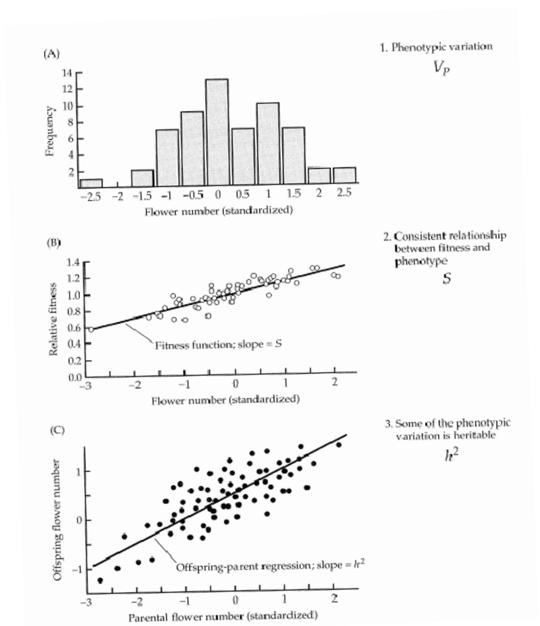
Natural Selection

Evolution by natural selection



Natural selection requires phenotypic variation

Selection occurs if variation in fitness is associated with variation in the phenotype (i.e., there is a covariance between fitness and phenotype)

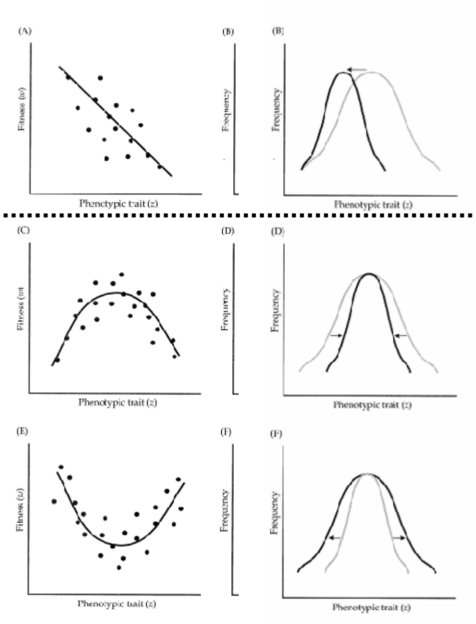
Evolution by natural selection can occur if part of the phenotypic variance is heritable (i.e., there is a covariance between phenotype and genotype)

Evolution by natural selection

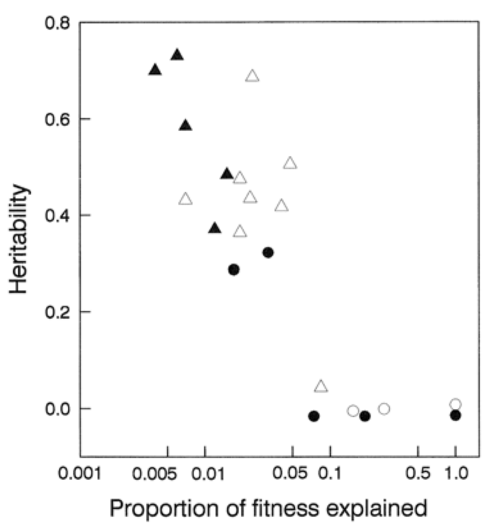
Directional Selection
(change in population mean and reduction in V_A)

Non-linear Selection
(stabilizing)
(reduction in V_A)

Non-linear Selection
(disruptive)
(increase in V_A)



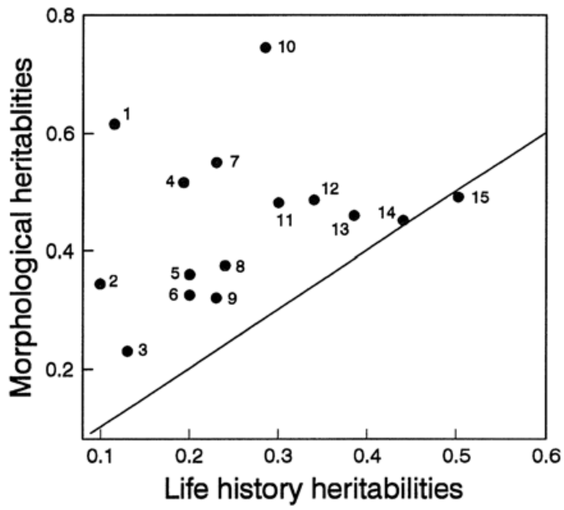
Prediction: Selection reduces the standing genetic variation in populations



Collared flycatcher
(*Ficedula albicollis*)

Gustaffson (1986)

Prediction: Selection reduces the standing genetic variation in populations

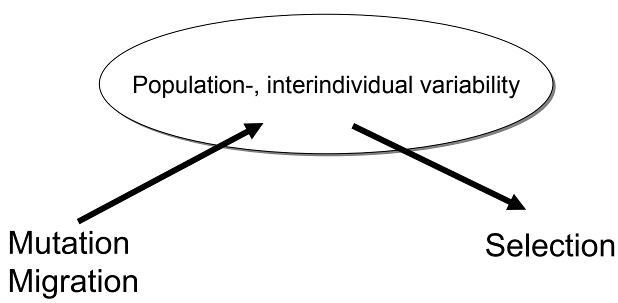


Across species comparison

Roff (1997)

Maintenance of heritable variation

Equilibrium between newly emerging genetic variability and selection removing genetic variants from the population.



Directional Selection

Selection differential:
Covariance between fitness and phenotype

The „Price Equation“ (Price, 1970)
(„Robertson-Price Identity“: Lynch and Walsh,1998)

$$\Delta z_i = \mathrm{cov}(w_i, z_i) = h^2 S = \beta V_a = \beta G$$

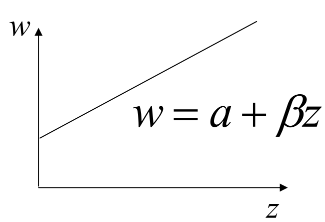
Δz = evolutionary change from generation *t* to *t*+1 (equivalent to R in breeders equation)
i = index-subscript for a particular phenotype/trait
β = selection gradient (slightly different from selection differential)
G = additive genetic variance (equivalent to V_A)
w_i = relative fitness $\left(\frac{W_i}{\overline{W}}\right)$

Directional Selection

Linear Regression

$$y = a + bx$$

Linear Fitness Equation



a: baseline fitness
β: directional selection gradient
z: phenotypic trait

Directional Selection differential (*S*): within-generational difference between mean phenotype after episode of selection (but before reproduction) and the mean before the selection episode (sometimes: “total selection”). Equivalent to regression of relative fitness on phenotype. Only for directional selection.

Selection gradient (*β*, *γ*): *partial* regression coefficients of relative fitness on a given trait (sometimes: “direct selection”). For directional, non-linear and correlational selection.

Directional Selection

$$R = h^2 S = \frac{V_a}{V_p} S = \frac{G}{P} S = G\frac{S}{P} = G\beta$$

univariate

$$\Delta\bar{\mathbf{z}} = \mathbf{G}\mathbf{P}^{-1}\mathbf{S} = \mathbf{G}\boldsymbol{\beta}$$

$$\xrightarrow{\textbf{hence}} \boldsymbol{\beta} = \mathbf{P}^{-1}\mathbf{S} = \frac{\mathbf{S}}{\mathbf{P}}$$

multivariate

(the bold upright font indicates matrix notation)

Non-linear Selection

Quadratic Regression

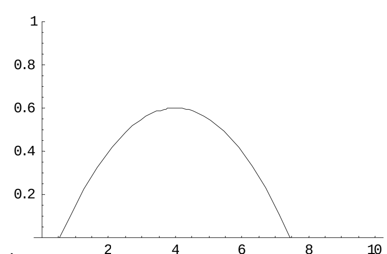
$$y = a + bx + cx^2$$

Non-linear fitness equation

$$w = a + \beta x + \frac{1}{2}\gamma x^2$$

Linear component (gradient)

Non-linear (quadratic) component (gradient)



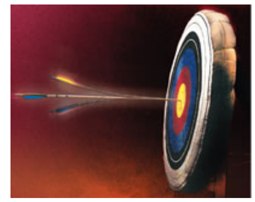
The non-linear selection gradient does not directly affect the change in the phenotypic mean from one generation to the next ($\Delta\bar{z}$). But it affect the genetic co-/variances.

Lande & Arnold 1983

Evolution by natural selection

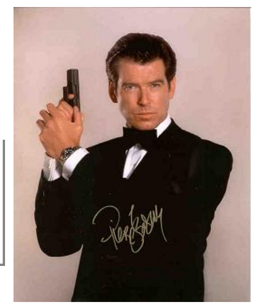
Of selective targets

Phenotypic trait under selection



and agents

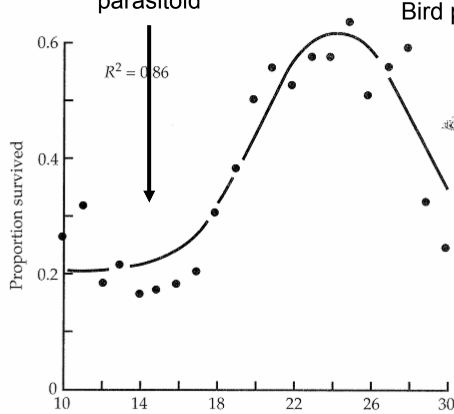
Ecological/social factor that generates a covariance between fitness and phenotype



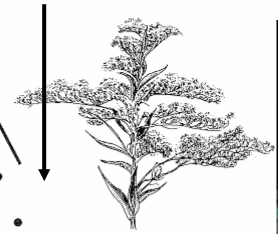
Evolution by natural selection

Agent 001 = parasitoid

Agent 002 = Bird predation



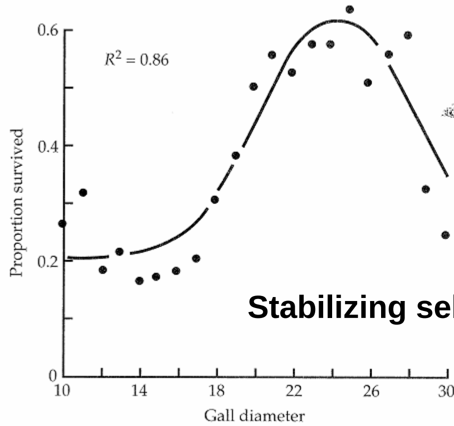
(Target)



Solidago altissima

Goldenrod = Goldrute

Example non-linear Selection



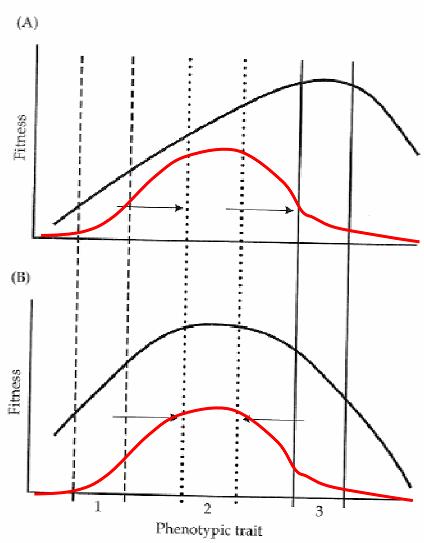
Stabilizing selection?

Solidago altissima

Goldenrod = Goldrute

Eurosta gall fly

Directional and Stabilizing Selection

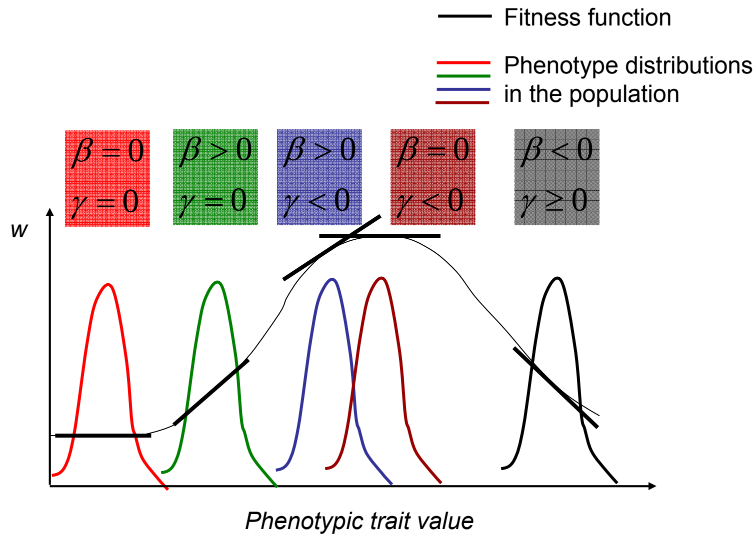


Fitness function

Phenotype distribution in the population

Stabilizing and directional selection are not mutually exclusive

Directional and Stabilizing Selection



Natural/Sexual Selection

Experimental Design

Definitions of Fitness

- Strict definition:
  A genotype's rate of increase in a population (e.g. Futuyma 1986)
- Working definitions:
  - **Fitness components**
    1. Individual survival (longevity)
    2. Fecundity (clutch size, hatching success, number of surviving offspring, number or reproducing offspring, fedundity of offspring, number of grand-children, ...)
    3. Insemination rate
    4. .... Often specific to the biology of the study organism.

Example: Estimating selection differentials and gradients

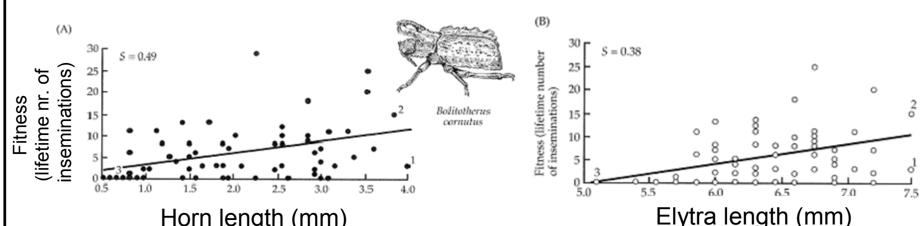


TABLE 6.1 *Estimates of total and direct selection in fungus beetles and Darwin's finches*

	Total selection (*S*)
Fungus beetles	
Elytra	0.38**
Horn	0.49***
Weight	0.39**

Fungus beetle
Bolithotherus cornutus

On the „+“ side

- Selection is observed as it is actually „happening“ in the population
- Estimation of indirect selection

On the „-“ side

- It is not possible to be completely sure to have causally isolated the „target of selection“*
- It is difficult to infer the „agents of selection“ causally*

*The problem of third variable causation (e.g., Ruxton and Colgrave, 2006)

Example:
Experimentally testing targets of selection

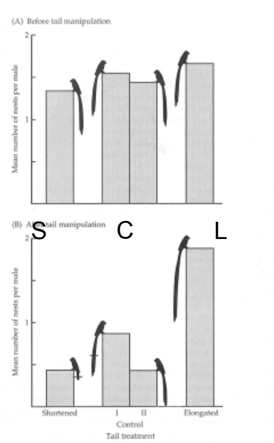
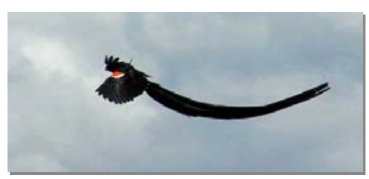


Figure 6.8 Results from experimental manipulation of widowbird tail lengths. The measure of fitness is the number of female nests per male. The top panel (A) shows the numbers before the tails were manipulated and the bottom (B) is after manipulation. Control I birds had their tails cut and glued back on, whereas control II birds were merely captured and banded. (After Andersson 1982.)



Long-tailed widow bird (*Euplectes progne*)

Anderson 1982.
Nature 299, 818-820

On the „+“ side

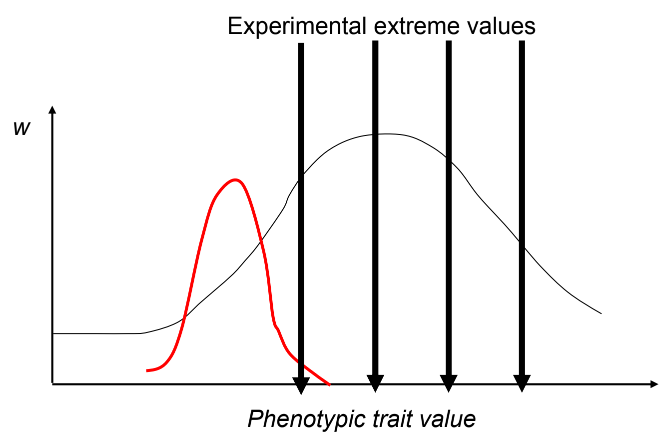
- Causal identification of target of selection
  (manipulation of target trait)
- Causal identification of agent of selection
  (manipulation of ecological factor)

On the „-“ side

- Univariate approach, usually one trait at a time
- Not all traits can be easily and directly
  manipulated
- Risk of generating exaggerated („unnatural“)
  variance in the trait

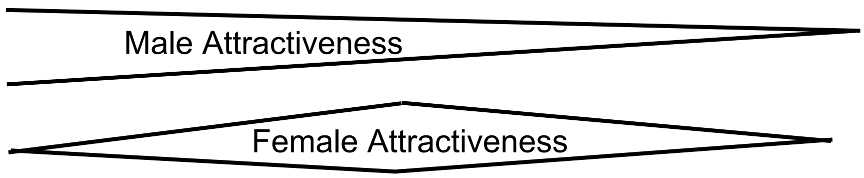
→ CAREFUL experimentation required

It can be interesting to experimentally create phenotypes that are outside the natural range



Example: sensory biases in the evolution of communication/signalling

Zebra finch (*Taenopygia guttata*)



Of 49 offspring reaching adulthood, 29 were reared by males with red colour bands, and 36 had mothers with orange bands.

Burley 1981, Science

Note on fitness components

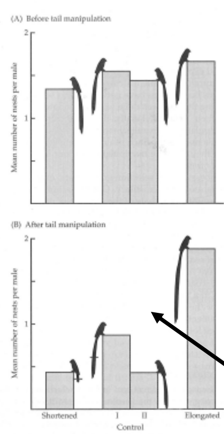


Figure 6.8 Results from experimental manipulation of widowbird tail lengths. The measure of fitness is the number of female nests per male. The top panel (A) shows the numbers before the tails were manipulated and the bottom (B) is after manipulation. Control I birds had their tails cut and glued back on, whereas control II birds were merely captured and banded. (After Andersson 1982.)

- In evolutionary and behavioural ecology, fitness components are often partitioned into a benefit part and a cost part
- Benefits and costs are often investigated separately
- But: what matters is the life-time value for the component (trade-offs involved)

Does this result mean that there is ongoing directional selection on male tail length in these widowbirds?

Note on fitness components