

## Lecture 12

# Individual Fitness and Measures of Univariate Selection

Bruce Walsh. jbwalsh@u.arizona.edu. University of Arizona.

ECOL 519A, March 2007. University of Arizona

Previous lectures examined the response to selection, assuming that the nature of selection is known. Here we are concerned with the complementary issue of measuring how selection acts on particular phenotypes (**phenotypic selection**). Estimating the amount and nature of selection provides a critical link between ecology and evolution. The estimation of selection involves two related issues: measuring individual fitness and measuring how the phenotype of a particular character influences individual fitness. The latter question is often phrased in terms of estimating  $W(z)$ , the expected fitness for an individual with character value  $z$ . Our focus here on individual fitness and selection on single traits. Selection on multiple traits is covered in Lectures 13 and 14.

### EPISODES OF SELECTION

Selection is often partitioned into components called **episodes of selection**. For example, a distinction is often made between **viability selection** (differences in survivorship) and **fertility selection** (differences in number of offspring per mating). **Tradeoffs** may be found, wherein a trait that does well in one episode does poorly in another. For example, large body size is usually favored in adults of Darwin's Medium Ground Finch *Geospiza fortis* (Boag and Grant 1981, Price et al. 1984), while small body size is apparently favored in juveniles (Price and Grant 1984). The possibility of tradeoffs between **natural** and **sexual selection**, first suggested by Darwin (1871), has also received significant attention. Sexual selection results from variance in male mating success due to male-male competition for females and/or female choice of particular males, while natural selection results from variance in all other fitness components, such as viability and fertility differences, differences in parental care, etc.

### Fitness Components

Loosely stated, the **lifetime** (or **total**) **fitness** of an individual is the number of descendants it leaves at the start of the next generation. When measuring the total fitness of an individual, care must be taken not to cross generations or to overlook any stage of the life cycle in which selection acts. To accommodate these concerns, lifetime fitness is defined as the total number of zygotes (newly fertilized gametes) that an individual produces. Measuring total fitness from any other starting point in the life cycle (e.g., from adults in one generation to adults in the subsequent generation) can result in a very distorted picture of true fitness of particular phenotypes (Prout 1965, 1969). If generations are crossed, measures of selection on a particular parental phenotype in reality are averages over both parental and offspring phenotypes, which may differ considerably.

Systems for measuring lifetime fitness have been especially well developed for laboratory populations of *Drosophila* (reviewed by Sved 1989). Measurements of lifetime fitness in field situations are more difficult and (not surprisingly) are rarely made. Attention instead is usually focused on particular episodes of selection or particular phases of the life cycle. Fitness components for each episode of selection are defined to be multiplicative. For example, lifetime fitness can be partitioned as (probability of surviving to reproductive age)·(number of mates)·(number of zygotes per mating). Number of mates is a measure of sexual selection, while the viability and fertility components measure natural selection. A commonly measured fitness component is **reproductive success**, the number of offspring per adult, which confounds natural (fertility) and sexual selection (in males, the number of matings per adult).

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). This decomposition allows us to ask questions of the form: do plants differ in number of seeds mainly because some plants have more stems, or more flowers per stem, or are there tradeoffs between these?

Estimates of fitness can be obtained from either **longitudinal** or **cross-sectional** studies. A longitudinal study follows a cohort of individuals over time, while a cross-sectional study examines individuals at a single point in time. Cross-sectional studies typically generate only two fitness classes (e.g., dead versus living, mating versus unmated). Analysis of cross-sectional studies involves a considerable number of assumptions (Lande and Arnold 1983, Arnold and Wade 1984b), and longitudinal studies are preferred. Unfortunately, these usually require far more work and may be impossible to carry out in many field situations. Age-structured populations pose further complications in that proper fitness measures require knowledge of the population's demography.

### Assigning Fitness Components

We now turn to the task of partitioning measures of individual fitnesses in a longitudinal study into 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  $j$ th episode of selection for the  $r$ th individual. For example, if we are following viability  $W_j$  is either zero (dead) or one (alive) at the census period. **Relative fitness** components  $w_j(r) = W_j(r)/\bar{W}_j$  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

$$\bar{W}_1 = \frac{1}{n} \sum_{r=1}^n W_1(r) \quad (12.1a)$$

We need to caution at this point that *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  $r$ th individual is  $w_1(r)/n$ , implying

$$\bar{W}_2 = \sum_{r=1}^n W_2(r) \cdot w_1(r) \cdot \left(\frac{1}{n}\right) \quad (12.1b)$$

In general, for the  $j$ th episode of selection,

$$\bar{W}_j = \sum_{r=1}^n W_j(r) \cdot w_{j-1}(r) \cdot w_{j-2}(r) \cdots w_1(r) \cdot \left(\frac{1}{n}\right) \quad (12.1c)$$

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

$$p_j(r) = w_j(r) \cdot p_{j-1}(r) = \frac{1}{n} \prod_{i=1}^j w_i(r) \quad (12.2a)$$

Thus, Equation 12.1c can also be expressed as  $\bar{W}_j = \sum W_j(r) \cdot p_{j-1}(r)$ . Using these weights allows fitness-weighted moments to be calculated, e.g., the mean of a particular character following the  $j$ th episode satisfies

$$\mu_{z(j)} = \sum z(r) \cdot p_j(r) \quad (12.2b)$$

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

**Example 12.1.** Total reproductive success and its components, mating success (number of mates) ( $W_1$ ) and fertility ( $W_2$ , eggs per successful mating), along with body size, were measured in 38 male bullfrogs (*Rana catesbeiana*) in a longitudinal study by Howard (1979). For illustrative purposes, we use part of this data set to compute these fitness components for five males.

Male	Size (mm)	$W_1$	$W_2$	$w_1$	$p_1$	$w_2$	$p_2$
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	0.000	0.000	0.000	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

Before selection, each male has frequency  $1/5 = 0.20$ , giving

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

While the *observed* frequencies of individuals have not changed after the first episode of selection (all are still present in the population), *fitness-weighted* frequencies change due to differences in acquiring mates. For male 2,  $p_1(2) = 0.2 \cdot 0.714 = 0.143$  (e.g., 14.3% of all matings in the population involve male 2), with the values for the other adults being computed similarly. Hence, if we were to take offspring from these adults after this episode of selection, then for a randomly-drawn offspring, the probability that it's parent is male 2 is 0.143. The mean fertility *per mating* is

$$\begin{aligned} \bar{W}_2 &= \sum W_2(r) \cdot p_1(r) \\ &= (25,820 \cdot 0.143) + (22,670 \cdot 0.143) + (7,230 \cdot 0.286) + (15,986 \cdot 0.429) \\ &= 15,860 \end{aligned}$$

If each reproducing male were weighted equally, average fertility per individual (independent of the number of times each mates) is  $(1/4) \cdot (25,820 + 22,670 + 7,230 + 15,986) = 17,927$ . The actual mean fertility *per mating*  $\bar{W}_2$  is lower because males 4 and 5 sired the most clutches, but had much lower fertility than the other (successful) males. Using  $w_2(r) = W_2(r)/(15,860)$  and recalling Equation 12.2a, the final fitness weighting for male 1 is  $(1/5) \cdot 0.714 \cdot 1.628 = 0.233$ . The remaining  $p_2$  values are computed similarly. Before selection the mean and variance for body size  $\bar{z}(0) = 140.0$  and  $\text{Var}[z(0)] = 59.5$ . From Equation 12.2b, the fitness-weighted mean body size following the first episode of selection is

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

Similarly,

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

Hence

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

Thus, if we again take a hypothetical offspring following the first episode of selection, the mean body size of the adult that produced a randomly-chosen offspring is 138.996.

## VARIANCE IN INDIVIDUAL FITNESS

How do we compare the amount of selection acting on different populations? At first thought, one might consider using the standardized selection differential (the selection intensity)  $i$  for comparing

the relative strength of individual selection between populations. The drawback with  $i$  as a measure of *overall* selection on individuals is that it is *character specific*. Hence,  $i$  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*. Two populations may have the same  $i$  value for a given character, but if that character is tightly correlated with fitness in one population and only weakly correlated in the other, selection is much stronger in the latter population. Further, considerable selection can occur without changing the mean (e.g., stabilizing selection). Standardized differentials also exist for the variance (see below), but the problem of character-specificity still remains.

A much cleaner measure (independent of the characters under selection), is  $I$ , the **opportunity for selection**, defined as the variance in *relative* fitness:

$$I = \sigma_w^2 = \frac{\sigma_W^2}{\bar{W}^2} \quad (12.3)$$

This measure was introduced by Crow (1958), who referred to it as the **Index of Total Selection** and was independently developed by O'Donald (1970).  $I$  is estimated by

$$\hat{I} = \text{Var}(w) = \frac{n}{n-1} (\overline{w^2} - 1) \quad (12.4)$$

Following Arnold and Wade (1984a,b) we call  $I$  the opportunity for selection, as any change in the distribution of fitness caused by selection represents an *opportunity* for within-generation change. The opportunity for selection bounds the maximum value of  $i$ . This follows by using (respectively), the definition of a correlation (Equation 1.15a), the Price-Robertson Identity (Equation 12.8, to be shortly discussed) which states that  $S = \sigma(z, w)$ , 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

$$|i| \leq \sqrt{I} \quad (12.5)$$

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

**Example 12.2.** To estimate  $I$  for the bullfrog data used in Example 12.1, we first compute the lifetime relative fitnesses as  $w = w_1 \cdot w_2$ , which gives relative lifetime fitnesses of 1.162, 1.020, 0, 0.652, and 2.160. Thus

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

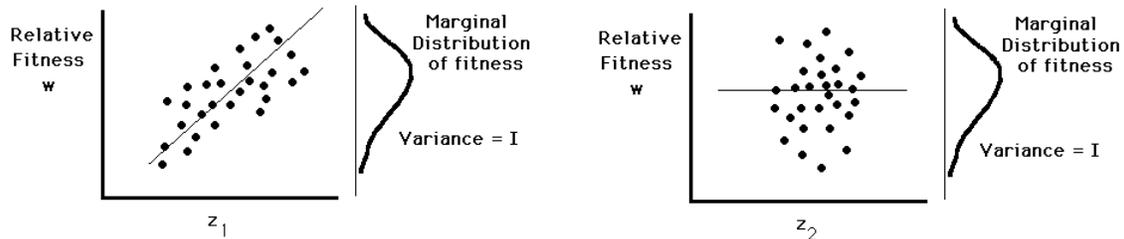
giving

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

Hence, the most selection can change the mean of any character within a generation is  $\sqrt{I} \simeq 0.79$  standard deviations. The observed change in male body size (in standard deviations) from Example 12.1 is  $(138.8 - 140)/\sqrt{59.5} = -0.155$ , less than one-fifth of the maximum absolute change of 0.79.

The usefulness of  $I$  as a bound of  $i$  depends on the correlation between relative fitness and the character being considered. Figure 12.1 shows scatterplots of relative fitness versus two characters ( $z_1$  and  $z_2$ ) measured in the same set of individuals. The marginal distributions of fitness are identical for both characters (since the same set of individuals was measured), and hence both have the same

opportunity for selection. The association between relative fitness and  $z_1$  is fairly strong, while there is no relationship between relative fitness and  $z_2$ , so that  $z_1$  realizes much, while  $z_2$  realizes none, of the opportunity for change.



**Figure 12.1.** The fraction of the opportunity for selection  $I$  that is translated into a change in the mean depends on the correlation between relative fitness and the character. Characters  $z_1$  and  $z_2$  have the same marginal distribution of fitness, but only the regression of  $w$  on  $z_1$  is significant. Thus (within a generation) selection changes the mean of  $z_1$  but not  $z_2$ .

In many cases individual fitnesses are not recorded. Rather, the average fitness for a number of phenotypic classes are estimated. In such cases, we can still obtain a lower bound for  $I$ , as the following example illustrates.

**Example 12.3.** O'Donald (1970, 1971) analyzed the data of Dowdeswell (1961) who looked for selection on eyespot number on the hindwing of the European butterfly *Maniola jurtina*. Dowdeswell compared the population distribution of eyespot number between a series of wild-collected females and a series of females reared from larvae. Presumably, the difference in distributions was due to selection on adults. By comparing the relative eyespot frequencies in reared and wild adults, fitnesses for each phenotypic class were estimated. These are given in the table, along with the number of adults in each size class from the sample of 237 reared females (presumably representing the population before selection).

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

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

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

Thus

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

and

$$\hat{I} = \frac{0.034}{0.838^2} \simeq 0.048$$

This is an *underestimate*, as to properly estimate  $I$  the distribution of *individual* fitnesses, rather than mean fitness for each phenotypic class (*character* fitnesses), is required. These data only allow us

to estimate the between-group variance in fitness (the variance in average fitness for the different eyespot classes) and hence this gives an *underestimate* of  $I$  because it neglects within-group variance (the variance in fitness among individuals with the same number of eyespots). Put another way,  $\sigma^2(w)$  is the variance in fitnesses between classes (which we have estimated) plus the variance within classes, which we have not.

### Some Caveats in Using the Opportunity for Selection

There are some subtle issues in the interpretation of  $I$ . To begin with, even though  $I$  appears to remove scaling effects due to different types of fitnesses, for estimates of  $I$  to be truly comparable, they must be based on consistent measures of fitness (Triall 1985).

A second point is that if the variance in fitness is not independent of  $\bar{W}$ , comparisons of  $I$  values between populations are compromised. This occurs in cross-sectional studies that measure sexual selection by simply counting the number of mating pairs (in such studies, an unequal sex ratio further biases comparisons of  $I$  between the sexes). If the time scale is such that only single matings are observed, the fitness of any individual is either 1 (mating) or 0 (not mating). The resulting fitness of randomly-drawn individuals is binomially distributed with mean  $p$  (the mean copulatory success for the sex being considered) and variance  $p(1 - p)$ , hence

$$I = \frac{p(1-p)}{p^2} \simeq \frac{1}{p} \quad \text{if } p \ll 1 \quad (12.6a)$$

The mean and variance in individual fitness are not independent, and the opportunity for selection depends entirely on mean population fitness. As the time window for observing mating pairs decreases, fewer matings are seen and  $p$  decreases, increasing  $I$ . Thus the opportunity for selection is often inflated if the observation period is short relative to the total mating period.

A second example of the lack of independence between  $\bar{W}$  and  $\sigma_W^2$  was given by Downhower et al. (1987). Assuming that the number of mates for any given male follows a Poisson distribution, the variance in number of mates equals the mean number of mates, giving

$$I = \frac{\bar{W}}{\bar{W}^2} = \bar{W}^{-1} \quad (12.6b)$$

where  $\bar{W}$  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  $\bar{W} = 0.05$ , while if 50 females mate,  $\bar{W} = 0.5$ . 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.

### DESCRIBING PHENOTYPIC SELECTION: INTRODUCTORY REMARKS

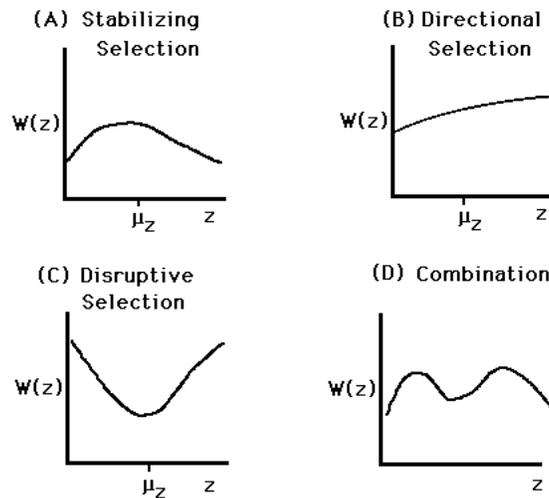
Most of our previous discussion so far has dealt with the fitness of individuals, independent of any knowledge of their phenotypes. Selection can favor certain phenotypes, leading to our second major topic — how do particular character values influence the fitness of an individual? Our interest in a particular character may be in predicting how selection changes it over time, which requires knowledge of the genetics of that character. Alternately, we may simply wish to explore the ecological implications of a character by examining how expected fitness changes with character value. While only the relationship of total fitness to the character is needed to describe the evolutionary response to selection, partitioning fitness across episodes of selection can enhance our understanding of the ecology of that character.

One general way of detecting selection on a character is to compare the (fitness-weighted) phenotypic distribution before and after some episode of selection. One important caveat is that

growth or other ontogenetic changes, immigration, and environmental changes can also change the phenotypic distribution. We must take great care to account for these factors. Typically, selection on a character is measured by considering changes in the mean and variance, rather than changes in the entire distribution. In many cases the entire selection response following a generation of selection can be reasonably predicted from the within-generation change in the mean and variance. As we will see below, there are a number of subtle issues in assigning fitnesses to phenotypes. Again, we remind the reader of the most important caveat, that of dealing with the effects of selection on correlated characters, which is considered in Lectures 13 and 14.

### Fitness Surfaces

$W(z)$ , the expected fitness of an individual with phenotype  $z$ , describes a **fitness surface** (or equivalently a **fitness function**), relating fitness and character value. The **relative fitness surface**  $w(z) = W(z)/\bar{W}$  is often more convenient than  $W(z)$ , and we use these two somewhat interchangeably. 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 (Figure 12.2). 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. As is illustrated in Figure 12.3D, when the local geometry of the fitness surface is complicated (e.g., multimodal) the simplicity of description offered by these three types of selection breaks down, as the population can experience all three simultaneously.



**Figure 12.2.** Selection is usually classified into three basic forms depending on the local geometry of  $W(z)$ : stabilizing (A), directional (B), and disruptive (C). As D illustrates, populations can simultaneously experience multiple forms of selection.

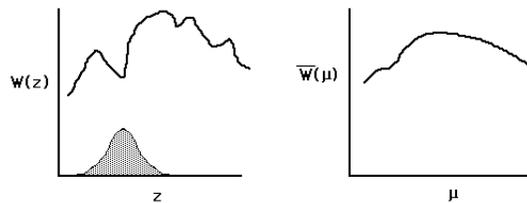
$W(z)$  may vary with genotypic and environmental backgrounds. In some situations (e.g., predators with search images, sexual selection, dominance hierarchies, truncation selection) the fitness of a phenotype depends on the frequency of other phenotypes in the population. In this case, fitnesses are said to be **frequency-dependent**.

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

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

Hence, mean fitness can be thought of as a function of the parameters  $\theta$  of the phenotypic distribution. For example, if  $z$  is normally distributed, mean fitness is a function of the mean  $\mu_z$  and variance  $\sigma_z^2$  for that population.

To stress the distinction between the  $W(z)$  and  $\bar{W}$  fitness surfaces, the former is referred to as the **individual fitness surface**, latter as the **mean fitness surface**. Knowing the individual fitness surface allows us to compute the mean fitness surface for any specified distribution of phenotypes  $p(z)$ , but the converse is not true. The importance of the mean fitness surface is that it provides one way of describing how the population changes under selection. When the breeders' equation holds, the first two partial derivatives of  $\bar{W}$  with respect to  $\mu_z$  describe the change in mean and variance. Mean fitness surfaces are considerably smoother than the individual fitness surfaces that generate them (Figure 12.3). The individual fitness surface may have discontinuities and rough spots — regions where very small changes in phenotypic value result in large changes in individual fitness. Mean population fitness averages over  $W(z)$ , smoothing out these rough spots.



**Figure 12.3.** In this example, a small change in  $z$  can result in a large change in the individual fitness surface  $W(z)$ . However, since the mean population fitness  $\bar{W}(\mu_z)$  averages individual fitnesses over the phenotypic distribution, shown as the stippled curve, small changes in  $\mu_z$  result in only small changes in  $\bar{W}(\mu_z)$ .

## DESCRIBING PHENOTYPIC SELECTION: CHANGES IN PHENOTYPIC MOMENTS

Selection for particular phenotypes changes in the phenotypic distribution (although it need not change all moments, for example, the mean may be unchanged). Thus, selection is detected by testing for differences between the distribution of phenotypes before and after some episode of selection. Nonparametric tests such as the Kolmogorov-Smirnov test have the advantage of making no assumptions about the form of the distribution, but suffer from low power. While complete distributions can be compared, the most common procedure for detecting selection is to test for changes in phenotypic moments. Standard statistical tests for differences in means ( $t$ -tests) and variances ( $F$ -tests) can be used, but these tests rely on normality assumptions that are often violated, and nonparametric tests are often more appropriate. Differences in means can be tested using the Wilcoxon-Mann-Whitney test, while Conover's squared rank test (Conover 1980) can be used to test for changes in variances. Other nonparametric tests for changes in variance exist, but care must be exercised, as some (e.g., the Siegel-Tukey test) are quite sensitive to differences in means. While these issues are important, the main problem in detecting selection on a character is that changes in the moments may be due entirely to selection on phenotypically correlated characters (Lectures 13, 14). Keeping this important caveat in mind, we now examine measures of selection for single characters.

### The Robertson-Price Identity

If  $p(z)$  is the density of phenotype  $z$  before selection, then the density after selection is

$$p_s(z) = \frac{W(z)p(z)}{\int W(z)p(z) dz} = \frac{W(z)p(z)}{\bar{W}} = w(z)p(z) \quad (12.7a)$$

The mean trait value following selection becomes

$$\mu_s = \int z p_s(z) dz = \int z w(z) p(z) dz = E[z w(z)] \quad (12.7b)$$

Note also that

$$\bar{w} = \int w(z) p(z) dz = \frac{1}{\bar{W}} \int W(z) p(z) dz = \bar{W}/\bar{W} = 1$$

i.e., the mean relative fitness in a population is always equal to one, and that since  $\mu = E(z) \cdot E(w) = E(z) \cdot 1$ , the directional selection differential may be rewritten as

$$S = \mu_s - \mu = E[z w(z)] - E(z) E(w) = \sigma[z, w(z)] \quad (12.8)$$

Thus, the *directional selection differential is equivalent to the covariance of phenotype and relative fitness*. This relationship, first noted by Robertson (1966), was greatly elaborated on by Price (1970, 1972). We refer to this very useful result as the **Robertson-Price identity**. It applies even when phenotypes vary in reproductive output, provided that the absolute fitnesses,  $W(z)$ , are weighted accordingly.

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

We have extensively discussed the standard measure of selection on the mean, the **directional selection differential**,  $S = \mu_s - \mu$ , the within-generation change in the mean. An alternative measure for the change in the mean follows from the Robertson-Price identity. Define the **directional selection differential**  $\beta$  by

$$\beta = \frac{S}{\sigma_z^2} = \frac{\sigma(z, w)}{\sigma_z^2} \quad (12.9)$$

Recall from Lecture 2 that the slope of the regression of  $y$  given  $x$  is  $\sigma(x, y)/\sigma_x^2$ . Thus,  $\beta$  is the slope of the least-squares linear regression of relative fitness ( $w$ ) on phenotypic value ( $z$ ),  $w(z) = 1 + \beta(z - \mu_z) + e$ . Substituting  $S = \sigma_z^2 \beta$  into  $R = h^2 S$  gives

$$R = \sigma_A^2 \beta \quad (12.10a)$$

Noting that  $\sigma_A^2 = h^2 \sigma_z^2$ , we can rearrange 12.10a to give

$$\frac{R}{\sigma_z^2} = h^2 \beta \quad (12.10b)$$

so that  $h^2 \beta$  is the expected response in units of phenotypic variance. The importance of the selection gradient is that under appropriate conditions it relates how a change in the trait mean maps into a change in the mean fitness of a population. In particular, if  $w(z)$  denotes the expected fitness of an individual with character value  $z$ , then when phenotypes are normally distributed, and fitness is frequency-independent (individual fitnesses are not a function of the mean of the character), Lande (1976) showed that the directional selection gradient satisfies

$$\beta = \frac{\partial \ln \bar{W}}{\partial \mu} \quad (12.10c)$$

Hence we can express the breeders equation as

$$R = \sigma_A^2 \left( \frac{\partial \ln \bar{W}}{\partial \mu} \right) \quad (12.10d)$$

Three measures of the within-generation change in phenotypic mean have thus far been introduced: the directional selection differential  $S$ , the standardized directional selection differential (selection intensity)  $i$ , and the directional selection gradient  $\beta$ . These measures are interchangeable for selection acting on a single character (e.g., Equations 9.5, 9.7, and 12.10a). However, when multiple characters are considered, the multivariate extension of  $\beta$  is the measure of choice, as it measures the amount of selection on a character over and above that attributable to selection on any other phenotypically correlated traits under consideration, while  $S$  (and hence  $i$ ) confounds these direct and indirect effects (Lectures 13 and 14).

### Quadratic Selection: Differentials ( $C$ ) and Gradients ( $\gamma$ )

Analogous measures to  $S$  and  $\beta$  can be defined to quantify the change in variance. At first glance this seems best described by  $\sigma_{z^*}^2 - \sigma_z^2$ , where  $\sigma_{z^*}^2$  is the phenotypic variance following selection. The problem with this measure is that directional selection reduces the variance. Lande and Arnold (1983) showed that

$$\sigma_{z^*}^2 - \sigma_z^2 = \sigma [w, (z - \mu_z)^2] - S^2 \quad (12.11a)$$

Hence, directional selection decreases the phenotypic variance by  $S^2$ . With this in mind, Lande and Arnold suggest a corrected measure, the **stabilizing selection differential**

$$C = \sigma_{z^*}^2 - \sigma_z^2 + S^2 \quad (12.11b)$$

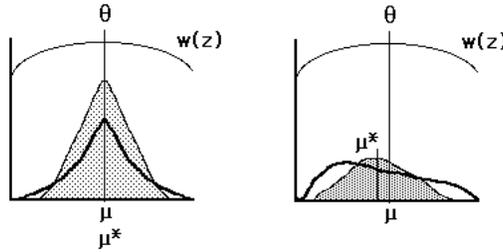
that describes selection acting directly on the variance. As we will see below, the term stabilizing selection differential may be slightly misleading, so following Phillips and Arnold (1989) we refer to  $C$  as the **quadratic selection differential**. Correction for the effects of directional selection is important, as claims of stabilizing selection based on a reduction in variance following selection can be due entirely to reduction in variance caused by directional selection. Similarly, disruptive selection can be masked by directional selection (e.g., Example 12.4).

**Example 12.4.** Boag and Grant (1981) observed intense natural selection in *Geospiza fortis* (Darwin's medium ground finch) during a severe drought on Daphne Major Island in the Galápagos. The estimated mean weight and variance of 642 adults before the drought were respectively, 15.79 and 2.37, while the estimated mean and variance of 85 surviving adults after the drought was 16.85 and 2.43. Thus  $\hat{S} = 16.85 - 15.79 = 1.06$  (with a standard error of 0.180), implying that the directional selection differential on body size is significantly positive. There appears to be very little selection on the variance when the uncorrected change in variance  $\text{Var}(z^*) - \text{Var}(z) = 2.43 - 2.37 = 0.06$  is used. However,

$$\hat{C} = 0.06 + 1.06^2 = 1.14$$

consistent with disruptive selection in addition to directional selection. The standard error for  $\hat{C}$  is 0.549. Thus  $\hat{C}$  is 2.08 standard errors above zero, suggesting that it is also significant.

Provided that selection does not act on characters phenotypically correlated with the one under study,  $C$  provides information on the nature of selection on the variance. Positive  $C$  indicates selection to increase the variance (as would occur with disruptive selection), while negative  $C$  indicates selection to reduce the variance (as would occur with stabilizing selection). As we discuss shortly,  $C < 0$  ( $C > 0$ ) is *consistent* with stabilizing (disruptive) selection, but not *sufficient*. A further complication in interpreting  $C$  is that if the phenotypic distribution is skewed, selection on the variance changes the mean. This causes a non-zero value of  $S$  that in turn inflates  $C$  (Figure 12.4).



**Figure 12.4.** Even when a population is under strict stabilizing selection, the mean can change if the phenotypic distribution is skewed. A standard fitness function for stabilizing selection is  $W(z) = 1 - b(\theta - z)^2$ . O'Donald (1968) found that, even if the population mean is at the optimum value ( $\mu_z = \theta$ ),  $S$  is nonnegative if the skew is nonzero ( $\mu_{3,z} \neq 0$ ) as  $S = -(b\mu_{3,z})/(1 - b\sigma_z^2)$ . **Left:** If phenotypes are distributed symmetrically about the mean ( $\mu_{3,z} = 0$ ), the distribution after selection (stippled) has the same mean when  $\mu_z = \theta$ . **Right:** If, however, the distribution is skewed, more of the distribution lies on one side of the mean than the other. Since the distribution is unbalanced, the longer tail experiences more selection than the shorter tail, changing the mean.

Analogous to  $S$  equaling the covariance between  $z$  and relative fitness, Equation 12.11 implies  $C$  is the covariance between relative fitness and the squared deviation of a character from its mean

$$C = \sigma [w, (z - \mu)^2] \quad (12.12)$$

As was the case with  $S$ , the opportunity for selection bounds the maximum possible within-generation change in variance (Arnold 1986). Expressing  $C$  as a covariance and using the definition of a correlation gives  $C = \rho_{w,(z-\mu)} \sigma_w \sigma [(z - \mu)^2]$ . Since  $\rho_{w,(z-\mu)}^2 \leq 1$ , we have

$$C^2 \leq \sigma_w^2 \sigma^2 [(z - \mu)^2] = I \cdot (\mu_{4,z} - \sigma_z^4)$$

The last equality follows from the definition of a variance,  $\sigma^2 [(z - \mu)^2] = E[(z - \mu)^4] - E[(z - \mu)^2]^2$ . Thus,

$$|C| \leq \sqrt{I (\mu_{4,z} - \sigma_z^4)} \quad (12.13a)$$

If  $z$  is normally distributed,  $\mu_{4,z} = 3\sigma_z^4$ , giving

$$|C| \leq \sigma_z^2 \sqrt{2I} \quad (12.13b)$$

The quadratic analogue of  $\beta$ , the **quadratic (stabilizing) selection gradient**  $\gamma$ , was suggested by Lande and Arnold (1983),

$$\gamma = \frac{\sigma [w, (z - \mu)^2]}{\sigma_z^4} = \frac{C}{\sigma_z^4} \quad (12.14)$$

### $\beta$ and $\gamma$ Measure the Geometry of the Fitness Surface

A conceptual advantage of  $\beta$  and  $\gamma$  is that they describe the average local geometry of the fitness surface when phenotypes are normally distributed. When  $z$  is normal and individual fitness are not frequency-dependent, Equation 12.10c implies that  $\beta$  can be expressed in terms of the geometry of the *mean* fitness surface,

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

the slope of the  $\bar{W}$  surface with respect to population mean.  $\beta$  can also be expressed as a function of the *individual* fitness surface. Lande and Arnold (1983) showed, provided  $z$  is normally distributed, that

$$\beta = \int \frac{\partial w(z)}{\partial z} p(z) dz \quad (12.15a)$$

implying that  $\beta$  is the average slope of the individual fitness surface, the average being taken over the population being studied. Likewise, if  $z$  is normally distributed,

$$\gamma = \int \frac{\partial^2 w(z)}{\partial z^2} p(z) dz \quad (12.15b)$$

which is the average curvature of the individual fitness surface (Lande and Arnold 1983). Thus,  $\beta$  and  $\gamma$  provide a measure of the geometry of the individual fitness surface averaged over the population being considered.

### $\beta$ and $\gamma$ Describe the Selection Dynamics

A final advantage of  $\beta$  and  $\gamma$  is that they appear as the only measures of phenotypic selection in equations describing selection response. We have already seen (Equation 12.10a) that under the constraints of the breeders' equation,  $\Delta\mu = \sigma_A^2\beta$ , which is independent of any other measure of the phenotype (note that  $\sigma_z^2$  is missing). Similarly, for predicting changes in variance under the infinitesimal model, from Equation 9.36b the expected change in variance from a single generation of selection is

$$\begin{aligned} \Delta\sigma_z^2 &= \frac{h^4}{2} \delta_{\sigma_z^2} = \frac{\sigma_A^4}{2\sigma_z^4} (C - s^2) \\ &= \frac{\sigma_A^4}{2} (\gamma - \beta^2) \end{aligned} \quad (12.16a)$$

More generally, Equation 9.38 becomes

$$d(t+1) = \frac{d(t)}{2} + \frac{\sigma_A^4(t)}{2} (\gamma(t) - \beta^2(t)) \quad (12.16b)$$

which decomposes the change in variance into changes due to selection on the variance ( $\gamma$ ) and changes due to directional selection ( $\beta$ ). Note that, when expressed in terms of gradients, the phenotypic variance term vanishes.

While the distinction between differentials and gradients seems almost trivial in the univariate case (only a scale difference), the multivariate versions are considerably different. As we will see in later lectures, gradients have the extremely important feature of removing the effects of phenotypic correlations.

## DESCRIBING PHENOTYPIC SELECTION: INDIVIDUAL FITNESS SURFACES

We can decompose the fitness  $W$  of an individual with character value  $z$  into the sum of its expected fitness  $W(z)$  plus a residual deviation  $e$ ,

$$W = W(z) + e$$

The residual variance for a given  $z$ ,  $\sigma_e^2(z)$ , measures the variance in fitness among individuals with phenotypic value  $z$ . Estimation of the individual fitness surface is thus a generalized regression problem, the goal being to choose a candidate function for  $W(z)$  that minimizes the average residual

variance  $E_z[\sigma_e^2(z)]$ . Since the total variance in fitness  $\sigma_W^2$  equals the sum of the within-group (phenotype) and between-group variance in fitness,

$$\frac{\sigma_W^2 - E_z[\sigma_e^2(z)]}{\sigma_W^2}$$

is the fraction of individual fitness variation accounted for by a particular estimate of  $W(z)$ , and this provides a measure for comparing different estimates. In the limiting case where fitness is independent of  $z$  (and any characters phenotypically correlated with  $z$ ),  $W(z) = \bar{W}$ , so that the between-phenotypic variance is zero while  $\sigma_e^2(z) = \sigma_W^2$ .

There are at least two sources of error contributing to  $e$ . First, there can be errors in measuring the actual fitness of an individual (these are almost always ignored). Second, the *actual* fitness of a particular individual can deviate considerably from the *expected value* for its phenotype due to chance effects and selection on other characters besides those being considered. Generally, these residual deviations are heteroscedastic. To see how this arises naturally, suppose fitness is measured by survival to a particular age. While  $W(z) = p_z$  is the probability of survival for an individual with character value  $z$ , the fitness for a particular individual is either 0 (does not survive) or 1 (survives). Thus the residual has only two possible values,  $e = 1 - p_z$  with probability  $p_z$  and  $e = -p_z$  with probability  $1 - p_z$ , giving  $\sigma_e^2(z) = p_z(1 - p_z)$ . Unless  $p_z$  is constant over  $z$ , the residuals are heteroscedastic. Note in this case that even after removing the effects attributable to differences in phenotypes, there still is substantial variance in individual fitness.

Inferences about the individual fitness surface are limited by the range of phenotypes in the population. Unless this range is very large, only a small region of the fitness surface can be estimated with any precision. Estimates of the fitness surface at the tails of the current phenotypic distribution are extremely imprecise, yet potentially very informative, suggesting what selection pressures populations at the margin of the observed range of phenotypes may be under. A further complication is that the fitness surface changes as the environment changes so that year to year estimates can differ and cannot be lumped together to increase sample size.

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

The individual fitness surface  $W(z)$  can be very complex and a wide variety of functions may be chosen to approximate it. The simplest and most straightforward approach is to use a low-order polynomial (typically linear or quadratic).

Consider first the simple linear regression of *relative* fitness  $w$  as a function of phenotypic value  $z$ . Since the directional selection gradient  $\beta = S/\sigma_z^2 = \sigma(w, z)/\sigma_z^2$ , it follows from regression theory (Lecture 2) that  $\beta$  is the slope of the least-squares linear regression of relative fitness on  $z$ ,

$$w = a + \beta z + e \tag{12.17a}$$

Hence the best linear predictor of relative fitness is  $w(z) = a + \beta z$ . Since the regression passes through the expected values of  $w$  and  $z$ , this can be written as

$$w = 1 + \beta(z - \mu_z) + e \tag{12.17b}$$

giving  $w(z) = 1 + \beta(z - \mu_z)$ . Assuming the fitness function is well described by a linear regression,  $\beta$  is the expected change in relative fitness given a unit change in  $z$ . From Equation 1.23, the fraction of variance in individual fitness accounted for by this regression is

$$r_{z,w}^2 = \frac{\text{Cov}^2(z, w)}{\text{Var}(z) \cdot \text{Var}(w)} = \hat{\beta}^2 \frac{\text{Var}(z)}{\hat{I}} \tag{12.18}$$

If the fitness surface shows curvature, as might be expected if there is stabilizing selection and/or disruptive selection, a **quadratic regression** is more appropriate,

$$w = a + b_1 z + b_2 z^2 + e \quad (12.19a)$$

We can also express this as

$$w = \alpha + b_1 z + b_2 (z - \mu)^2 + e \quad (12.19b)$$

The regression coefficients are the same in 12.19a and, while the intercepts differ.

The regression coefficients  $b_1$  and  $b_2$  nicely summarize the local geometry of the fitness surface. Evaluating the derivative of Equation 12.19 at  $z = \mu_z$  gives

$$\left. \frac{\partial w(z)}{\partial z} \right|_{z=\mu_z} = b_1 \quad \text{and} \quad \left. \frac{\partial^2 w(z)}{\partial z^2} \right|_{z=\mu_z} = 2b_2 \quad (12.20)$$

Hence  $b_1$  is the slope and  $2b_2$  the second derivative (curvature) of the best quadratic fitness surface around the population mean.  $b_2 > 0$  indicates that the best-fitting quadratic of the individual fitness surface has an upward (positive) curvature (**concave selection**), while  $b_2 < 0$  implies the curvature is downward (negative, for **convex selection**). Lande and Arnold (1983) suggest that  $b_2 > 0$  indicates disruptive selection, while  $b_2 < 0$  indicates stabilizing selection. Their reasoning follows from elementary geometry in that a *necessary* condition for a local minimum is that a function curves upward in some interval, while a necessary condition for a local maximum is that the function curves downward. Mitchell-Olds and Shaw (1987) and Schluter (1988) argue that this condition is not *sufficient*. Stabilizing selection is generally defined as the presence of a local maximum in  $w(z)$  and disruptive selection by the presence of a local minimum, while  $b_2$  indicates curvature, rather than the presence of local extrema. Hence, we use concave and convex selection to describe the sign of curvature (i.e., the sign of the second derivative of the individual fitness surface).

We solve for the regression coefficients  $b_1$  and  $b_2$  by transforming Equation 12.19 into a standard multiple regression problem by setting  $x_1 = z$  and  $x_2 = (z - \mu_z)^2$  and applying the methods of Lecture 2. To proceed, we need expressions for  $\sigma(x_1, x_2)$ ,  $\sigma(x_1, w)$ , and  $\sigma(x_2, w)$ . From Lynch and Walsh's Equation A1.14,  $\sigma(x_1, x_2) = \sigma(z, (z - \mu_z)^2) = \mu_{3,z}$ , the skew of the phenotypic distribution before selection. Likewise, from Equations 12.8 and 12.11a,  $\sigma(x_1, w) = \sigma(z, w) = S$  and  $\sigma(x_2, w) = \sigma((z - \mu_z)^2, w) = C$ . Substituting these into Equations 2.13, and noting that  $\sigma^2((z - \mu_z)^2) = \mu_{4,z} - \sigma_z^4$ , gives

$$b_1 = \frac{\sigma^2(x_2) \cdot \sigma(x_1, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{(\mu_{4,z} - \sigma_z^4) \cdot S - \mu_{3,z} \cdot C}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2} \quad (12.21a)$$

$$b_2 = \frac{\sigma^2(x_1) \cdot \sigma(x_2, w) - \sigma(x_1, x_2) \cdot \sigma(x_2, w)}{\sigma^2(x_1) \cdot \sigma^2(x_2) - \sigma^2(x_1, x_2)} = \frac{\sigma_z^2 \cdot C - \mu_{3,z} \cdot S}{\sigma_z^2 \cdot (\mu_{4,z} - \sigma_z^4) - \mu_{3,z}^2} \quad (12.21b)$$

The estimators of  $b_1$  and  $b_2$  are obtained by replacing  $\mu_{k,z}$  with their sample estimates and using  $\hat{C}$  and  $\hat{S}$ .

Provided  $z$  is normally distributed before selection,  $\mu_{3,z} = 0$  and  $\mu_{4,z} - \sigma_z^4 = 2\sigma_z^4$ . In this case, Equations 12.9 and 12.14 imply, respectively, that  $b_1 = \beta$  and  $b_2 = \gamma/2$ , giving the univariate version of the **Lande-Arnold regression**,

$$w = \alpha + \beta z + \frac{\gamma}{2} z^2 + e \quad (12.22)$$

developed by Lande and Arnold (1983), motivated by Pearson (1903). The Lande-Arnold regression thus provides a connection between selection differentials (directional and stabilizing) and quadratic approximations of the individual fitness surface.

An important point from Equation 12.21a is that if skew is present ( $\mu_{3,z} \neq 0$ ),  $b_1 \neq \beta$  and the slope term in the linear regression (the best *linear* fit) of  $w(z)$  differs from the slope term in the quadratic regression (the best *quadratic* fit) of  $w(z)$ . This arises because the presence of skew generates a covariance between  $z$  and  $(z - \mu_z)^2$ . The biological significance of this can be seen by reconsidering Figure 12.4, wherein the presence of skew in the phenotypic distribution results in a change in the mean of a population under strict stabilizing selection (as measured by the population mean being at the optimum of the individual fitness surface). Skew generates a correlation between  $z$  and  $(z - \mu_z)^2$  so that selection acting only  $(z - \mu_z)^2$  generates a correlated change in  $z$ . From the Robertson-Price identity (Equation 12.8), the within-generation change in mean equals the covariance between phenotypic value and relative fitness. Since covariances measure the amount of *linear* association between variables, in describing the change in mean, the correct measure is the slope of the best *linear* fit of the individual fitness surface. If skew is present, using  $b_1$  from the quadratic regression to describe the change in mean is incorrect, as this quadratic regression removes the effects on relative fitness from a linear change in  $z$  due to the correlation between  $z$  and  $(z - \mu_z)^2$ .

### Schluter's Cubic-Spline Estimate

A serious problem with quadratic regressions as estimators of  $W(z)$  is that the fitted curve allows for at most only a single local maximum or minimum. Fitness surfaces with multiple local maxima are thus very poorly described by a quadratic. In order to more reliably estimate the fitness function, Schluter (1988, Schluter and Nychka 1994) has developed a non-parametric method that makes no assumptions about the functional form of the fitness surface. Schluter's approach fits the data using a series of cubic splines (a series of cubic polynomials that join smoothly together) using a jackknife method as the best fit criterion. This requires assumptions about the distribution of the residuals  $e$  as a function of phenotypic value  $z$ . A program to estimate  $W(z)$  assuming either normally, binomially, or Poisson distributed residuals is available from Schluter. Binomially distributed residuals arise naturally with survival data, while Poisson distributed residuals are a reasonable model for number of offspring or mates. Schluter's program also has a resampling procedure that generates rough confidence intervals on estimates of  $W(z)$ . Interestingly, when one of one of the classic examples of stabilizing selection, the data of Karn and Penrose (1951) relating survival and human birth weight, is reanalyzed using Schluter's method, the local maximum is not significant. Parametric tests of the significance of estimated local maximum/minimum are discussed by Mitchell-Olds and Shaw (1987) for quadratic regressions, while nonparametric tests are discussed by Schluter (1988).

### Complications from Unmeasured Correlated Variables

As discussed in Lecture 14, a major complication with the estimation of both linear and quadratic gradients are correlated traits (or other factors) not included in the analysis. For example, selection might be entirely based on height, while we measure body weight. The two traits are correlated, and hence we would observe a relationship between relative fitness and body weight. In Lecture 14, we show that by including all traits under selection, unbiased estimates of  $\beta$  and  $\gamma$  are obtained. For our hypothetical example, using this approach we would obtain a non-zero estimate of the gradient associated with height, but not with weight.

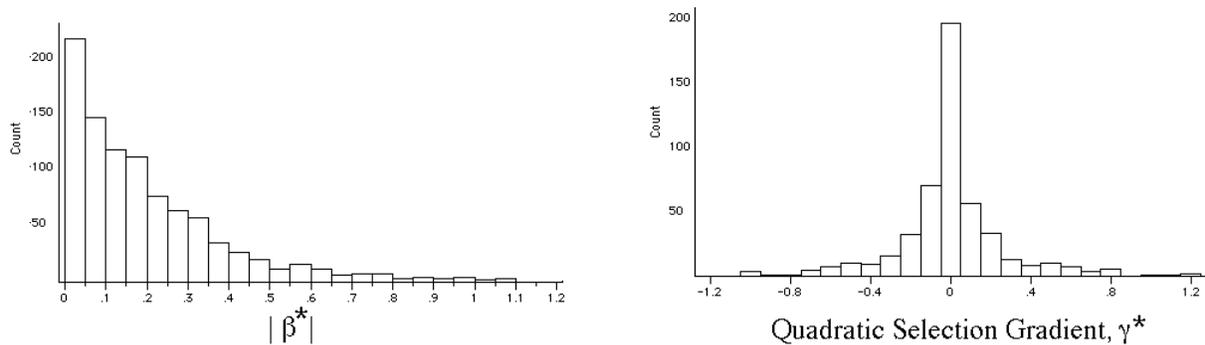
A more interesting complication is when the environment influences both fitness and the trait of interest. For example, suppose that plants growing in rich soil have more seed and also are able to generate more plant secondary compounds. If we were simply focused on the secondary compounds, we might find an association between them and fitness, entirely due to the shared environmental effect. As with phenotypically correlated traits, if we knew these environmental factors, we could include them in the model, which would result in unbiased estimates of gradients. In reality, we are unlikely to know critical environmental factors. Rauscher (1992) proposes a simple solution to this, replace phenotypic values of traits with estimates of their breeding values. While

estimates of breeding values are often non-trivial to obtain, this approach (replacing the trait value  $z$  of an individual by its estimated breeding value  $A$  in a Lande-Arnold analysis) completely removes any bias due to shared environmental effects.

**Example 12.5.** Kruuk et al. (2002) examined antler size in red deer on the Inner Hebrides Isle of Rum in Scotland. They found that 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,  $h^2 = 0.22 \pm 0.12$ , so that one would expect a significant response to natural selection, given both heritability in the trait and strong selective pressure for change. However, despite selection and heritability, no significant changes were observed response over 30 years of study. The authors suggest that antler size and male fighting ability is heavily dependent upon an individual's nutritional state, and hence selection is on this environmental component, rather than any genetic component. As a result, there is no response to selection.

### Strength of Selection in Natural Populations

Just how strong is selection in natural populations? Attempts at measuring selection on quantitative traits in nature trace back to Bumpus (1899) and Weldon (1895). Endler (1986) was the first to attempt to summarize the average strength of selection, while more recently Kingsolver (Kingsolver et al. 2001, Hoekstra et al. 2001) summarized over 2,500 estimates of  $\beta$  and  $\gamma$  from natural populations (Figure 12.5).



**Figure 12.5.** Summary of estimates of directional and quadratic selection in the wild. All estimates are scaled in terms of phenotypic standard deviations ( $\beta^* = \beta/\sigma_z$ ,  $\gamma^* = \gamma/\sigma_z$ ). Data from the summary of Kingsolver et al. 2001. **Left:** Plot of roughly 1,000 estimated directional selection gradients in natural populations. The distribution of  $|\beta^*|$  was not significantly different from an exponential distribution. The medium value for  $|\beta^*|$  was 0.16. **Right:** Plot of roughly 470 estimates of  $\gamma^*$  from natural populations. The medium value of  $|\gamma^*|$  was 0.10.

A couple of surprising results emerge from the meta-analysis of Kingsolver. First, the distribution of the absolute value of (scaled) directional selection gradients essentially follows an exponential distribution with a medium (50% value) of 0.16. Note that a  $\beta^*$  of 0.16 implies at a one standard deviation change in the trait changes relative fitness by 16%. Thus, most directional selection in nature is fairly weak, although (due to the long tail of the exponential), there are a few large estimates of  $|\beta^*|$  (10% of the estimates in Kingsolver's summary exceeded 0.5). Kingsolver notes that most of the large estimates for  $|\beta^*|$  occur in studies with small sample sizes, with most estimates below 0.1 when the sample size was 1,000 or greater. Hence, it is possible that some of the large  $\beta^*$  value are simply

a consequence of sampling error due to small sample size. Second, the wide-spread belief is that stabilizing selection is far more common than disruptive selection. However, Kingsolver observed an essentially symmetric distribution of  $\gamma^*$  values, mean positively- and negatively-curved fitness surfaces were equally common. Further, the average strength of quadratic selection was weak, with  $|\gamma^*|$ . However, Blows and Brooks (2003) point out that the univariate estimators of  $\gamma$  likely significantly *underestimate* the strength of quadratic selection when multiple traits are considered. We discuss this point in Lecture 14.

As pointed out by Connner (2001), even “weak” selection can be very efficient. Consider the medium value of  $\beta^* = 0.16$ , or  $\beta = 0.16 \cdot \sigma_z$ . From Equation 12.10b., the single-generation change in phenotypic standard deviations is  $h^2 \cdot 0.16$ . Hence, with a typically heritability of 0.4, only 16 generations of selection are required to shift the population mean by one standard deviation.

## The Importance of Experimental Manipulation

Several authors have stressed that regression approaches should be viewed as only the preliminary step in any analysis of the actual agents of selection, treating any regression estimates as an initial hypothesis to be further tested by experimental manipulation. Spurious correlations between a character and fitness can be generated in a variety of ways: environmental correlations between character value and fitness, selection on unmeasured characters correlated with the observed character, and loci with direct fitness effects having pleiotropic effects on the character being measured. Likewise, when individuals in the population differ in amount of inbreeding (such as occurs in many plants), highly inbred individuals may suffer a reduction in fitness due to inbreeding depression. If the measured character being considered also suffers inbreeding depression, this generates a correlation between with fitness that is due entirely to levels of inbreeding rather than intrinsic differences between phenotypic values (Willis 1993).

Mitchell-Olds and Shaw (1987) and Wade and Kalisz (1990) suggest that interactions between environmental effects and fitness are extremely important. For example, Breden and Wade (1989) observed a positive relationship between group size and fitness in the imported willow leaf beetle. However, when predators were excluded, there was no relationship. Thus, in this case  $\beta$  is correlated with the environment (presence/absence of predators). A second (hypothetical) example is the case where individuals reared in higher-quality environments both obtain a larger size and also have more offspring than individuals from lower-quality environments. This generates a correlation between body size and fitness. However, it is the quality of the environment, not body size *per se*, that is the causal agent influencing the number of offspring in this case. Wade and Kalisz suggest computing fitness regressions in several different environments, and looking for correlations between  $\beta$  (and/or  $\gamma$ ) and the environmental treatment. Such correlations strongly imply that the environmental character is a causal agent of selection.

## Lecture 12 Problems

1. Consider the data in Example 12.1 after one episode of selection. Consider the regression of mating success on body size.

a: Compute  $S$

b: Compute  $\beta$

c: Compute  $C$

d: Compute  $\gamma$

e: Given a-d, what can you say about the nature of selection?

f: Suppose  $\sigma_A^2 = 25$ . What is the expected change in mean?

g: Further assuming no prior selection ( $d(0) = 0$ ), what is the additive genetic variation and heritability after one generation of selection?

## Solutions to Lecture 12 Problems

1: Recall from Example 12,1 that we have  $\mu^* = 138.996$ ,  $\mu = 140$ ,  $\sigma_{z^*}^2 = 6.39$ ,  $\sigma_z^2 = 59.5$ .

a:  $S = \mu^* - \mu = 138.996 - 140 = -1.004$

b:  $\beta = S/\sigma_z^2 = -1.004/59.5 = -0.017$

c:  $C = \sigma_{z^*}^2 - \sigma_z^2 + S^2 = 6.39 - 59.5 + 1.004^2 = -52.10$

d:  $\gamma = C/\sigma_z^4 = -52.10/59.5^2 = -0.0147$

e: Given a-d, what can you say about the nature of selection?

f: Suppose  $\sigma_A^2 = 25$ . What is the expected change in mean?  $R = \sigma_A^2\beta = 0.25 \cdot (-0.017) = -0.42$

g: Further assuming no prior selection ( $d(0) = 0$ ), what is the additive genetic variation and heritability after one generation of selection?

$$d(1) = \frac{d(0)}{2} + \frac{\sigma_A^4(0)}{2} (\gamma(0) - \beta^2(0)) = 0 + \frac{25^2}{2} (-0.0147 - 0.017^2) = -4.69$$

Hence,

$$\sigma_A^2(1) = 25 + d(1) = 20.31, \quad \text{and} \quad h^2(1) = \frac{\sigma_A^2(0) + d(1)}{\sigma_z^2(0) + d(1)} = \frac{25 - 4.69}{59.5 - 4.69} = 0.371$$

Note that  $h^2(0) = 25/59.5 = 0.42$ .