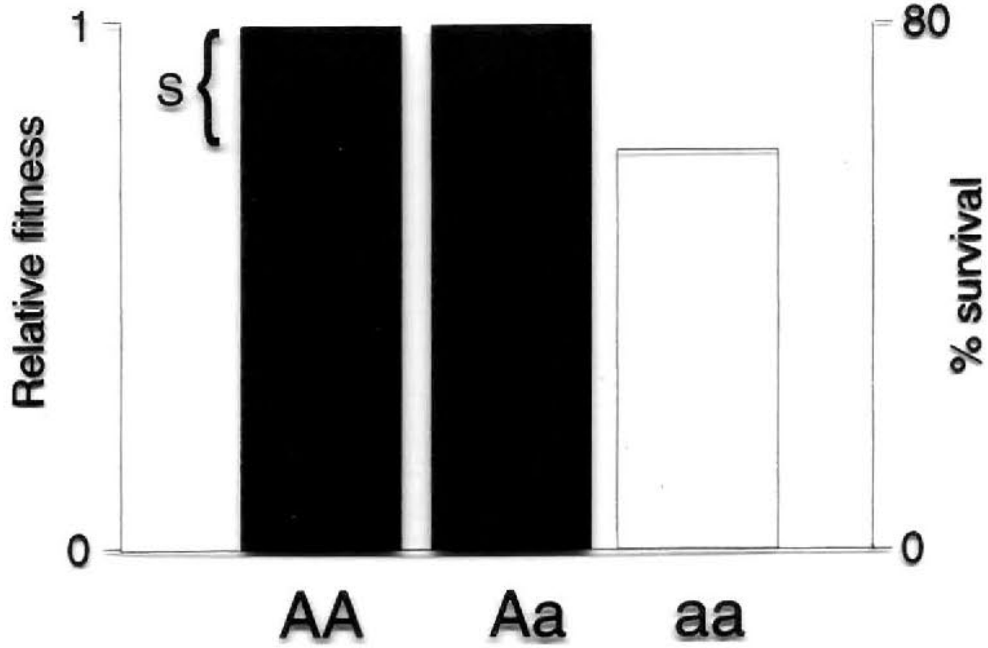



$$S = \overline{Z}_{after} - \overline{Z}_{before}$$

Kingsolver et al (2001) 1984-1997 literature survey

# 3) How common is natural selection?

How selection on discrete traits was measured using "*s*"
in Endler (1986) survey



# 3) How common is natural selection?

## Strength of selection ($s$) on discrete traits

Undisturbed populations

Perturbations field cages
stressful environments

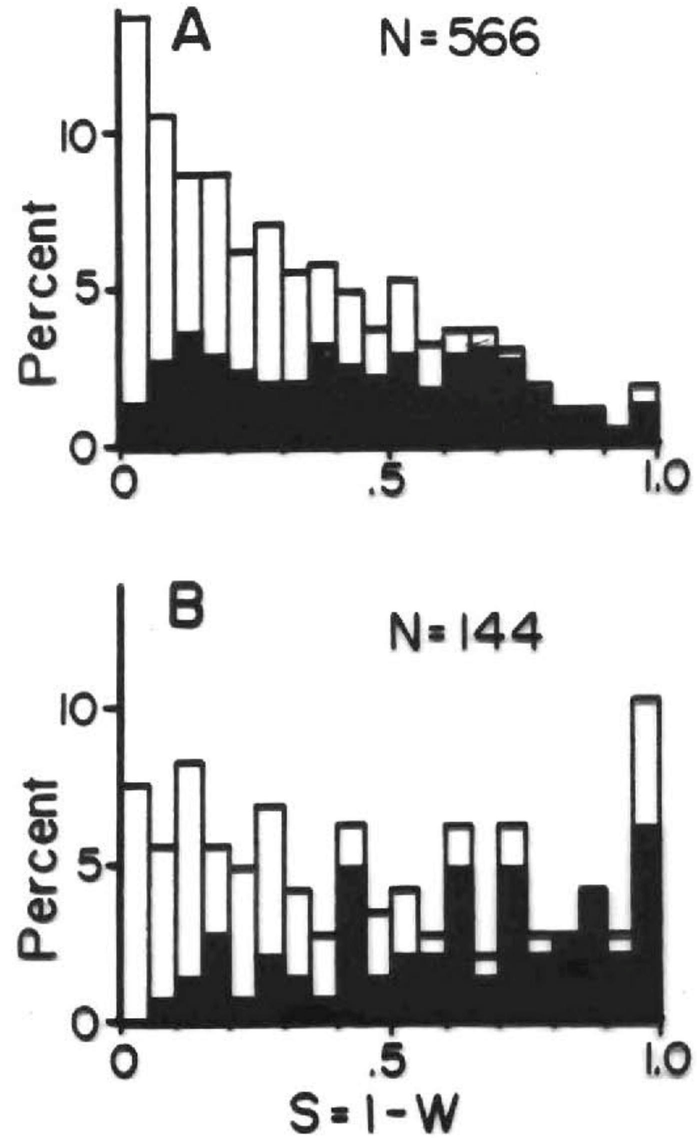



FIGURE 7.1. The distribution of selection coefficients $S$ for polymorphic traits. The total height of each bar indicates the percentage of $S$ values in each interval, and the shaded portion indicates $S$ that are significantly different from zero at the 0.05 level. *A*, data from undisturbed populations; 36 species, 239 of 566 $S$ values significant. *B*, data from perturbations, field cages, or stressful environments; 12 species, 70 of 144 $S$ significant. *C*, data from mortality selection; 34 species, 154 of 394 $S$ significant. *D*, data from fecundity, fertility, and sexual selection; 13 species, 92 of 172 $S$ significant.

# 4) What do we know about its causes?

Experimental studies can help

# 4) What do we know about its causes?

## Mimicry in *Heliconius* butterflies

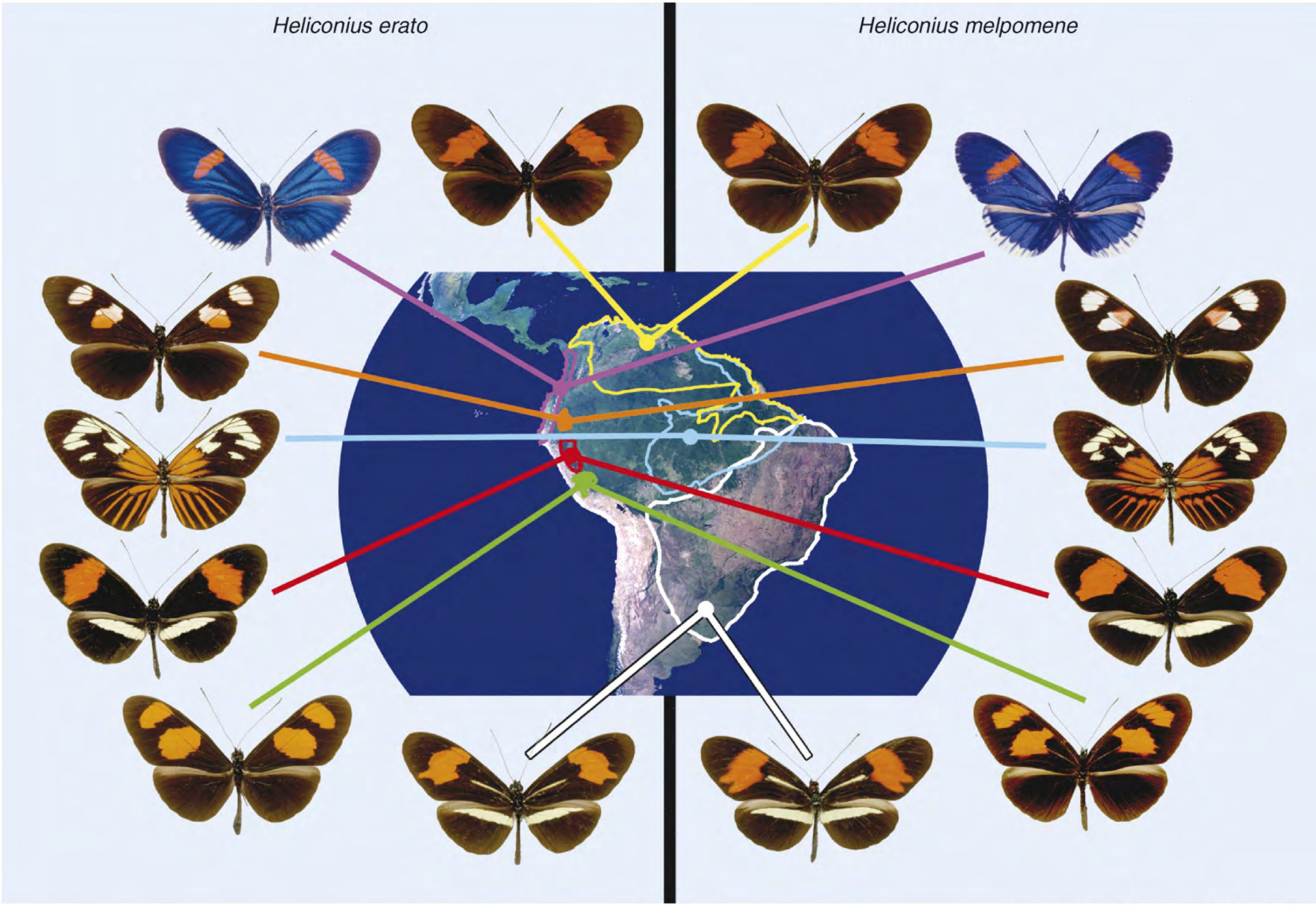
postman rayed

*H. melpomene*

*H. erato*

http://en.wikipedia.org/wiki/File:Heliconius_mimicry.png

# 4) What do we know about its causes?

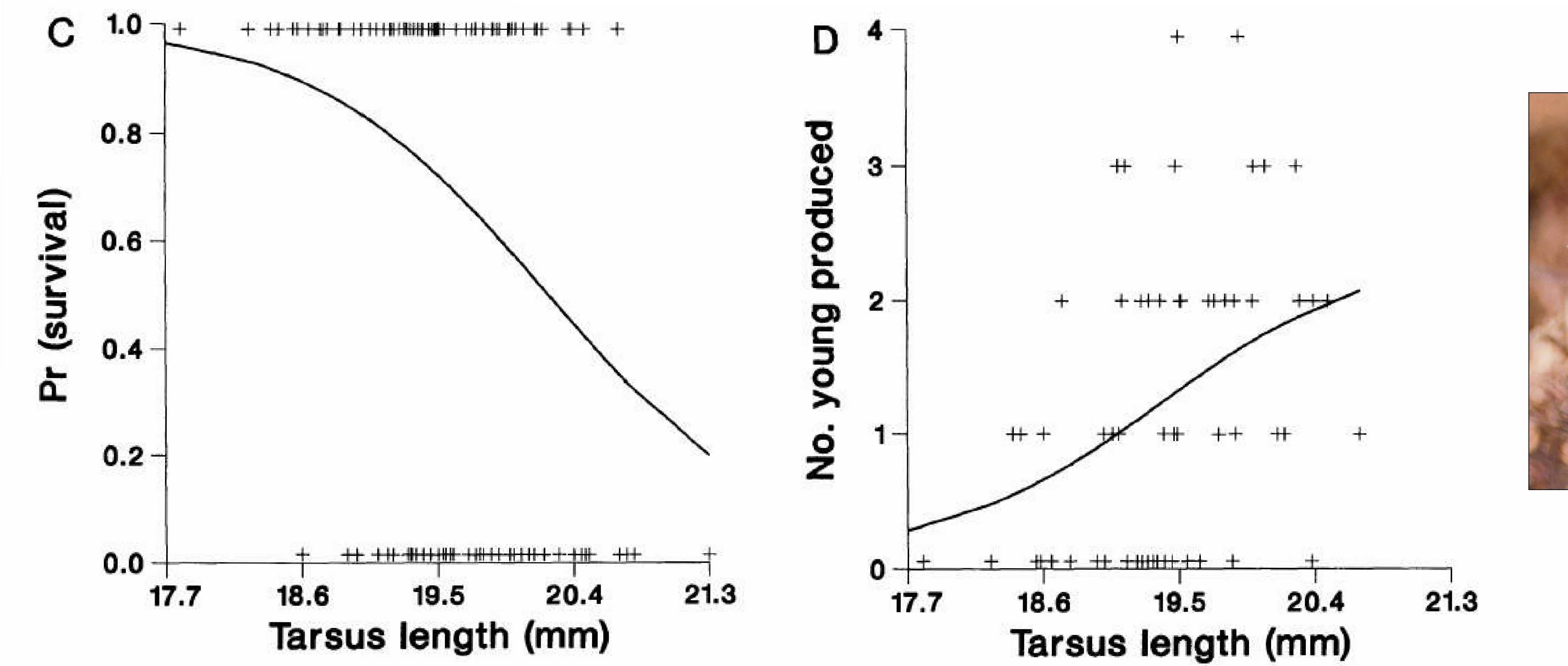



Parchem et al. (2007)

Current Opinion in Genetics & Development

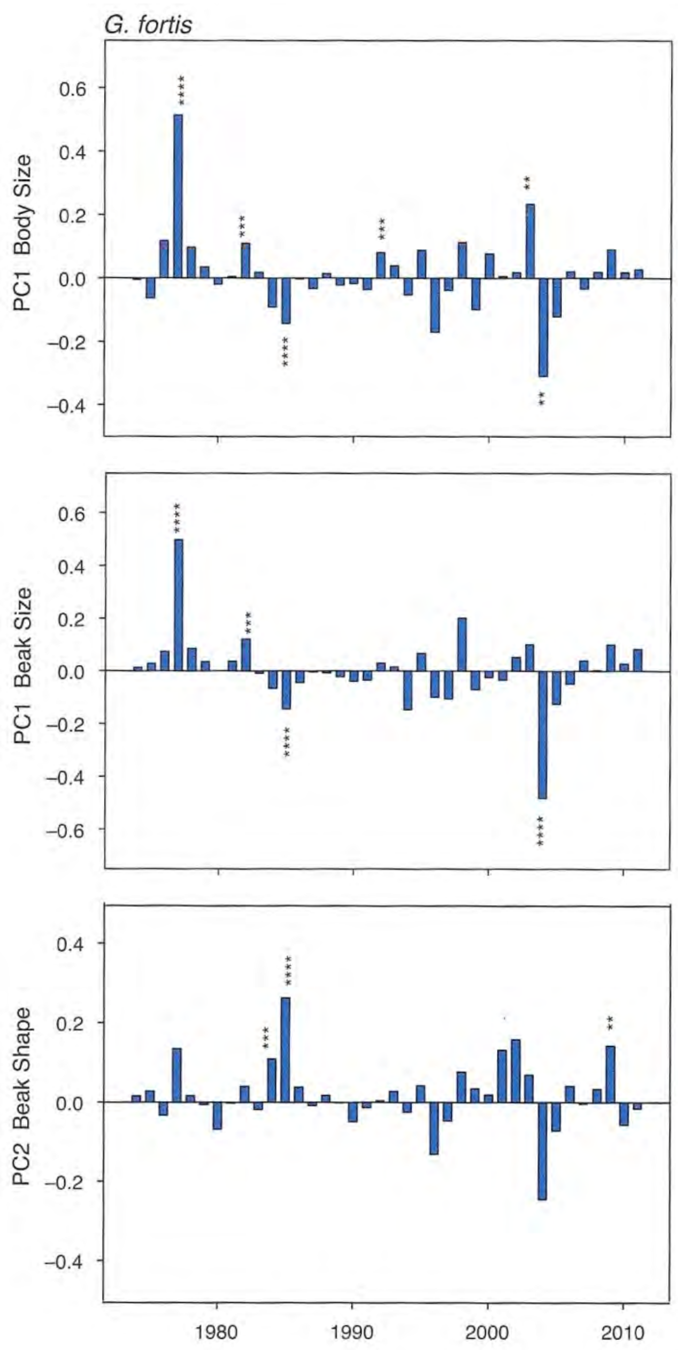
# 5) How variable is selection?

Selection at one life stage
may be counteracted by selection at another




http://animal.discovery.com/guides/wild-birds/s-y/song-sparrow.html

# 5) How variable is selection?

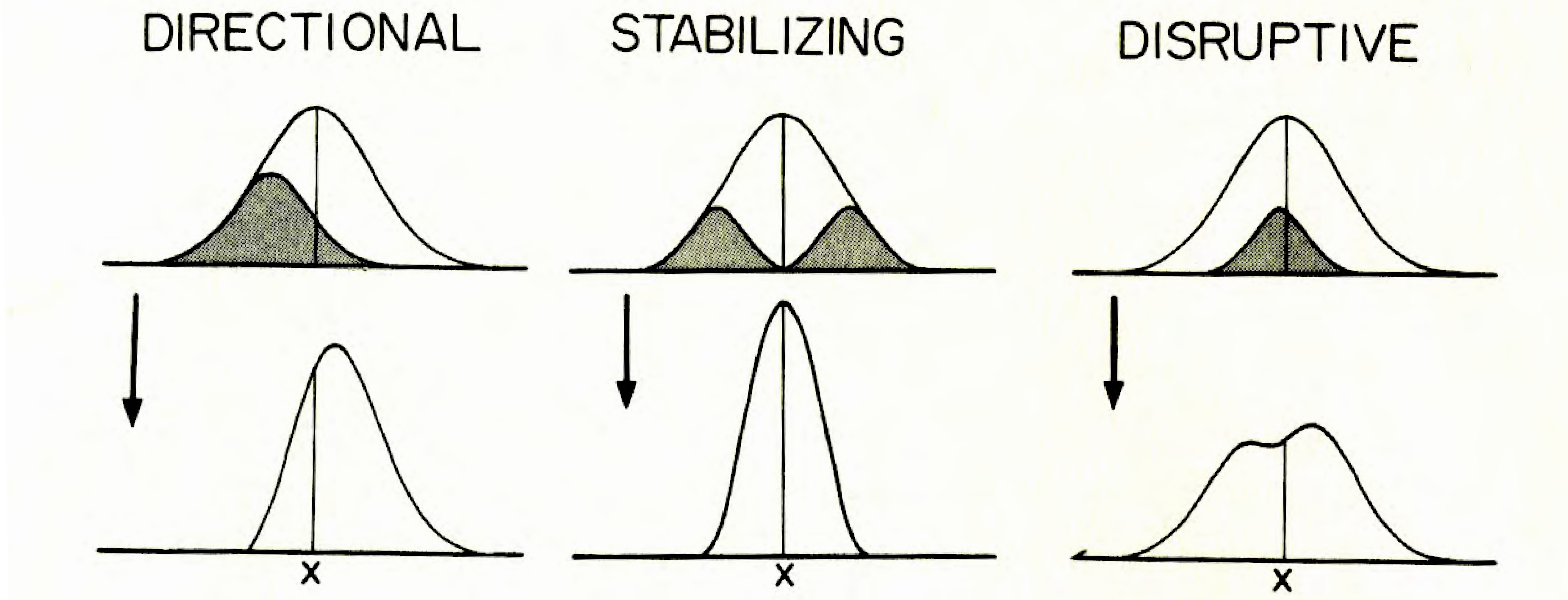



Selection can oscillate between years

Standardized selection differentials ($S$), calculated for each sample surviving from year $x$ to year $x + 1$.

Fig. 11.1 Standardized selection differentials (coefficients) for *fortis*.

# 6) What are the forms of natural selection?



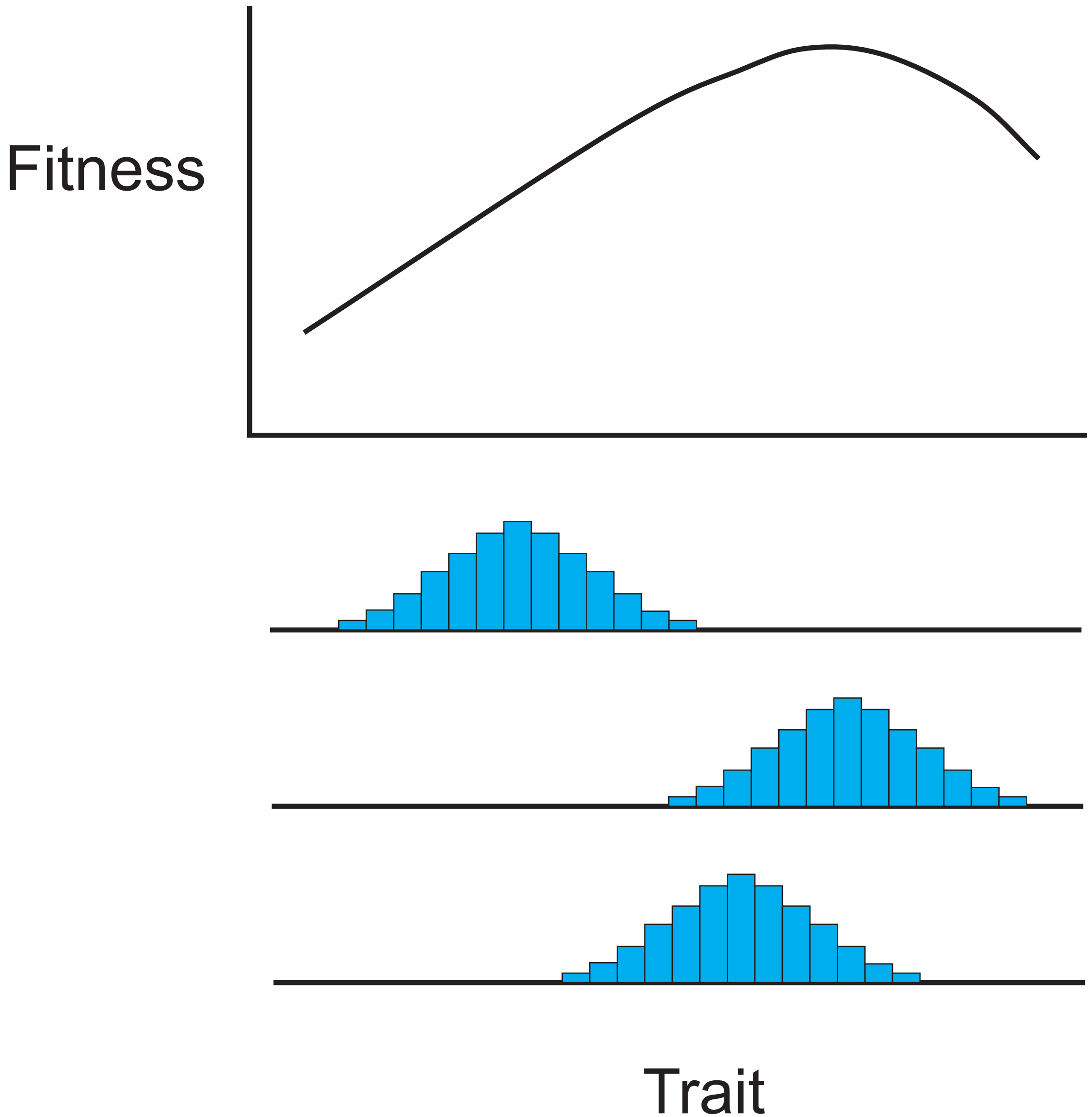

Directional selection: Average fitness is higher on one side of the population mean value than the other.

Stabilizing selection: The maximum fitness lies within the range of trait values in the population (between the extremes)

Disruptive selection: The minimum fitness lies within the range of trait values in the population (between the extremes)

Endler (1986)

# 6) What are the forms of natural selection?




This population experiences

...only directional selection

...only stabilizing selection

...both types of selection

# 6) What are the forms of natural selection?

## “Correlational” selection in song sparrows

Correlational selection: stabilizing or disruptive selection on a combination of traits

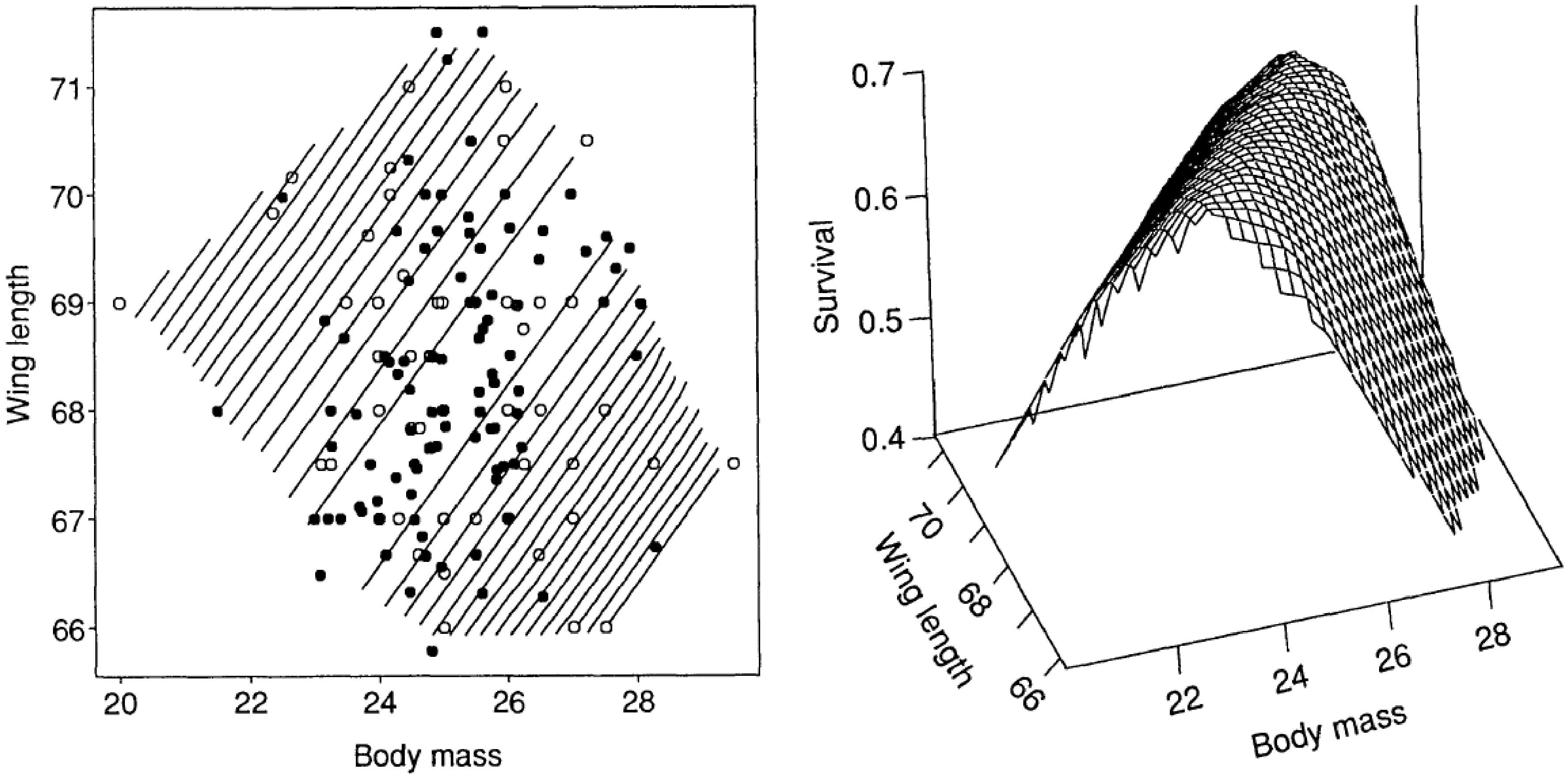



FIG. 3.—Survival (recruitment) of juvenile male song sparrows in relation to wing length and body mass.

Schluter (1988) *Evolution*

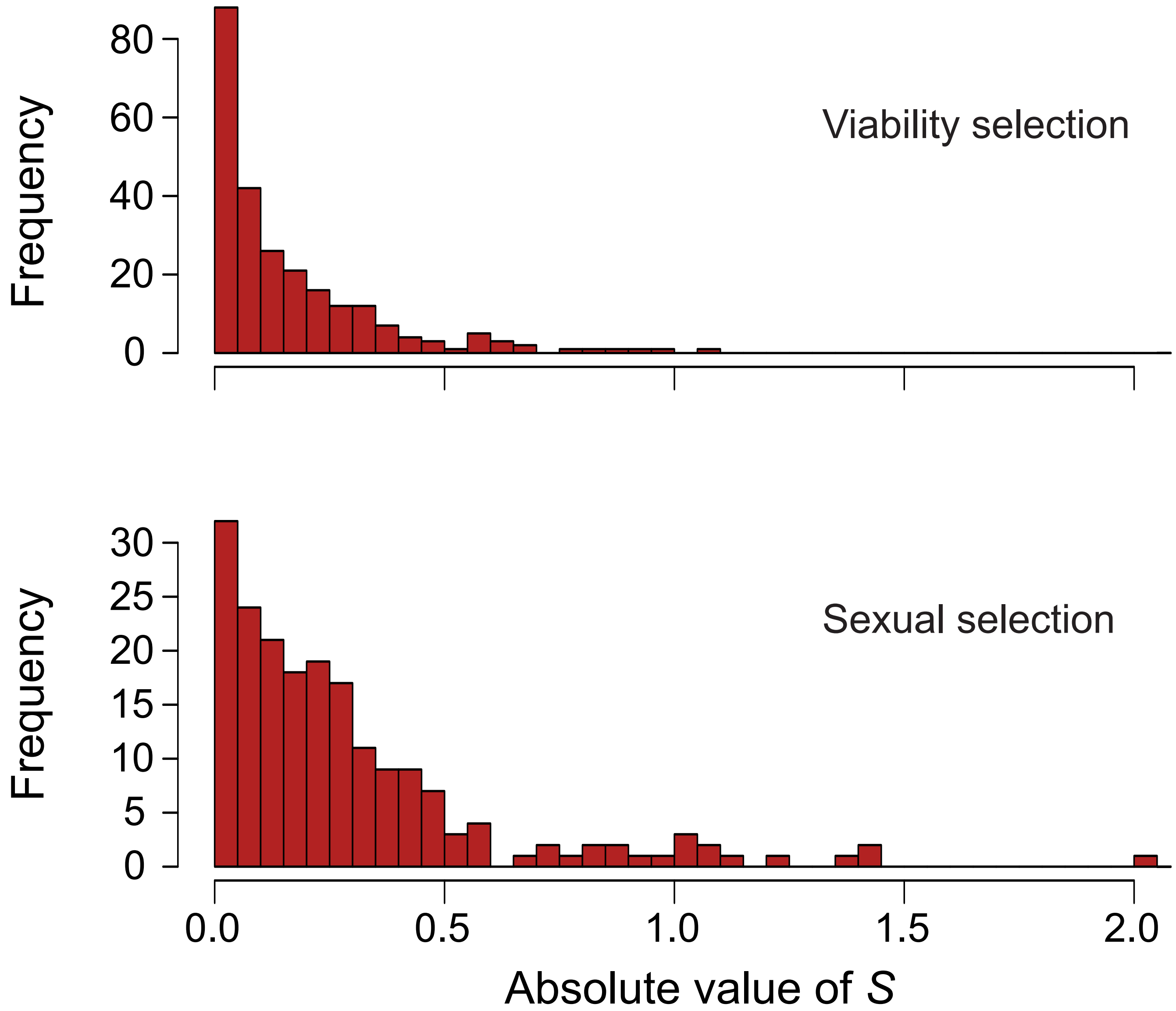
# 7) What is sexual selection?

Like natural selection, but is called sexual selection when the fitness component is <u>mating success</u>

http://commons.wikimedia.org/wiki/File:Male_and_female_superb_fairy_wren.jpg

# 7) What is sexual selection?

Directional selection coefficients are frequently higher for sexual selection than viability selection (in units of standard deviations)

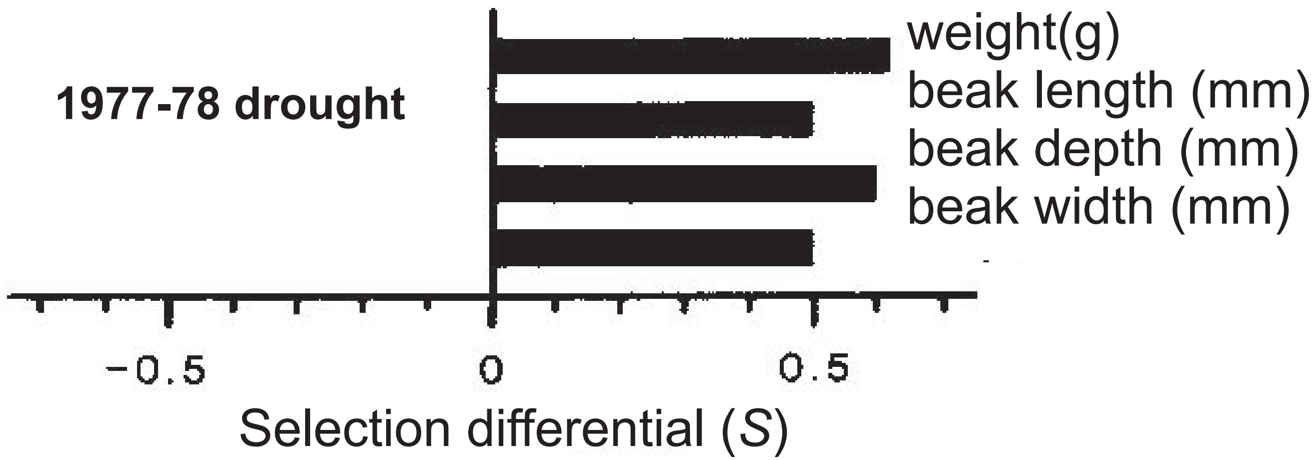



Kingsolver et al (2001) 1984-1997 literature survey

# 8) The problem of correlated traits

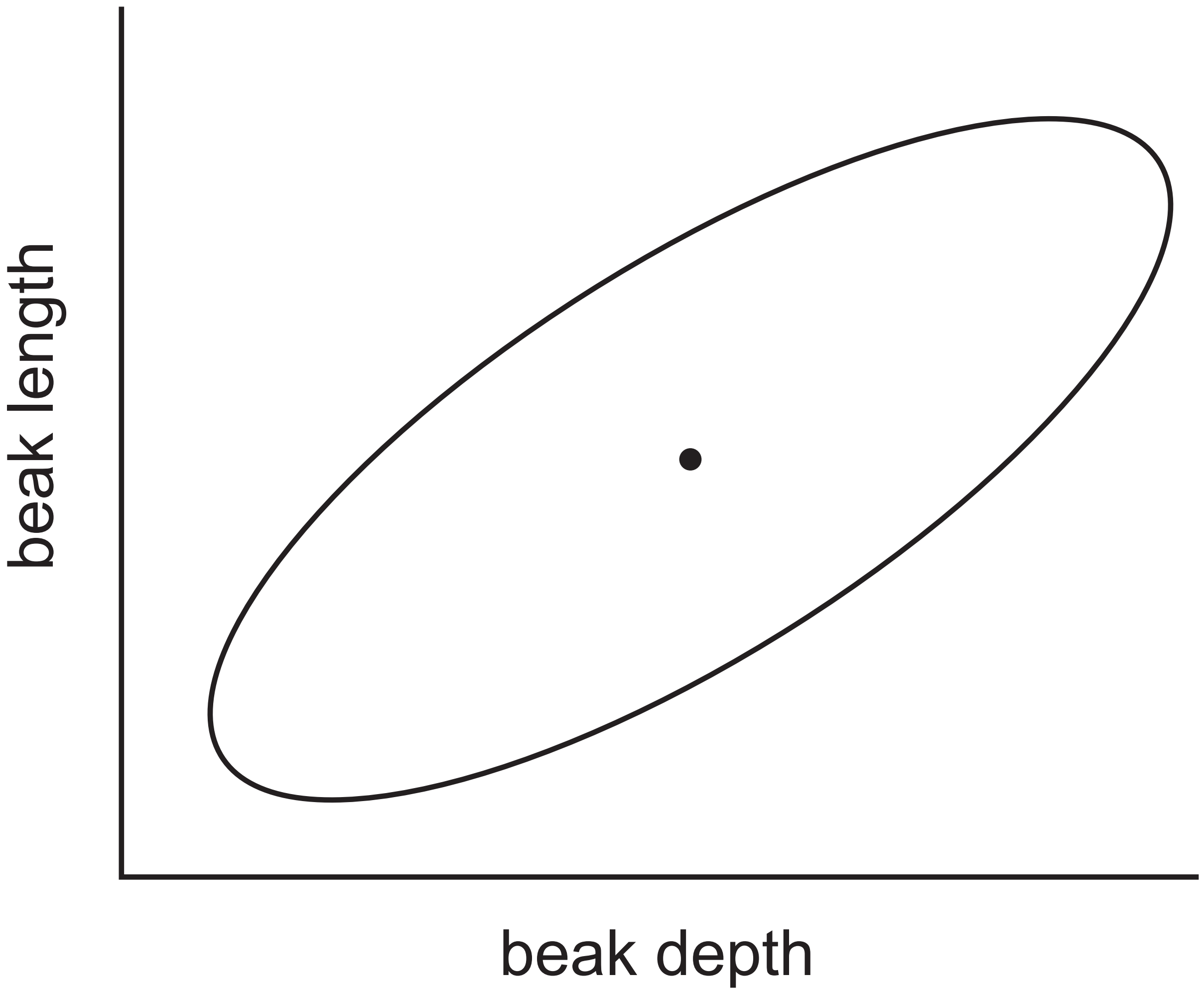
## Directional selection <u>differentials</u> in the medium ground finch

$$S = \overline{Z}_{after} - \overline{Z}_{before}$$




| | ***S*** |
|---|---|
| **weight (g)** | **<u>0.62</u>** |
| **beak length** | **<u>0.49</u>** |
| **beak depth** | **<u>0.60</u>** |
| **beak width** | **<u>0.49</u>** |

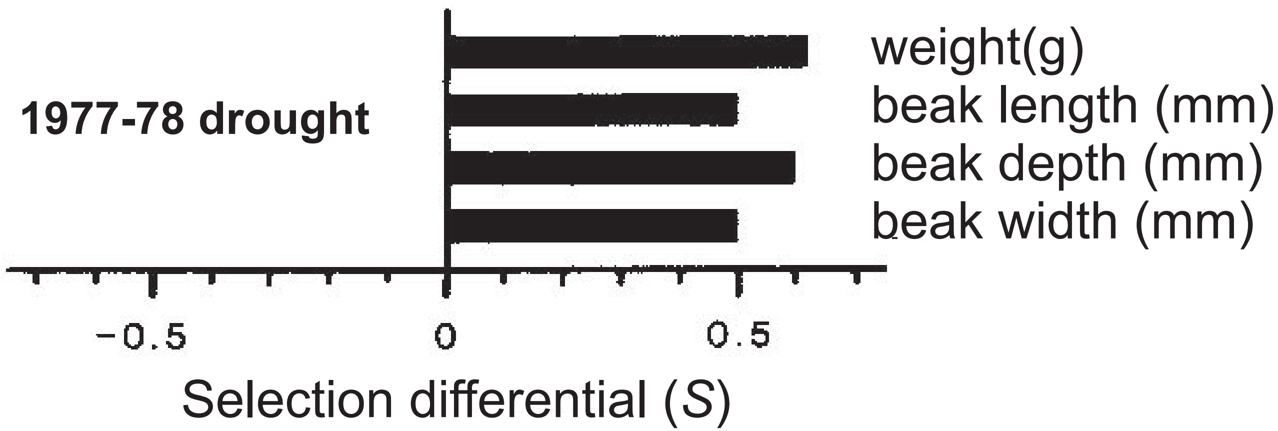
# 8) The problem of correlated traits



# 8) The problem of correlated traits

## Directional selection gradients in the medium ground finch

$$S = \overline{Z}_{after} - \overline{Z}_{before}$$




| | **S** | **β** |
|---|---|---|
| **weight (g)** | **0.62** | **0.51** |
| **beak length** | **0.49** | **0.17** |
| **beak depth** | **0.60** | **0.79** |
| **beak width** | **0.49** | **-0.47** |

# 8) The problem of correlated traits

The directional selection differential (*S*):

The shift in the mean trait value after selection minus before selection.

A selection differential results from selection on a trait and from selection on correlated traits.

A non-zero differential for a trait might result from selection on the trait, but it can also result without selection on the trait and instead from selection on correlated traits.

The directional selection gradient ($\beta$):

The strength of directional selection on a trait.

If there is no selection directly on the trait the gradient is zero, even if the trait has a non-zero selection differential resulting from selection on correlated traits.

# 9) Example exam questions on this section

What is the difference between natural selection and evolution?

What is the difference between stabilizing and directional natural selection?

What is the difference between a selection differential and a selection gradient?

Some researchers argue that natural selection acts only on genes, whereas others say that natural selection acts on phenotypes of individuals. Which view is correct? Explain.

The table below [not shown here] shows the estimated selection differential and selection gradient on several traits associated with survival in a population of fungus beetles. The gradients are not the same as the differentials, indeed they are sometimes of different sign. Why might this be the case?