- ***Phenotypic selection***
  How selection acts on particular phenotypes

- ***Response to selection***
  Change in a trait distribution across generations.

- ***Episodes of selection***
  Selection is often subdivided into components

- ***Viability selection***
  Differences in survivorship

- ***Fertility selection***
  Differences in number of offspring per mating

- ***Tradeoffs***
  A trait that does well in one episode does poorly in another. Large body size favored in adult Ground Finch, small body size is favored in juveniles.

- ***Natural*** Vs ***sexual selection*** (Darwin 1859)

- ***Reproductive success***
  Number of offspring per adult, which confounds natural (fertility) and sexual selection (in males, the number of matings per adult).

- ***Lifetime*** (or ***total***) *fitness* of an individual
  the number of descendants it leaves at the start of the next generation.

Fitness components can themselves be further decomposed. For example, fertility in plants might be decomposed as (seeds per plant) = (number of stems per plant)·(number of inflorescences per stem)·(average number of seed capsules per inflorescence)·(average number of seeds per capsule).

Longitudinal vs. ***cross-sectional*** studies.

- Longitudinal study follows a cohort of individuals over time

- Cross-sectional study examines individuals at a single point in time. Cross-sectional studies typically generate only two fitness classes (e.g., dead vs. living, mating vs. unmated). Analysis of cross-sectional studies involves a considerable number of assumptions, and longitudinal studies are preferred.

Assigning Fitness Components

A cohort of n individuals (indexed by $1 \leq r \leq n$) is followed through several episodes of selection. Let $W_j(r)$ be the fitness measure for the jth episode of selection for the rth individual. For example, if we are following viability W_j is either zero (dead) or one (alive) at the census period.

Relative fitness components $w_j(r) = W_j(r)/\overline{W}_j$ will turn out to be especially useful.

At the start of the study, the frequency of each individual is $1/n$, giving for the first (observed) episode of selection

$$\overline{W}_1 = \frac{1}{n}\sum_{r=1}^{n} W_1(r) \tag{19.1a}$$

Caution: *considerable selection may have already occurred prior to the life cycle stages being examined*.

Following the first episode of selection, the new fitness-weighted frequency of the rth individual is $w_1(r)/n$, implying

$$\overline{W}_2 = \sum_{r=1}^{n} W_2(r) \cdot w_1(r) \cdot \left(\frac{1}{n}\right) \tag{19.1b}$$

In general, for the jth episode of selection,

$$\overline{W}_j = \sum_{r=1}^{n} W_j(r) \cdot w_{j-1}(r) \cdot w_{j-2}(r) \cdots w_1(r) \cdot \left(\frac{1}{n}\right) \tag{19.1c}$$

Note that if $W_j(r) = 0$, further fitness components for r are unmeasured.

Letting $p_j(r)$ be the fitness-weighted frequency of individual r *after* j episodes of selection, it follows that $p_0(r) = 1/n$ and

$$p_j(r) = w_j(r) \cdot p_{j-1}(r) = \frac{1}{n} \prod_{i=1}^{j} w_i(r) \tag{19.2a}$$

Equation 19.1c can also be expressed as

$$\overline{W}_j = \sum W_j(r) \cdot p_{j-1}(r)$$

Using these weights allows fitness-weighted moments to be calculated, e.g., the mean of a particular character following the jth episode satisfies

$$\mu_{z(j)} = \sum z(r) \cdot p_j(r) \tag{19.2b}$$

where $z(r)$ is the character value of individual r.

VARIANCE IN INDIVIDUAL FITNESS

How do we compare the amount of selection acting on different populations?

One might consider using the standardized selection differential (the selection intensity) $\overline{\imath} = S/\sigma_z$ for comparing the relative strength of individual selection between populations — drawback is that it is *character specific*.

$\overline{\imath}$ is appropriate if we are interesting in comparing the strength of selection on a particular *character*, but inappropriate if we wish to compare the overall strength of selection on *individuals*.

- ***Opportunity for selection,*** I

Much cleaner measure (independent of the characters under selection)

Defined as the variance in *relative* fitness:

$$I = \sigma_w^2 = \frac{\sigma_W^2}{\overline{W}^2} \tag{19.3}$$

I is estimated by

$$\widehat{I} = Var(w) = \frac{n}{n-1}\left(\overline{w^2} - 1\right) \tag{19.4}$$

I bounds the maximum value of $\overline{\imath}$. This follows by using (respectively), the definition of a correlation, the covariance definition of $S = Cov(z, w)$, and the fact that $|\rho| < 1$, to give

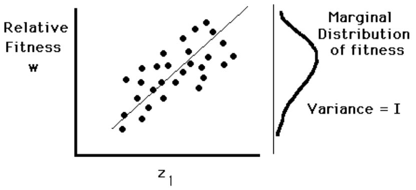
$$|\,\rho_{z,w}\,| = \frac{|\sigma_{z,w}|}{\sigma_z \sigma_w} = \frac{|S|}{\sigma_z \sqrt{I}} \leq 1,$$

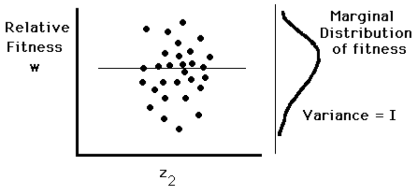
implying

$$|\,\overline{\imath}\,| \leq \sqrt{I} \tag{19.5}$$

Thus, the most that any mean can be shifted within a generation is $\sqrt{I}$ phenotypic standard deviations.

The usefulness of I as a bound of $\bar{\imath}$ depends on the correlation between relative fitness and the character being considered.





Caveats in Using the Opportunity for Selection

If the variance in fitness is not independent of $\overline{W}$, comparisons of I values between populations are compromised.

Example 1: With probability p organism mates (or survives), else does not mate (or dies).

$$I = \frac{p(1-p)}{p^2} \simeq \frac{1}{p} \quad if\ p << 1 \tag{19.9}$$

The mean and variance in individual fitness are not independent, and the opportunity for selection depends entirely on mean population fitness.

Example 2: Number of mates for any given male follows a Poisson distribution, the variance in number of mates equals the mean number of mates, giving

$$I = \frac{\overline{W}}{\overline{W}^2} = \overline{W}^{-1}$$

where $\overline{W}$ is the mean number of mates per male. Thus, differences in I between populations do not necessarily indicate *biological* differences in male mating ability. For example, in a population of 100 males, if only 5 females mate, average male mating success is $\overline{W} = 0.05$, while if 50 females mate, $\overline{W} = 0.5$. For this example, differences in I come solely from variation in the number of mating females, not biological differences between males in their ability to acquire mates.

Measuring Phenotypic Selection: Changes in Mean

- The selection differential, $S = \mu_{z^*} - \mu_z$
  S is the fitness-weighted mean after selection minus the mean before selection
- Robertson-Price Identity, $S = cov(z, w)$
- The directional selection gradient β

$$\beta = \frac{S}{\sigma_z^2} = \frac{cov(z,w)}{\sigma_z^2}$$

- β is the slope of the best (least-squares) linear regression of relative fitness on phenotype,

$$w = a + bz = 1 + beta(z - \mu)$$

Measuring Phenotypic Selection: Changes in Variance

Stabilizing selection decreases the phenotypic variance

Disruptive selection increases the variance

Problem: Directional selection also decreases the variance.

Hence, for a proper measure of the selection on the variance, we must first remove the directional selection effects.

- ***Quadratic selection differential,*** C

$$C = \sigma^2_{z^*} - \sigma^2_z + s^2$$

- Like S, we can express C as a covariance,

$$C = \sigma\left[w, (z-\mu)^2\right] \tag{19.12}$$

- As was the case for S, we can use I to bound C,

$$|C| \leq \sqrt{I\left(\mu_{4,z} - \sigma^4_z\right)} \tag{19.13a}$$

- The ***quadratic (stabilizing) selection gradient*** γ is the variance analogue of β, with

$$\gamma = \frac{\sigma\left[w, (z-\mu)^2\right]}{\sigma^4_z} = \frac{C}{\sigma^4_z}$$

- Just as β was the slope of the best linear regression of w on z, γ is the slope of the best quadratic regression of w on z, with

$$w = a + b(z-u) + (\gamma/2)(z-\mu)^2$$

If the distribution of z shows no skew, then $b = \beta$, giving the ***Pearson-Lande-Arnold Fitness regression***

$$w = 1 + \beta(z-u) + \frac{\gamma}{2}\left((z-\mu)^2 - \sigma^2_z\right)$$

Graidents and Fitness Surfaces

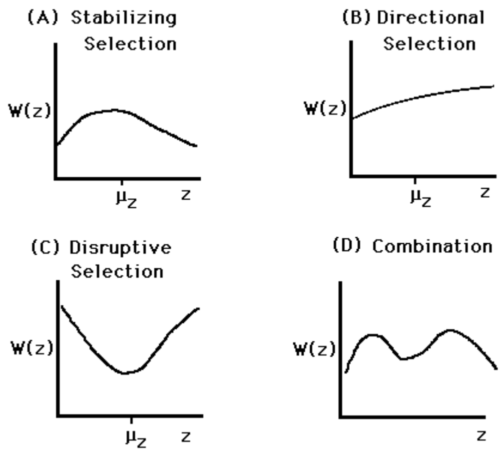
$w(z)$ is the expected fitness of an individual with trait value z, and this is called the ***individual fitness surface***.

- The nature of selection on a character in a particular population is determined by the local geometry of the individual fitness surface over that part of the surface spanned by the population

- If fitness is increasing (decreasing) over some range of phenotypes, a population having its mean value in this interval experiences ***directional selection***

- If $W(z)$ contains a local maximum, a population with members within that interval experiences ***stabilizing selection***

- If the population is distributed around a local minimum, ***disruptive selection*** occurs.



- ***Mean population fitness*** $\overline{W}$ is also a fitness surface, describing the expected fitness of the population as a function of the distribution of phenotypes in that population,

$$\overline{W} = \int W(z)\, p(z)\, dz$$

- Mean fitness a function of the parameters of the phenotypic distribution, e.g. $\overline{W}(\mu_z, \sigma_z^2)$

- When the trait z is normally distributed and individual fitness are not frequency-dependent, β can be expressed in terms of the geometry of the *mean* fitness surface,

$$\beta = \frac{\partial \ln \overline{W}}{\partial \mu_z} = \frac{1}{\overline{W}} \frac{\partial \overline{W}}{\partial \mu_z}$$

- If the trait is normally distributed, then β and γ are the average slope and curvature of the fitness surface,

$$\beta = \int \frac{\partial w(z)}{\partial z}\, p(z)\, dz$$

$$\gamma = \int \frac{\partial^2 w(z)}{\partial z^2}\, p(z)\, dz$$

- β and γ describe changes in the mean and variance,

$$\Delta\mu_z = \sigma_A^2\, \beta$$

$$\Delta\sigma_z^2 = \frac{\sigma_A^4}{2} \left(\gamma - \beta^2\right)$$