

# Individual Fitness and Measures of Univariate Selection

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Uppsala EQG 2012 course  
version 6 Feb 2012

In previous lectures, we assumed the nature of selection was known, and our goal was to estimate response.

Our interest here is how selection acts on particular phenotypes (**phenotypic selection**)

This involves two issues:

- Measurement of fitness in individuals
- Quantification of any association between fitness and trait values

# Episodes of Selection

Selection often broken into components, or episodes of selection.

**Viability selection** (differences in survivorship)

**Fertility selection** (differences in number of offspring/mating)

Natural vs. sexual selection

**Sexual selection** results from variance in mating success.

# Assigning Fitness Components

**Longitudinal studies**, which follow a cohort of individuals through time, are strongly preferred when possible.

**Cross-sectional** studies examine individuals at a single point in time, and typically return only two fitness classes (e.g., dead/alive, mated/unmated). Their analysis requires a considerable number of assumptions.

To see how fitness components are assigned when there are several episodes of selection, suppose we measure a cohort of  $n$  individuals (indexed by  $1 \leq r \leq n$ ) over several episodes of selection

One must remember that considerable selection may have already occurred prior to our study.

Let  $W_j(r)$  denote the fitness of individual  $r$  for the  $j$ -th episode of selection. For example,  $W$  could be 0 or 1 (dead/alive), or number of mates, or number of offspring

The relative fitness is just  $w_j(r) = W_j(r) / \bar{W}_j$

At the start of our study, all individuals are equally-weighted, so that the mean fitness for episode 1 is

$$\bar{W}_1 = \frac{1}{n} \sum_{r=1}^n W_1(r)$$

Thus after the first episode of selection, the  $r$ -th individual now has a fitness-weighted frequency of  $(1/n) w_1(r)$

Thus, the mean fitness for episode 2 is the average of the fitness of individuals times their frequencies,

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

In general, the mean fitness for episode  $j$  is

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



$p_j(r)$ , the fitness-weighted frequency of  $r$  at the *start* of the  $j$ -th episode

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

We can also write the mean fitness of the  $j$ -th episode as

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

With the fitness-weighted frequencies for individuals after  $j$  episodes of selection, we can compute the fitness-weighted trait means and variances.

$$\mu_{z(j)} = \sum z(r) * p_j(r)$$

$$E[z^2(j)] = \sum z^2(r) * p_j(r)$$

$$\sigma_j^2(z) = E[z^2(j)] - \mu_{z(j)}^2$$

Example: Howard's (1979) data on mating success (number of mates)  $W_1$  and eggs per mating ( $W_2$ ) for male bullfrogs (*Rana*) as a function of their size

Male	Size	$W_1$	$W_2$	$w_1$	$p_1$	$w_2$	$p_2$
1	145	1	25,820	0.714	0.143	1.628	0.233
2	128	1	22,670	0.714	0.143	1.429	0.204
3	148	0	0	0	0	0	0
4	138	2	7,230	1.429	0.286	0.456	0.130
5	141	3	15,986	2.143	0.429	1.008	0.432

$$\bar{W}_1 = \frac{1}{5} (1+1+0+2+3) = \frac{7}{5} = 1.4, \quad \text{giving } w_1(r) = \frac{W_1(r)}{1.4}$$

$$\bar{W}_2 = \sum W_2(r) * p_1(r)$$

$$= (25,820 * 0.143) + (22,670 * 0.143) + (7,230 * 0.286) + (15,986 * 0.429)$$

$$= 15,860$$

Example: Howard's (1979) data on mating success (number of mates)  $W_1$  and eggs per mating ( $W_2$ ) for male bullfrogs (*Rana*) as a function of their size

Male	Size	$W_1$	$W_2$	$w_1$	$p_1$	$w_2$	$p_2$
1	145	1	25,820	0.714	0.143	1.628	0.233
2	128	1	22,670	0.714	0.143	1.429	0.204
3	148	0	0	0	0	0	0
4	138	2	7,230	1.429	0.286	0.456	0.130
5	141	3	15,986	2.143	0.429	1.008	0.432

$$\bar{z}(1) = 145 \cdot 0.143 + 128 \cdot 0.143 + 148 \cdot 0 + 138 \cdot 0.286 + 141 \cdot 0.429 = 138.996$$

$$\overline{z^2}(1) = 145^2 \cdot 0.143 + 128^2 \cdot 0.143 + 148^2 \cdot 0 + 138^2 \cdot 0.286 + 141^2 \cdot 0.429 = 19,325$$

$$\text{Var}[z(1)] = \frac{5}{4} (19,325 - 138.996^2) = 6.39$$

# Variance in Individual Fitness

How can we compare the amount of selection acting on different populations (independent of the actual traits under selection)?

While the selection intensity  $i$  allows us to compare different populations, it is *character-specific*

Further, selection can occur without changing the mean (such as stabilizing selection)

A character-independent measure for the overall strength of selection on a population that is trait-independent is  $I$ , the *opportunity for selection*,

I is just the **variance in relative fitness**

$$I = \sigma_w^2 = \frac{\sigma_W^2}{\bar{W}^2}$$

Which can be estimated by

$$\hat{I} = \text{Var}(w) = \frac{n}{n-1} \left( \overline{w^2} - 1 \right)$$

I was introduced by Crow (1958), who called it the index of total selection. The term opportunity for selection was introduced by Arnold and Wade (1984a,b)

I bounds the maximum possible selection intensity  $i$  for any trait in a population.

To see this, we first use the Robertson-Price identity,  $S = \sigma(z,w)$ , namely that the selection differential is the covariance between trait value and relative fitness

Since the absolute value of a correlation is bounded by 1,

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

Thus, the absolute selection intensity is bounded by the square root of  $I$  for *any character*

$$|i| \leq \sqrt{I}$$

The most that selection can change any trait in one generation is  $I^{1/2}$  phenotypic standard deviations.

## Example: return to our frog data

Here,

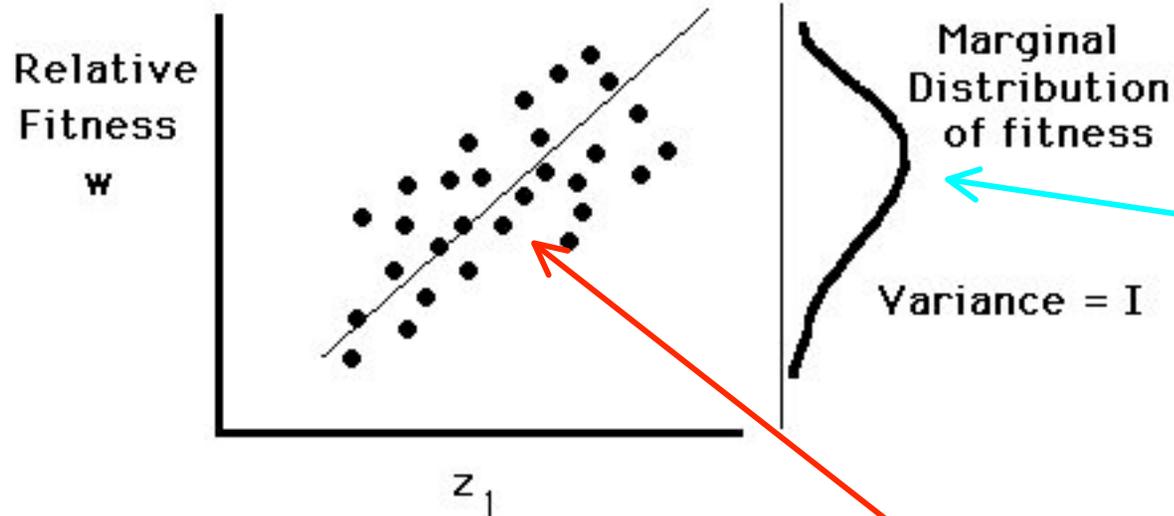
$$\overline{w^2} = (1/5) (1.162^2 + 1.020^2 + 0^2 + 0.652^2 + 2.160^2) = 1.496$$

Hence,

$$\hat{I} = \frac{5}{4} (1.496 - 1) = 0.62$$

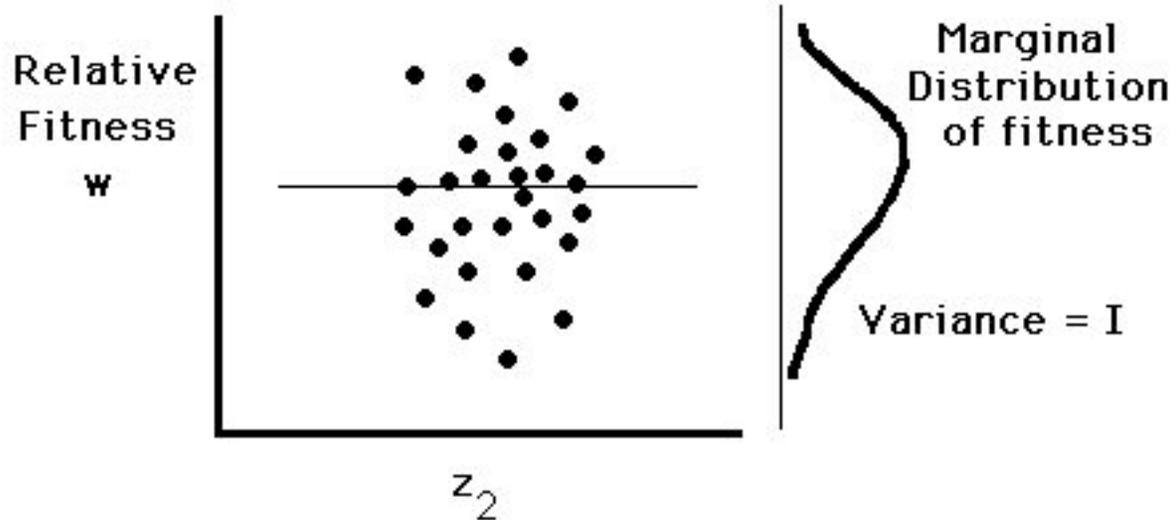
Thus for this population, the maximum any trait can change over a single generation is  $0.62^{1/2} \approx 0.71$  SD

Note that the change in male body size (in SD) was just -0.155, less than 1/5 of the maximum absolute possible change



For any set of individuals, this distribution does not change over traits

What does change is the association (i.e. regression) of trait value on fitness,  $\sigma(w, z) / \sigma^2_z = S / \sigma^2_z$



Same set of individuals, hence the same distribution of relative fitness values, but different trait = different regression

In some cases, we do not have data on individual fitness, but rather the fitnesses of phenotypic classes. In such cases we can still place a lower bound on  $I$

Example: O'Donald looked at selection on wing eyespot number in the butterfly *Maniola* by comparing the distribution of eyespot number in wild-caught individuals vs. those reared in the lab

Eyespot number	Fitness	Number
0	1.000	124
1	0.699	67
2	0.657	34
3	0.548	10
4	0.000	2

$$\overline{W} = \frac{1}{237} [(1 * 124) + (0.699 * 67) + (0.675 * 34) + (0.548 * 10)] \simeq 0.838$$

$$\overline{W^2} = \frac{1}{237} (1^2 * 124) + (0.699^2 * 67) + (0.675^2 * 34) + (0.548^2 * 10) \simeq 0.736$$

$$\text{Var}(W) = \frac{237}{236} (0.736 - 0.838^2) \simeq 0.034 \quad \hat{I} = \frac{0.034}{0.838^2} \simeq 0.048$$

Hence,  $I \geq 0.048$ , as

$\text{Var} = \text{Var}(\text{between groups}) + \text{Var}(\text{within groups})$

$I = 0.048 + \text{Var}(\text{within groups})$

# Caveats with using I

If the variance in fitness is not independent of mean fitness  $\bar{W}$ , then comparisons of I values across populations are compromised.

For example, suppose we look over some short time period and score mating vs. not mating. Mean fitness is simply  $p$ , the fraction that have mated. As we look over longer time windows,  $p$  should increase.

In this case, fitness follows a binominal distribution, with mean  $p$  and variance  $p(1-p)$ , giving I as

$$I = \frac{p(1-p)}{p^2} \simeq \frac{1}{p} \quad \text{if } p \ll 1$$

In this case, as we change our sampling interval, which increases or decreases  $p$ , we also change  $I$

A second example where there is a lack of independence between mean fitness and variance in fitness is when individual fitness follows a Poisson distribution, in which case the mean = variance, and  $I = 1/\text{mean fitness}$

Suppose we have a population of 100 males, but only have 5 females mate, giving mean fitness as 0.05. However, if 50 females mate, mean fitness is now 0.5. Differences between  $I$  in these two settings come solely from variation in the number of mating females, not any biological differences between males in mating ability.

# Describing Phenotypic Selection

One way to describe selection on a trait is to compare the (fitness-weighted) distributions before and after an episode of selection

In addition to selection on the trait itself, growth (or other ontogenetic changes), immigration, environment change, selection on phenotypically-correlated traits can all shift this distribution

We typically speak of **fitness surfaces** for traits, which map trait value into fitness

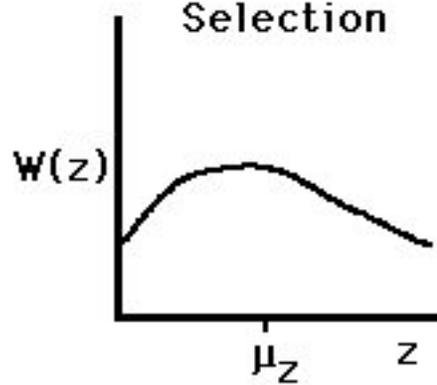
**$W(z)$**  = average fitness of an individual with trait value  $z$

$W(z)$  is called the **individual fitness surface**.

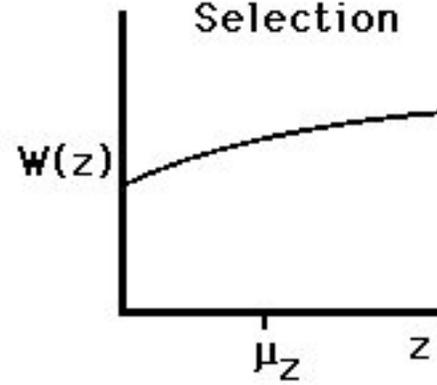
The geometry of the fitness surface describes the  
Nature of selection:

- **Directional selection:** fitness increases (or decreases with trait value) -- **linear relationship** between fitness and trait value
- **Stabilizing selection:** The fitness surface has a peak --- **convex quadratic relationship** btw  $w$  and  $z$
- **Disruptive selection:** The fitness surface has a valley --- **concave quadratic relationship** btw  $w$  and  $z$

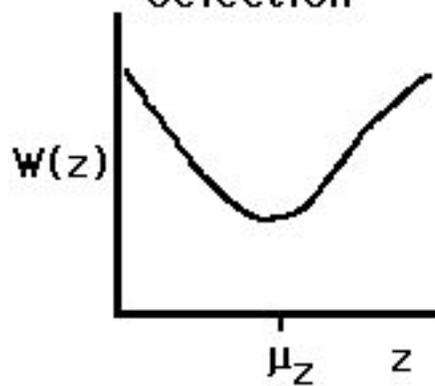
(A) Stabilizing Selection



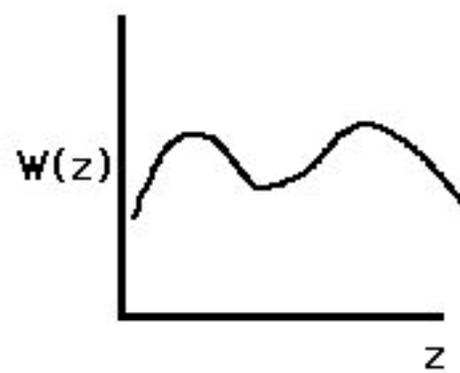
(B) Directional Selection



(C) Disruptive Selection



(D) Combination



$W(z)$  may vary with genotypic and environmental backgrounds

When the fitness of an individual depends on the distribution of trait values of other individuals (e.g, truncation selection, search imagines, dominance hierarchies), fitness is said to be **frequency-dependent**.

The second type of fitness surface is the **mean fitness surface**, the average fitness given the distribution of phenotypes.

As an analogy, we measure breeding values for individuals, while the summary statistic for the population is the additive variance

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

While the mean fitness surface depends on all of the parameters of the distribution, how it changes as we change the population mean is usually what is considered.



# The Robertson-Price Identity

Robertson (1966) and Price (1970, 1972) showed that  $S = \text{cov}(w, z)$ , the covariance between relative fitness  $w$  and trait value  $z$ . This is a *completely general relationship* and makes no assumptions.

To see this, first note that the distribution of the trait after selection is

$$p_s(z) = \frac{W(z) p(z)}{\int W(z) p(z) dz} = \frac{W(z) p(z)}{\bar{W}} = w(z) p(z)$$

Thus, we can write the mean after selection as

$$\mu_s = \int z p_s(z) dz = \int z w(z) p(z) dz = E[ z w(z) ]$$

# The Robertson-Price Identity

Thus, we can write the mean after selection as

$$\mu_s = \int z p_s(z) dz = \int z w(z) p(z) dz = E[ z w(z) ]$$

Thus, we can express the selection differential as

$$S = \mu_s - \mu = E[ z w(z) ] - E(z) E(w) = \sigma[ z, w(z) ]$$

This follows since  $E(w) = 1$ , so that  $\mu = \mu * 1 = E(z) * E(w)$

# Directional Selection: Directional Differentials (S) And Gradients ( $\beta$ )

Changes in the mean (within a generation) are measured by the **directional** selection differential  $S$  and the selection gradient  $\beta$ , where

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

Note that  $\beta$  is the **slope of a regression** of relative fitness  $w$  on trait value  $z$ ,

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

Since  $S = \beta \sigma^2_z$ , we can write the breeders' equation as  $R = h^2 (\beta \sigma^2_z) = (\sigma^2_A / \sigma^2_z) (\beta \sigma^2_z)$

giving

$$R = \beta \sigma^2_A$$

The real importance of  $\beta$  arises when we consider multiple traits (Lecture 13)

When phenotypes are normally-distributed and fitnesses are frequency-independent, then (Lande 1976)

$$\beta = \frac{\partial \ln \bar{W}}{\partial \mu}$$

Thus,  $\beta$  is the **gradient** (with respect to  $\mu$ ) of the mean fitness surface, hence its name

# Summary of measures of the within-generation change in the mean

For a single character under selection, we have introduced three measures for change in mean

$$S = \mu^* - \mu \quad i = S/\sigma_z \quad \beta = S/\sigma_z^2$$

The (**directional**) **selection differential**  $S$ , the observed change in the mean

The **selection intensity**  $i$ , the observed, change in the mean in phenotypic standard deviations. The measure for comparing selection on particular traits

The **selection gradient**  $\beta$ , the slope of the regression of relative fitness on trait value

While these three measures are just scaled values of each other for a single trait, they behave very differently when we consider their vector extensions for multiple traits

## Changes in the Variance: The Quadratic Selection Differential $C$ and Quadratic Selection Gradient ( $\gamma$ )

Now let's consider changes in variances.

At first though, you might consider the variance analogue to  $S$  to simply be the within-generation change in variance,  $\sigma_{z^*}^2 - \sigma_z^2$

The problem is that Lande and Arnold (1983) showed that

$$\sigma_{z^*}^2 - \sigma_z^2 = \sigma \left( w, (z - \mu_z)^2 \right) - S^2$$

Observed within-generation  
change in the phenotypic variance

Directional selection decreases the  
variance, by an amount  $S^2$


$$\sigma_{z^*}^2 - \sigma_z^2 = \sigma \left( w, (z - \mu_z)^2 \right) - S^2$$

Robertson-Price like term for  
quadratic effects

Based on this expression, Lande & Arnold defined  
the quadratic selection differential  $C$  by

$$C = \sigma_{z^*}^2 - \sigma_z^2 + S^2$$

Lande and Arnold originally called  $C$  the **stabilizing selection differential**, but (for a variety of reasons to be discussed) quadratic is much less misleading

Note that since directional selection reduces the variance

- A reduction in variance is not, by itself, an indication that stabilizing (or more properly **convex**) selection has occurred.
- An increase in variance due to disruptive (or more properly **concave**) selection can be masked by a decrease in the variance from directional selection (a change in the mean) has occurred.

Example: natural selection in Darwin's finches on Daphne Major Island (Galapaagos)

Boag and Grant (1981) observed intense selection on body size in *Geospiza fortis* during a severe drought

The mean and variance of 642 adults before the drought were 15.79 and 2.37. The mean/variance of the 85 surviving adults was 16.85 / 2.43. There appeared very little selection in the variance ( $2.43 - 2.37 = 0.06$ )

However,  $S = 16.85 - 15.79 = 1.06^2$ , giving the quadratic selection differential as

$$C = 0.06 + 1.06^2 = 1.14$$

Hence, a combination of directional and concave (disruptive) selection likely occurred.

## Convex / Concave Selection vs. Stabilizing / Disruptive selection

**Convex selection:** The individual fitness surface has a **negative curvature**

**Stabilizing selection:** The individual fitness surface has a negative curvature AND has a **maximum** within the **range of phenotypes seen in the population**

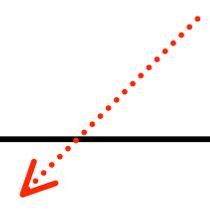
**Concave selection:** The individual fitness surface has a **positive curvature**.

**Disruptive selection:** The individual fitness surface has a positive curvature AND has a **minimum** within the **range of phenotypes seen in the population**

Since  $C = \sigma[ w, (z- \mu_z)^2 ]$ , we can also use arguments akin to leading to a bound on  $S$  based on  $I$ , the opportunity for selection

Specifically,

4-th moment about the mean,  
 $E[(x-\mu)^4]$ , -- **kurtosis**

$$|C| \leq \sqrt{I (\mu_{4,z} - \sigma_z^4)}$$


For a normally-distributed trait, the 4th moment is  $3 \sigma_z^4$ , giving

$$|C| \leq \sigma_z^2 \sqrt{2I}$$

## Quadratic Selection Gradient ( $\gamma$ )

The **Quadratic Selection Gradient** ( $\gamma$ ) is defined by

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

As we will see shortly,  $\gamma$  (like  $\beta$ ) is also a coefficient in a fitness regression, here on quadratic terms.

Likewise (again like  $\beta$ )  $\gamma$  is a measure of the average geometry of the individual fitness surface, in particular The average slope.

$\beta$  and  $\gamma$  describe the average geometry of the fitness surface

Provided phenotypes are normally distributed,

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

Slope of the individual fitness surface at trait value  $z$

$\beta$  = average slope, no matter how messy the fitness surface

$\beta$  and  $\gamma$  describe the average geometry of the fitness surface

Provided phenotypes are normally distributed,

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

$\gamma$  = average curvature, no matter how messy the fitness surface

Curvature of the individual fitness surface at trait value  $z$



$\beta$  and  $\gamma$  fully describe the effects of phenotypic selection in the response equations

Change in mean

$$\Delta \mu = \sigma_A^2 \beta$$

$$\Delta \sigma_z^2 = \frac{h^4}{2} \delta \sigma_z^2 = \frac{\sigma_A^4}{2 \sigma_z^4} (C - S^2)$$

Change in variance (one generation of selection)

$$= \frac{\sigma_A^4}{2} (\gamma - \beta^2)$$

Change in variance (general)

$$d(t+1) = \frac{d(t)}{2} + \frac{\sigma_A^4(t)}{2} (\gamma(t) - \beta^2(t))$$

## Linear and Quadratic Approximations of $W(z)$

To simplify expressions somewhat we first rescale our trait to have mean zero (i.e, subtract off the mean)

The best linear regression predicting relative fitness  $w$  given trait value  $z$  is

$$w = 1 + \beta z + \varepsilon$$

The slope of the best-fitting **linear** regression is given by  $\sigma(w,z) / \sigma^2_z = \beta$ .

$$r^2_{z,w} = \frac{\text{Cov}^2(z, w)}{\text{Var}(z) * \text{Var}(w)} = \hat{\beta}^2 \frac{\text{Var}(z)}{\hat{I}}$$

Now consider the best quadratic regression

$$w = 1 + b_1 z + b_2 z^2 + \varepsilon$$

The regression coefficients  $b_1$  and  $b_2$  nicely summarize the local geometry

What are  $b_1$  and  $b_2$  for the best-fitting regression?

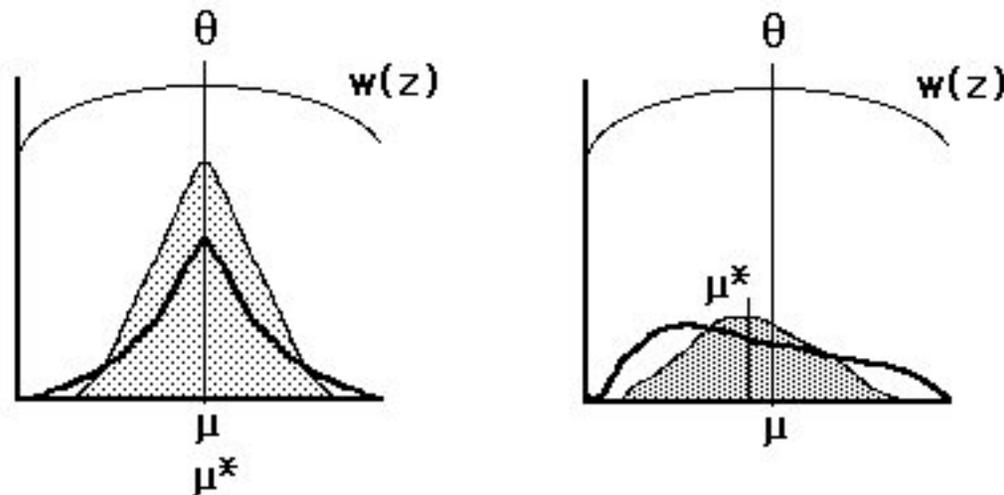
$$\left. \frac{\partial w(z)}{\partial z} \right|_{z=\mu_z} = b_1, \quad \left. \frac{\partial^2 w(z)}{\partial z^2} \right|_{z=\mu_z} = 2b_2$$

Slope of the fitness surface  
evaluated at the mean is  $b_1$

$(1/2)b_2$  is the curvature  
of the surface at the mean

$b_1$  is NOT necessarily  $\beta$ !

An interesting feature of quadratic selection is that it can result in a change in the mean, even when no direct selection on the mean is apparent.



Both populations are under strict stabilizing selection, with the mean under the optimal value  $\theta$ . The phenotypic distribution on the left is symmetric and does not experience directional selection.

However, the population on the right has skewed its phenotypic variance, and hence the stabilizing selection unevenly shifts the distribution after selection, resulting in a change in mean.

# Find the regression coefficients by OLS

$$w = 1 + b_1 z + b_2 z^2 + \varepsilon$$

$$b_1 = \frac{\sigma^2(x_2) \cdot \sigma(x_1, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{(\mu_{4,z} - \sigma_z^4) \cdot S - \mu_{3,z} \cdot C}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2}$$
$$b_2 = \frac{\sigma^2(x_1) \cdot \sigma(x_2, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{\sigma_z^2 \cdot C - \mu_{3,z} \cdot S}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2}$$

If skew is present, the linear slope is influenced by the quadratic selection differential. Likewise the quadratic slope is influenced by the directional selection differential.

# Find the regression coefficients by OLS

$$w = 1 + b_1 z + b_2 z^2 + \varepsilon$$

$$b_1 = \frac{\sigma^2(x_2) \cdot \sigma(x_1, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{(\mu_{4,z} - \sigma_z^4) \cdot S - \mu_{3,z} \cdot C}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2}$$

$$b_2 = \frac{\sigma^2(x_1) \cdot \sigma(x_2, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{\sigma_z^2 \cdot C - \mu_{3,z} \cdot S}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2}$$

If skew is absent,  $b_1 = \beta$ .

If skew is absent,  $b_2 = C/(\mu_z^4 - \sigma_z^4)$ . If  $z$  is normally distributed, then  $\mu_z^4 - \sigma_z^4 = 3\sigma_z^4 - \sigma_z^4 = 2\sigma_z^4$ , giving  $b_2 = C/(2\sigma_z^4) = \gamma/2$

Thus, when  $z$  is normal, the regression reduces to

$$w = 1 + \beta z + (\gamma/2)z^2 + \varepsilon$$

This is the **Lande-Arnold regression**, or **Lande-Arnold fitness estimation**.

# Nonparametric estimators of the fitness surface

If the fitness surface have higher order curvature beyond the quadratic, the fitted quadratic regression terms can be potentially misleading. For example, with multiple peaks/values, a quadratic regression assumes (at most) only one extreme point.

This has lead to **nonparametric** (distribution-free) estimates of the fitness (**response**) surface.

Schulter (1988) produced a method using a local series of splines (cubic polynomials)

**Thin-plate spline** methods have also been used, fitting "plates" instead of lines

## Complications with Unmeasured Variables

Our estimates are biased if there are traits under selection that are phenotypically correlated with our trait.

Happily, traits under selection that are not phenotypically correlated do not bias our results (even if they are genetically correlated)

A potentially more serious issue is when the environment influences both our trait and also fitness.

For example, suppose plants in good soil environments produce both larger plants and more seeds. If we do not know soil type, we will assume larger plants have a higher fitness.

## Complications with Unmeasured Variables

An interesting example is Kruuk et al. (2002) who looked at antler size in red deer.

Males with larger antlers enjoy increased lifetime breeding success (antlers being involved in male-male competition), resulting in a  $\beta = 0.44 \pm 0.18$

Further, antler size is also heritable,  $h^2 = 0.22 \pm 0.12$

Despite selection and heritability, no observed response over 30 years of study

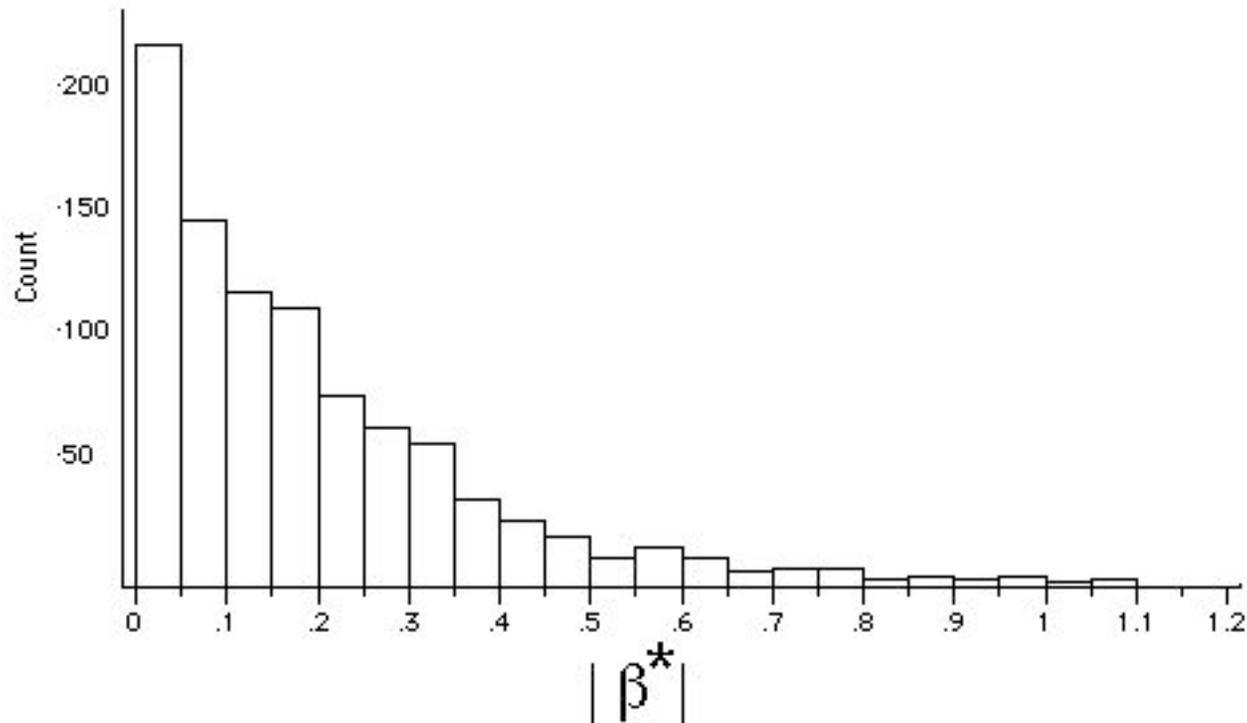
Authors suggest that antler size and male fighting ability heavily dependent upon an individual's nutritional state

## How Strong is Selection in Natural Populations?

Bumpus (1899) and Weldon (1901) were the first to publish attempts to detect selection on quantitative traits in nature

Endler (1986) was the first to make a serious attempt at summarizing the average strength of selection

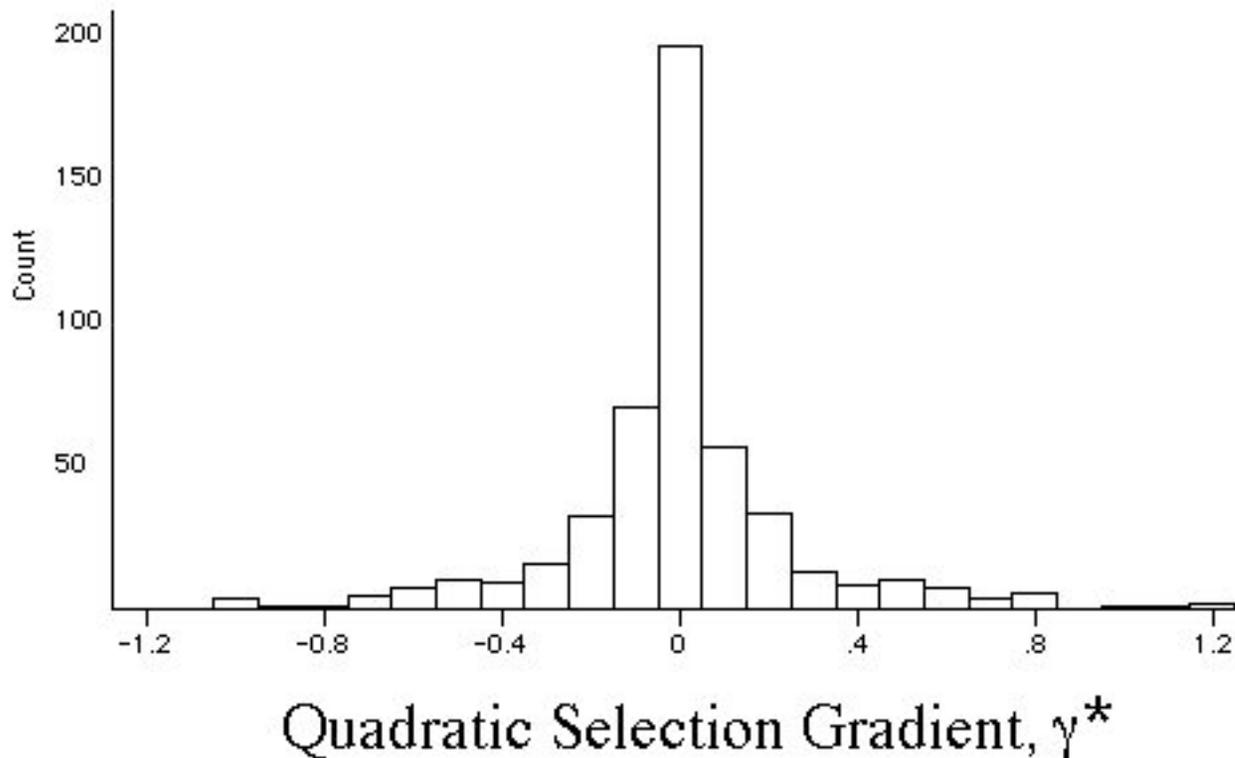
Kingsolver and colleagues (2001) provide the most recent summary, with other 2,500 estimates of  $\beta$  and  $\gamma$  from natural populations



$\beta$  values fit an exponential distribution, with medium (50%) values of scaled  $\beta = 0.16$ . This means that a one SD change in the trait changes fitness by 16%

Selection is generally weak, with few (<10%) of the  $\beta > 0.5$

Most large estimates of  $\beta$  occur in small populations. For samples sizes  $> 1000$ , most estimates of  $\beta$  are below 0.1



Medium value of  $|\gamma|$  was 0.10

Distribution of the estimated  $\gamma$  is symmetric, with concave (“disruptive”) selection ( $\gamma < 0$ ) as common as convex (“stabilizing”) selection ( $\gamma > 0$ ).

Blows & Brooks (2003) point out issues with estimating selection from the  $\gamma_{ii}$  terms in a multivariate analysis (we will return to this)

# The Importance of Experimental Manipulation

As we have tried to stress, unmeasured (but phenotypically correlated) traits, environmental factors that influence both the trait and fitness, changes in the environment and additional complications (such as inbreeding depression) can seriously bias estimates of fitness-trait associations.

Hence, the final analysis should always try to include direct experimental manipulation to demonstrate that a detected correlation really has a direct effect.