

5

Short-term Changes in the Mean: Response For Special Traits

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While the basic breeders' equation is indeed the foundation for much of the theory of selection response in quantitative traits, its simple form $R = h^2 S$ arises because of certain simplifying assumptions. In this chapter we consider the implications of relaxing some of those assumptions. The first assumption is that traits are continuously distributed, examining the response with both binary (presence/absence) and Poisson-distributed traits. The second class of assumptions we start to relax here deal with the environment, by allowing for parents to pass along some of their environmental component to their offspring (which is critical to considering material traits) as well as an initial exploration of the implications of genotype X environment interactions when considering response in natural populations.

RESPONSE WITH DISCRETE TRAITS: BINARY CHARACTERS

A potentially interesting complication for the analysis of quantitative traits are **binary characters**, presence/absence (such as normal/diseased). Our basic model to this point has assumed a continuous character that is influenced by both genetic and environmental value, which initially seem a bit at odds with the notion of a continuous trait. The connection (LW Chapters 11 and 25) is that we assumed some underlying continuous trait that maps into the observed discrete trait.

The Threshold/Liability Model

As discussed in LW Chapters 11 and 25, discrete characters can often be modeled by assuming an underlying continuous character z (usually referred to as the **liability**) that maps to the observed discrete character states (Figure 5.1). Consider the simplest case where the character is either present ($z \geq T$) or absent ($z < T$). Let μ_t be the mean liability and q_t the frequency of individuals displaying the character in generation t . If liability is well enough behaved to satisfy the assumptions of the breeders' equation (e.g., a linear biparental-offspring regression, no epista-

sis, genotype-environmental interactions or correlations), then $\mu_{t+1} = \mu_t + h^2 S_t$. We index the selection differential S_t by generation, as the amount of selection on threshold characters changes each generation. The problem is to estimate μ_t from the observed frequencies of character states. Our analysis will be restricted to a single threshold, but extension to multiple thresholds is straightforward (see Lande 1978).

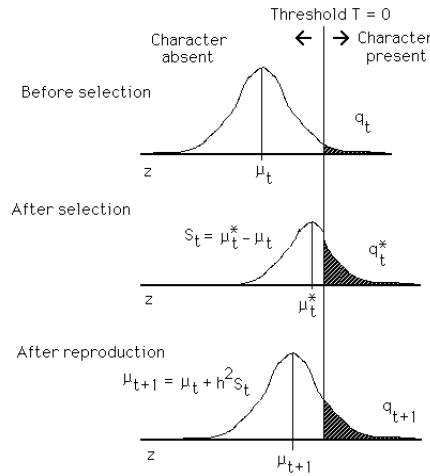


Figure 5.1. Selection on a character with a single threshold T . z is the value on the underlying scale of liability. Assuming z is a well-behaved quantitative character, $\mu_{t+1} = \mu_t + S_t h^2$, where $S_t = \mu_t^* - \mu_t$. Using the probit transform (Equation 4.15) we can translate from q , the frequency of individuals displaying the character, to μ , the mean of z .

If the values on the underlying scale are normally distributed, we can choose a scale that sets the threshold value at $T = 0$ and assigns z a variance of one. Since $z - \mu_t$ is a unit normal, $\Pr(z \geq 0) = \Pr(z - \mu_t \geq -\mu_t) = \Pr(U \geq -\mu_t) = q_t$ and from Equation 6.16

$$\mu_t = -z_{[1-q_t]} \tag{5.1}$$

where $z_{[p]}$, the probit transformation of p is given by Equation 4.15. For example, if 5% of a large population displays the trait, $\mu = -z_{[0.95]}$. From normal probability tables, $\Pr(U < 1.645) = 0.95$, hence $z_{[0.95]} = 1.645$ and $\mu = -1.645$. For small samples, estimation of μ requires the use of order statistics.

The response to selection, as measured by the change in the frequency of the

character, is

$$\begin{aligned}
 q_{t+1} &= \Pr(U \geq -\mu_{t+1}) \\
 &= \Pr(U \geq -\mu_t - h^2 S_t) \\
 &= \Pr(U \geq z_{[1-q_t]} - h^2 S_t)
 \end{aligned} \tag{5.2}$$

It remains to obtain $S_t = \mu_t^* - \mu_t$, where μ^* is the mean value of z in the selected parents in generation t . The selected population may consist entirely of adults displaying the character. However, more individuals than this may be required to keep the population at constant size, especially if q_t and the number of sampled individuals are small. In this case, the selected adults consist of two populations: those displaying the trait (hence $z \geq 0$) and those not ($z < 0$). Letting p_t be the fraction of selected adults displaying the character,

$$\mu_t^* = (1 - p_t) E(z|z < 0; \mu_t) + p_t E(z|z \geq 0; \mu_t) \tag{5.3}$$

Applying LW Equation 2.14 and noting that the unit normal density function satisfies $\varphi(x) = \varphi(-x)$, gives

$$\begin{aligned}
 E(z|z \geq 0; \mu_t) &= \mu_t + \frac{\varphi(\mu_t)}{q_t} \\
 E(z|z < 0; \mu_t) &= \mu_t - \frac{\varphi(\mu_t)}{1 - q_t}
 \end{aligned}$$

Substituting into Equation 5.3 gives

$$S_t = \mu_t^* - \mu_t = \frac{\varphi(\mu_t)}{q_t} \frac{p_t - q_t}{1 - q_t} \tag{5.4}$$

As expected, if $p_t > q_t$, $S_t > 0$. S_t depends critically on q_t and is very unlikely to remain constant over several generations of selection. Maximal selection occurs if only individuals displaying the trait are saved ($p_t = 1$), in which case Equation 5.4 reduces to $S_t = \varphi(\mu_t)/q_t$.

Example 1. Consider a threshold character whose liability has heritability $h^2 = 0.25$. What is the expected response to selection if the initial frequency of individuals displaying the character is 5% and selection is practiced by selecting only adults displaying the character? As was calculated earlier, $q_0 = 0.05$ implies $\mu_0 = -1.645$. In each generation, only individuals displaying the trait are saved. Thus

$$S_0 = \varphi(-1.645)/0.05 \simeq 0.106./0.05 \simeq 2.064$$

giving

$$\mu_1 = \mu_0 + 0.25, \quad S_0 = -1.645 + 0.25 \times 2.062 = -1.129$$

and hence

$$q_1 = \Pr(U \geq 1.129) = 0.129$$

After one generation of selection, the character frequency is expected to increase to 12.9%. Changes in q and S after further iterations are plotted in Figure 5.2.

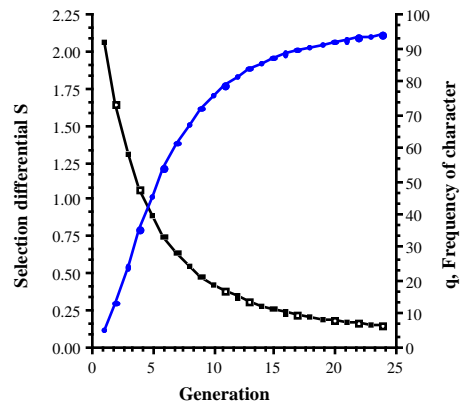


Figure 5.2. Response to selection on a threshold character. The initial frequency of individuals displaying the trait is 5%. Selection occurs by only allowing adults displaying the trait to reproduce ($p_t = 1$). Solid circles denote q_t , open squares denote S_t . The liability is assumed to have $h^2 = 0.25$.

Why did we not estimate μ_t^* using $z_{[1-q_t^*]}$? The reason is that the distribution of z values in selected parents is a weighted average of two truncated normal density functions. This distribution is not normal. However, we assume that normality is restored in the next generation due to segregation plus the addition of the environmental value. We examine the validity of this assumption in Chapter 10XX.

The Logistic Regression/Probit Model

The threshold approach is one way to model the mapping from some underlying continuous variable with both genetic and environmental influences into a discrete

character state. This is a deterministic approach, in that all individuals with liability values above the threshold value T show the trait, all those below the threshold do not display the trait. A potentially more realistic model might (at first blush) appear to be more stochastic, with the underlying liability mapping into a probability of displaying the trait. Under the threshold model, this probability is zero above T , zero below T . From a biological standpoint, a more appealing model might be that the probability of displaying the trait is a monotonically increasing function of the underlying liability value, which approaches zero for very low liability values and approaches one for very high liability values. Under this model, a high value of the liability does not imply that the trait is always shown, nor does a low liability value imply that the trait is never shown. A standard approach for such modeling is the logistic regression/probit approach, where the function that translates a liability value z into a probability of showing the trait, $\Pr(X = 1 | z)$, is given by a logistic regression,

$$\Pr(X = 1 | z) = \frac{1}{1 + e^{-\alpha z}}$$

where α is a scaling factor. Note that for $z \ll -1$, $\Pr(X = 1) \simeq 0$, while for $z \gg 1$, $\Pr(X = 1) \simeq 1$.

While the threshold and probit models appear to be rather different, they are actually essentially identical in terms of their analysis.

Suppose an individual's liability value is g . What is the probability that they will display the trait (i.e. $X = 1$)?

$$\Pr(X = 1 | g) = \int_T^\infty \varphi(z + g) dz = \Pr(U > T - g)$$

$$\Pr(U > T - g) \simeq 1 - \frac{1}{1 + e^{-\theta(T-g)}}, \quad \text{where } \theta = \pi/\sqrt{3}$$

DISCRETE TRAITS: POISSON-DISTRIBUTED CHARACTERS

With some discrete characters, such as number of leaves on a tree, we can essentially treat this as a continuous trait with little error. What about a trait that is discrete, but also has a rather compact distribution, such as number of eggs (**clutch size** for a bird, which may range from (say) 0 to 10 in our observed sample with a mean of (say) 4. How can we handle such a trait? One approach, motivated from the generalized linear model approach, is to assume some underlying liability value determines the mean of a random variable that then follows a Poisson distribution. Individuals with higher liability values have large mean values.

$$\Pr(Y = k) = e^{-\lambda} \frac{\lambda^k}{k!} \tag{5.xx}$$

$$\lambda = \exp(z), \quad \ln(\lambda) = z = \mu + g + e$$

Given there is a distribution of z values, the distribution of the observed trait value is

$$\Pr(Y = k) = \int e^{-\lambda} \frac{\lambda^k}{k!} p(\lambda) d\lambda$$

$z \sim N(\mu, \sigma_z^2)$, transformation of variables
mean value

$$E[\lambda] = \int \exp(z) p(z) dz = \int \exp(\mu + e) p(e) de = \exp(\mu) \int \exp(e) p(e) dz \quad (5.xx)$$

$$\int \exp(e) p(e) dz = \int \exp(e) \exp\left(\frac{-e^2}{2\sigma_z^2}\right) \frac{1}{\sqrt{2\pi\sigma_z^2}} = \exp(\sigma_z^2/2) \quad (5.xx)$$

Hence,

$$E[\lambda] = \exp(\mu) \exp(\sigma_z^2/2) = \exp(\mu + \sigma_z^2/2)$$

Hence,

$$E[\lambda_{t+1}] = \exp(\mu_t + h_t^2 S_t + \sigma_z^2/2)$$

giving the response as

$$R_Y = E[\lambda_{t+1}] - E[\lambda_t] = \exp(\mu_t + h_t^2 S_t + \sigma_z^2/2) - \exp(\mu_t + \sigma_z^2/2)$$

$$R_Y = \exp(\mu_t + \sigma_z^2/2) (\exp(h_t^2 S_t) + 1) = \mu_t (\exp(h_t^2 S_t) + 1)$$

Breeder's equation translates the mean of z after selection into the mean of z in the next generation, as the change in mean is just $h^2 S$. hence, it remains to translate from $\mu(Y^*)$ and $\mu(Y)$, the means in the observed trait before and after selection into $\mu(z^*)$ and $\mu(z)$

$$E[Y^*] = \exp(\mu^* + \sigma_z^2)$$

$$E[Y] = \exp(\mu + \sigma_z^2)$$

hence,

$$\frac{\mu_{Y^*}}{\mu_Y} = \exp([\mu^* + \sigma_z^2] - [\mu + \sigma_z^2]) = \exp(\mu^* - \mu) = \exp(S_x)$$

hence

$$S_x = \ln \left(\frac{\mu_{Y*}}{\mu_Y} \right) = \ln \left(\frac{\mu_Y + S_Y}{\mu_Y} \right) = \ln \left(1 + \frac{S_Y}{\mu_Y} \right)$$

RESPONSE DUE TO ENVIRONMENTAL CORRELATION

As Equation 4.25 indicates, shared parent-offspring environmental effects (e.g., $\sigma(E_p, E_o) \neq 0$) can influence response. We show here that this contribution is also transient. Consider a character whose variation is entirely environmental, in which case the phenotypic value can be decomposed as

$$z = \mu + E = \mu + e_{fa} + e_{mo} + e$$

where μ is the mean value of the character when environmental effects are randomly distributed, and the environmental value E has been decomposed into the maternal and paternal contributions to the offspring due to shared environmental effects (e_{mo} and e_{fa}) and a residual due to special environmental effects (e). In order to predict the shared environmental contribution from a parent, we assume the simplest model, that a fraction b of the total environmental value of a parent is passed onto its offspring. This model serves as a useful introduction to some of the dynamics that can occur with maternal effects (which are examined in the next section). Thus, the expected contribution from a father to his offspring is $e_{fa} = b E_{fa} = b(z_{fa} - \mu)$ where E_{fa} is the father's total environmental value. To simplify matters further, we assume that this regression coefficient is independent of the sexes of the parent and offspring, although this can easily be relaxed. If we assume that parents and offspring have the same phenotypic variance, then $b = \rho/2$, where ρ is the midparent-offspring correlation. Note that ρ can be negative. For example, suppose parents and offspring compete for a limited amount of common resource. Larger parents may gather a disproportionate share of resources, resulting in smaller offspring.

Provided E_{fa} and E_{mo} are independent, the expected value of an offspring from parents with phenotypic values z_{fa} and z_{mo} is

$$E(z_o | z_{mo}, z_{fa}) = \mu + \frac{\rho}{2}(z_{fa} - \mu) + \frac{\rho}{2}(z_{mo} - \mu) \quad (4.33)$$

Denoting the mean of adults selected in generation t by μ_t^* , the mean at generation $t + 1$ is given by

$$\mu_{t+1} = \mu + \rho(\mu_t^* - \mu)$$

where $(\mu_t^* - \mu)$ is the environmental deviation in selected parents at generation t , ρ of which is passed on to their offspring. Rewriting the mean after selection as $\mu_t^* = \mu_t + S_t$,

$$\mu_{t+1} = \mu + \rho(\mu_t + S_t - \mu) \quad (4.34)$$

The change in mean in generation t , $\Delta\mu_t = \mu_{t+1} - \mu_t$, is

$$\begin{aligned}\Delta\mu_t &= [\mu + \rho(\mu_t + S_t - \mu)] - [\mu + \rho(\mu_{t-1} + S_{t-1} - \mu)] \\ &= \rho[(\mu_t - \mu_{t-1}) + (S_t - S_{t-1})] \\ &= \rho[\Delta\mu_{t-1} + (S_t - S_{t-1})]\end{aligned}\quad (4.35a)$$

Suppose that constant selection (with differential S) is applied starting at generation 1. Here, $\Delta\mu_0 = 0$, $S_0 = 0$, and $S_t = S$ for $t \geq 1$. Equation 4.35a gives $\Delta\mu_1 = \rho S$. Further iterations yield

$$\Delta\mu_t = \rho^t S \quad (4.35b)$$

which decreases each generation, approaching zero for large t . Hence, even under continued selection, the response to selection eventually stops. The reason for this decline in the per generation rate of response can be seen from Equation 4.35b. Changes in the character mean due to previous generations of selection decay, countering selection in the current generation. Only ρ of the change from generation $t - 1$ is passed on, and, in general, only ρ^k of the response from generation $t - k$ persists by generation t . Summing over Equation 4.35b, the total response to selection after t generations is

$$R(t) = \mu_{t+1} - \mu_0 = \sum_{i=1}^t \Delta\mu_i = S \sum_{i=1}^t \rho^i \quad (4.35c)$$

Recalling the partial sum of a geometric series (Equation 4.29), this reduces to

$$R(t) = S \frac{\rho}{1 - \rho} (1 - \rho^t) \quad (4.36)$$

Thus, no matter how long selection is applied, the mean can never change by more than $S\rho/(1 - \rho)$. Further, none of this response is permanent. Suppose selection is stopped after t generations, giving $S_t = S$, $S_{t+\tau} = 0$ for $\tau \geq 1$. Substituting into Equation 4.35a and using Equation 4.35b, the expected change in generation $t + 1$ is

$$\Delta\mu_{t+1} = \rho^\tau (\Delta\mu_t - S) = -S\rho^\tau (1 - \rho^t) \quad (4.37)$$

By generation $t + \tau$ the cumulative response is

$$R(t + \tau) = R(t) - S(1 - \rho^t) \sum_{i=1}^{\tau} \rho^i = \rho^\tau R(t) \quad (4.38)$$

which converges to zero, with the rate of decay being set by the amount of environmental correlation, ρ (Figure 5.3). Hence, while there can be some selection

response when the resemblance between relatives is entirely environmental, any response is transient, decaying away once selection stops.

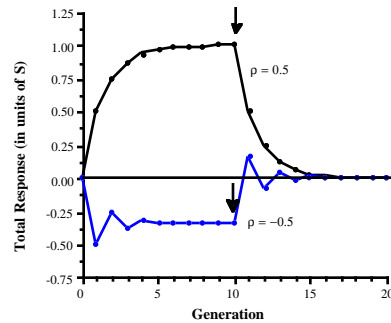


Figure 5.3. Response when resemblance between relatives is due entirely to correlation between environmental values in parents and offspring. Selection with constant differential S starts at $t = 0$ and continues until generation 10 (indicated by the arrow), at which point selection is stopped. Note the interesting dynamics that occur if environmental values are negatively correlated. The response to selection is **reversed** with respect to the selection differential. In this case, selection for *increased* character value results in a *decreased* mean value, with the total response eventually converging to $-S/3$ (for $\rho = -0.5$). Once selection is relaxed there is an initial positive response (generation 11), although response quickly decays to zero.

MATERNAL EFFECTS

Any influence that the mother's phenotype has on the phenotype of her offspring (beyond being a predictor of breeding value) is considered a **maternal effect** (LW Chapter 23). Body size, amount of care invested in offspring, and endosperm production are examples of **maternal performance characters** that potentially influence a variety of characters in the progeny. **Paternal effects** are also possible, especially in situations where the father plays some role in caring for the offspring. While paternal effects are not considered here, they can be treated in exactly the same fashion as maternal effects.

Assuming a maternal effect, the phenotype of a character can be decomposed as $z = G + M + e$, the sum of a genotypic value G plus a maternal component M plus an environmental deviation e (this assumes no interactions between G , M , and e). There are a number of subtle (and important) features with this apparently simple model. First, how many characters are we really considering?

The maternal effect may be regarded as either a direct function of the character being considered, or it may be due to a character (or suite of characters) correlated with the one being considered. For example, weight may be correlated with the amount of lactation, in which case maternal weight can influence offspring weight indirectly because larger females tend to have increased lactation. In the latter case, if there is a genetic basis to the maternal effect, selection on the direct character (e.g., body weight) is expected to give a correlated response in the maternal performance characters (e.g., lactation), and vice versa (Kirkpatrick and Lande 1989). We return to these points when we discuss evolution of correlated characters in Chapters 17-20. For now attention is restricted to single-character models.

Response under Falconer's Model

The simplest model of maternal effects (motivated by the inheritance of litter size in mice) is that of Falconer (1965), which deals with a single maternal character: the only character that has a maternal influence on z is z itself (reviewed in LW Chapter 23). Falconer assumes the maternal contribution is a linear function of the maternal phenotype z_{mo} , so that $M = m z_{mo}$ and the phenotypic decomposition becomes

$$z = G + m z_{mo} + e \quad (4.39)$$

Conceivably, M could be a nonlinear function of z_{mo} , but linearity is assumed for tractability. We refer to Equation 4.39 as the **dilution model**, as the effect of the maternal phenotype is diluted over several generations. The parameter m can be regarded as the partial regression coefficient (holding genotypic value constant) of offspring phenotype on maternal phenotype and can be estimated as the difference between the mother- and father-offspring regression slopes (LW Equation 23.13). Negative estimates of m have been reported. Falconer (1965) estimated $m = -0.15$ for litter size in mice and Janssen et al. (1988) estimated m values of -0.58 and -0.40 for age of maturity in two replicate lines of springtails. Maternal effects can result in unusual dynamics such as time lags. This is not surprising considering the dynamics of selection response when variation in the character is entirely environmental (Figure 5.4).

Assume that the joint distribution of phenotypes and breeding values in parents and offspring is multivariate normal. Further assuming no epistasis, the expected phenotypic value of an offspring whose mother has phenotypic value z_{mo} is

$$E(z_o | A_{mo}, A_{fa}, z_{mo}) = \frac{A_{mo}}{2} + \frac{A_{fa}}{2} + m z_{mo} \quad (4.40a)$$

where A_{mo} and A_{fa} are the maternal and paternal breeding values (see example 7 in LW Chapter 8). Averaging over the selected parents, the mean in generation $t + 1$ is

$$\mu_z(t + 1) = \frac{A_{fa}^*(t) + A_{mo}^*(t)}{2} + m \mu_{mo}^*(t) \quad (4.40b)$$

where $A_{fa}^*(t)$ and $A_{mo}^*(t)$ are the mean breeding values of the selected parents and $\mu_{mo}^*(t)$ the mean phenotypic value of selected mothers in generation t . Using the regression of breeding value on phenotype,

$$A = \mu_A + b_{Az} (z - \mu_z) + e$$

allows us to predict the breeding value A of an individual from its phenotypic value z . Thus we can rewrite $A_{mo}^*(t)$ as

$$\begin{aligned} E_s(A_{mo}) &= E_s \left(\mu_A(t) + b_{Az} [z_{mo} - \mu_z(t)] + e \right) \\ &= \mu_A(t) + b_{Az} S_{mo}(t) \end{aligned} \quad (4.41)$$

where $E_s(\)$ denotes the expected value over the selected parents. A similar expression holds for $A_{fa}^*(t)$. In the absence of maternal effects, $b_{Az} = h^2$. However, the dilution model generates a covariance between M and A , specifically $\sigma_{A,M} = m \sigma_A^2 / (2 - m)$, which in turn alters the covariance between z and A (Falconer 1965, Kirkpatrick and Lande 1989, LW Chapter 23). The resulting regression slope (at equilibrium) is

$$b_{Az} = h^2 \frac{2}{2 - m} \quad (4.42)$$

(Falconer 1965, Van der Steen 1985, Kirkpatrick and Lande 1989). If there is a negative maternal effect ($m < 0$), $b_{Az} < h^2$, reducing the correlation between breeding value and phenotype. Conversely, $m > 0$ increases the correlation between breeding value and phenotype above h^2 . Applying Equations 4.40–4.42 and using $\mu_{mo}^*(t) = \mu_z(t) + S_{mo}(t)$, gives

$$\mu_z(t+1) = \mu_A(t) + \frac{h^2}{2 - m} \left(S_{mo}(t) + S_{fa}(t) \right) + m \left(\mu_z(t) + S_{mo}(t) \right) \quad (4.43)$$

(Van der Steen 1985, Kirkpatrick and Lande 1989). The change in population mean over one generation, $\Delta\mu_z(t)$, is thus

$$\begin{aligned} \Delta\mu_z(t) &= \mu_z(t+1) - \mu_z(t) = \\ &= \left[\mu_A(t) + \frac{h^2}{2 - m} \left(S_{mo}(t) + S_{fa}(t) \right) + m \left(\mu_z(t) + S_{mo}(t) \right) \right] \\ &\quad - \left[\mu_A(t-1) + \frac{h^2}{2 - m} \left(S_{mo}(t-1) + S_{fa}(t-1) \right) + m \left(\mu_z(t-1) + S_{mo}(t-1) \right) \right] \\ &= \frac{h^2}{2 - m} \left(S_{mo}(t) + S_{fa}(t) \right) + m S_{mo}(t) + m \left(\Delta\mu_z(t-1) - S_{mo}(t-1) \right) \end{aligned} \quad (4.44)$$

The last simplification follows from the regression of breeding value on phenotype, with

$$\mu_A(t) = \mu_A(t-1) + \frac{h^2}{2-m} \left(S_{mo}(t-1) + S_{fa}(t-1) \right)$$

Equation 4.44 can be interpreted as follows: the first two terms are the change in character value resulting from selection in generation t due to genetic ($h^2 / [2 - m]$) and maternal (m) contributions. The final term, which can also be expressed as $m[\mu_z(t) - \mu_z^*(t-1)]$, represents the decay in the maternal contribution from the previous generation.

Starting with an unselected base population, the response to a single generation of selection is

$$\Delta\mu_z(1) = S_{mo}(1) \left(\frac{h^2}{2-m} + m \right) + S_{fa}(1) \frac{h^2}{2-m} \quad (4.45)$$

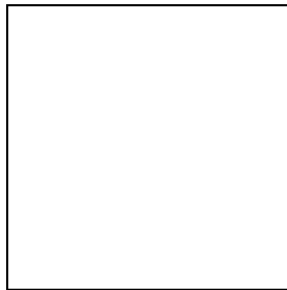
An interesting consequence of Equation 4.45 is that if $m < 0$, there is some possibility of a **reversed response**, where $\Delta\mu_z$ has opposite sign of S . If $S_{fa} = S_{mo} = S$, a reversed response is expected if

$$m < 1 - \sqrt{1 + 2h^2} \quad (4.46a)$$

If selection is only occurring on females, this condition is

$$m < 1 - \sqrt{1 + h^2} \quad (4.46b)$$

An example of an apparently maternally-induced reversed response was seen by Falconer (1960, 1965) in his selection experiments on litter size in mice. This character shows a negative maternal effect, with m and h^2 estimated to be -0.13 and 0.11 , respectively. Since selection for litter size occurs only in females, Equation 4.46b implies that a reversed response in the first generation is expected (as $1 - \sqrt{1 + 0.11} \simeq -0.05 > m$). As Figure 5.4 shows, a reversed response was indeed observed.



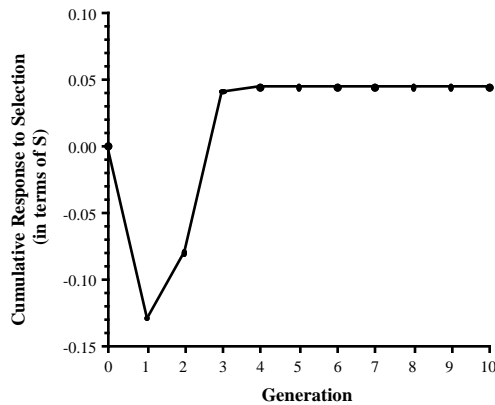


Figure 5.4. **Top:** Falconer's (1960, 1965) experiments on selection response for litter size in mice. The dashed line is the response to selection for small litters, the thick line selection for large litters, and the thin line the control. Note the reversed response in the first generation in both the up- and down-selected lines. **Bottom:** Prediction from the model, using Falconer's estimated values of $h^2 = 0.11$ and $m = -0.13$. The predicted change in population mean following a single generation of selection on females with $S_{mo} > 0$ is plotted. There is a reversed response in the first generation, even though the net genetic change is to increase the character. By generation 3, the nongenetic change in phenotypic mean has largely decayed away, revealing the net genetic change of $S_{mo} h^2 / [(1 - m)(2 - m)] = 0.044S_{mo}$.

An observed reversed response is misleading because the *permanent* response is expected to have the same sign as S , while the initial observed response also includes a transient component that (in this case) is of opposite sign and of larger magnitude than the permanent response component. It may take several generations for this transient component to decay and reveal the actual genetic changes (Figure 5.4), which from Equation 4.52 is (for a single generation of selection) $S h^2 [2 / (2 - m)(1 - m)]$.

The possibility of reversed response hints at some of the complicated dynamics that can appear when maternal effects are present. To examine these dynamics in more detail, consider the dilution model with constant directional selection occurring equally on both sexes. i.e., $S_{fa}(t) = S_{mo}(t) = S$ for $t \geq 1$. Iteration of Equation 4.44 gives

$$\Delta\mu_z(t) = S \left[\frac{2h^2}{(1 - m)(2 - m)} (1 - m^t) + m^t \right] \quad (4.47a)$$

which converges (for $|m| < 1$) to

$$\Delta\mu_z = S \frac{2h^2}{(1-m)(2-m)} \quad (4.47b)$$

Thus after a sufficient number of generations, the per generation change is constant. If $|m|$ is near zero, the per generation response rapidly converges to the asymptotic value, while if $|m|$ is near one, the rate of convergence is considerably slower. Summing over the single-generation changes (Equation 4.57a) the cumulative response to t generations of selection is

$$R(t) = \frac{S}{1-m} \left[t \frac{2h^2}{2-m} + m(1-m^t) \left(1 - \frac{2h^2}{(1-m)(2-m)} \right) \right] \quad (4.48a)$$

which converges (for $|m| < 1$) to

$$\frac{S}{1-m} \left[\frac{2h^2}{2-m} \left(t - \frac{m}{1-m} \right) + m \right] \quad (4.48b)$$

How much of this response is permanent? Suppose selection ends at generation t , and denote by τ the number of generations since selection was stopped. Iterating Equation 4.44 with $S(t) = S$, $S(t+\tau) = 0$ for $\tau \geq 1$ yields

$$\Delta\mu_z(t+\tau) = m^\tau (\Delta\mu_z(t) - S) \quad (4.49)$$

where $\Delta\mu_z(t)$ is given by Equation 4.47a. Thus, *response continues even after the cessation of selection*. Summing Equation 4.49 over τ yields the cumulative response *following* the last generation of selection,

$$R^*(\tau) = \frac{m(1-m^\tau)}{1-m} (\Delta\mu_z(t) - S) \quad (4.50)$$

which converges as $\tau \rightarrow \infty$ to

$$R^* = S \frac{m(1-m^t)}{1-m} \left[\frac{2h^2}{(1-m)(2-m)} - 1 \right] \quad (4.51)$$

Summing Equations 4.48b and 4.51, the permanent response to t generations of selection is

$$R(t) + R^* = t h^2 S \frac{2}{(1-m)(2-m)} \quad (4.52)$$

If R^* is opposite in sign to S , there is some erosion of the cumulative response upon relaxation of selection (we have already seen a special case of this with reversed response). For $|m| < 1$, erosion in response occurs if

$$0 < m < \frac{3 - \sqrt{1 + 8h^2}}{2} \quad (4.53a)$$

On the other hand, if maternal effects are either negative ($m < 0$) or sufficiently large

$$m > \frac{3 - \sqrt{1 + 8h^2}}{2} \tag{4.53b}$$

the response continues for a few generations following the relaxation of selection. Figure 5.5 plots some sample trajectories.

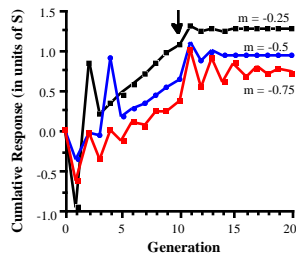
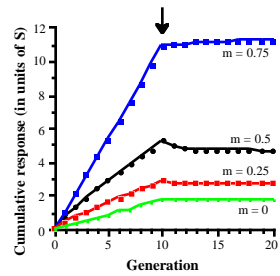


Figure 5.5. Examples of the predicted selection response with maternal effects under Falconer’s dilution model. Selection starts at generation zero, with $S_{fa} = S_{mo} = S$ until generation 10 (arrow), at which point selection stops. We assume $h^2 = 0.35$, with the different curves corresponding to different maternal effect values, m . **Top:** Positive maternal effects ($m > 0$). For this value of h^2 , Equations 4.53b gives the critical m value as 0.52, so that for $m = 0.75$ response continues after selection is relaxed, while response decays for $m = 0.5$ and 0.25. **Bottom:**

Negative maternal effects. The dynamics here are considerably more interesting. For this h^2 value, Equation 4.53a implies that response continues once selection stops for all values of $m < 0$. Compare with Figure 5.4.

In summary, the presence of maternal effects introduces several complications. First, predicting the response to selection requires not only of the inheritance parameters (m, h^2) and current selection differential, but also requires knowledge of previous selection ($\Delta\mu_z(t-1), S_{mo}(t-1)$). Second, after selection is stopped, the mean is likely to continue to change due to lag effects (e.g., Figure 5.4). If $m < 0$, the response will continue, while if $m > 0$ the response can either continue or decay. This clearly causes problems if we are trying to estimate the nature of selection acting on a character by comparing changes in means between generations. For example, an observed cross-generation decrease in a character could be due to four very different causes: (i) $S < 0$, (ii) $S > 0$ and a reversed response due to maternal effects, (iii) no selection in the observed generation but a previous history of $S > 0$, with the decrease in mean due to a positive maternal effect (reflecting a decay in response), or (iv) no current selection but a previous history of $S < 0$, with the decrease in mean due to a negative (or sufficiently large positive) maternal effect (reflecting a continuation of response).

Other Models of Maternal Effects

Willham (1963, 1972), expanding on the early results of Dickerson (1947), obtained covariances between relatives under a more general model that assumes the maternal effect can be further decomposed as $M = G_M + e_M$. G_M is the contribution to z resulting from the mother's genotypic value for the maternal performance character, while e_M is the contribution resulting from the environmental value of the maternal performance character (reviewed in LW Chapter 23). Hence, even though from the offspring's standpoint, M is treated as an environmental effect, it can have both a genetic and environmental basis in the mother. As Kirkpatrick and Lande (1989) have pointed out, this model is really a two-character model: the character directly being followed z (e.g., body weight) and some other character z_M (e.g., lactation) that has a maternal effect on z . Generalizations of the Dickerson-Willham model have been proposed by Riska et al. (1985) and Kirkpatrick and Lande (1989), but we will defer further discussion of these multiple character models until we discuss the evolution of correlated characters in Chapters 17-20. Mueller and James (1985) examine selection on maternal characters with overlapping generations.

MODIFYING THE BREEDERS' EQUATION FOR NATURAL POPULATIONS

One of the most serious limitations to applying the breeders' equation in natu-

ral populations is that selection can occur on (unmeasured) characters that are correlated with the particular character under consideration. Further, genotype-environment correlations can be a concern, as (for example) larger individuals may be able to obtain the best environments. Just how these complications can bias the breeders' equation was examined by van Tienderen and de Jong (1994). They assume complete additivity (no dominance or epistasis), multivariate normality, and linear parent-offspring regressions. As is discussed in Chapter 9, under these conditions a more general expression than the breeders' equation for the response to selection is given by Robertson's Secondary Theorem of Natural Selection, which states that response equals the covariance between relative fitness w and breeding value A , $R = \sigma(w, A)$. van Tienderen and de Jong use a path analysis argument (LW Appendix 2) to explore the relationship between response R and the selection differential S when complications such as selection on correlated characters and genotype-environment correlations exist.

To present their analysis, we first decompose the phenotype z as

$$z = A + E + E_s$$

where A is the additive genetic value, E the general environmental value (for example, the average value for a particular macrohabitat) and E_s the special environmental value unique to each individual (LW Chapter 6). By construction, E_s is independent of other variables (so that the total environmental variance is $\sigma_E^2 + \sigma_{E_s}^2$), but A and E may be correlated. Consider the path diagrams (LW Appendix 2) in Figure 5.6, which shows possible paths of how the environment value E , the genotypic value A , and the phenotypic value z can influence fitness. The standard breeders' equation assumes E and A influence fitness only through phenotypic value z . van Tienderen and de Jong examines the more general situation when E and A can influence fitness independent of (or in addition to) their effects on z , such as can occur if the character is phenotypically or genetically correlated with under characters under selection. If fitness is entirely set by the phenotypic value of the character of interest, there should be no expected differences in fitness of individuals with the same phenotypic value z but different underlying genetic (A) or environmental values (E). However, if other correlated characters are under selection, then individuals with the same z value can have different fitnesses as correlations between the A and /or E values with the genetic and/or environmental values at these other characters with have influences on fitnesses (also see Chapters 15-17).

To quantify the effects from these different paths to influencing fitness, van Tienderen and de Jong consider the multiple regression of relative fitness w as a function of z , A , and E , viz.,

$$w = \alpha + \beta_z z + \beta_A A + \beta_E E + \epsilon$$

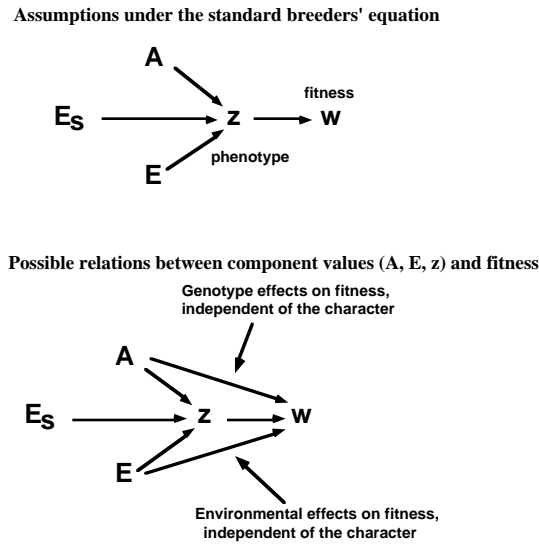


Figure 5.6. The pathways by which the components of a character, here its phenotype z , additive genetic value A , common environmental effect E , and special environmental effect E_s , influence fitness w . **Top.** The breeders' equation assumes that only the phenotype (z) of a character influences fitness. This may not be an unreasonable starting assumption for artificial selection wherein the breeder directly chooses individuals on the basis of phenotypes and randomized environments with respect to phenotypes. **Bottom.** Other pathways by which the components of a character can influence fitness. In addition to possible effects from the phenotype, either (or both) of the additive genetic or environmental value can influence fitness independent of their influence on phenotype. For example, an environmental value can influence both the character of interest and independently influence fitness. This creates an association between character value and fitness so that we might observe a character mean being changed within a generation without that character itself being under any selection.

The partial regression coefficients β represent the expected change in fitness holding the other variables constant (LW Chapter 8). For example, β_z is the effect of phenotype on fitness, holding the other variables (A and E) constant. From multiple regression theory (LW Chapter 8), the partial regression coefficients satisfy

$$\begin{pmatrix} \sigma(w, z) \\ \sigma(w, A) \\ \sigma(w, E) \end{pmatrix} = \begin{pmatrix} S \\ R \\ \sigma(w, E) \end{pmatrix} = \begin{pmatrix} \sigma_z^2 & \sigma(z, A) & \sigma(z, E) \\ \sigma(z, A) & \sigma_A^2 & \sigma(A, E) \\ \sigma(z, E) & \sigma(A, E) & \sigma_E^2 \end{pmatrix} \begin{pmatrix} \beta_z \\ \beta_A \\ \beta_E \end{pmatrix} \quad (4.57)$$

Recall that $S = \sigma(w, z)$ follows from the Robertson-Price identity and $R = \sigma(w, A)$ from Robertson's Secondary Theorem. The first vector contains the covariances

between relative fitness and the predictor variables (z , A , and E), while the matrix is the variance-covariance matrix for these predictor variables. Note that

$$\sigma(z, A) = \sigma(A + E + E_s, A) = \sigma_A^2 + \sigma(E, A)$$

Likewise, $\sigma(z, E) = \sigma_E^2 + \sigma(E, A)$. Using these identities and taking the first two rows of the above matrix equation gives

$$\begin{aligned} S &= \sigma_z^2 \beta_z + (\sigma_A^2 + \sigma(E, A)) \beta_A + (\sigma_E^2 + \sigma(E, A)) \beta_E \\ &= \sigma_z^2 \beta_z + \sigma_A^2 \beta_A + \sigma_E^2 \beta_E + \sigma(E, A) (\beta_A + \beta_E) \end{aligned} \quad (4.58a)$$

and

$$\begin{aligned} R &= (\sigma_A^2 + \sigma(E, A)) \beta_z + \sigma_A^2 \beta_A + \sigma(E, A) \beta_E \\ &= \sigma_A^2 \beta_z + \sigma_A^2 \beta_A + \sigma(E, A) (\beta_z + \beta_E) \end{aligned} \quad (4.58b)$$

If there are no genotype-environment correlations [$\sigma(E, A) = 0$],

$$R = \sigma_A^2 (\beta_z + \beta_A) \quad (4.59a)$$

and

$$S = \sigma_z^2 \beta_z + \sigma_A^2 \beta_A + \sigma_E^2 \beta_E \quad (4.59b)$$

Multiplying both sides of Equation 4.59b by h^2 and rearranging gives

$$\sigma_A^2 \beta_z = h^2 \sigma_z^2 \beta_z = h^2 (S - [\sigma_A^2 \beta_A + \sigma_E^2 \beta_E])$$

Substituting into Equation 4.59a gives

$$R = h^2 S + \sigma_A^2 (1 - h^2) \beta_A - h^2 \sigma_E^2 \beta_E \quad (4.59c)$$

Hence, selection entirely on additive genetic values ($\beta_A \neq 0$) inflates response over the breeders' equation, while selection on entirely environmental values ($\beta_E \neq 0$) decreases response relative to the breeders' equation. Following this same approach gives the general solution [when $\sigma(E, A) \neq 0$] of

$$R = h^2 S + \sigma_A^2 (1 - h^2) \beta_A - h^2 \sigma_E^2 \beta_E + \sigma(E, A) (\beta_z - h^2 \beta_A + (1 - h^2) \beta_E) \quad (4.40)$$

If selection acts only on the phenotype of the character being considered, then $\beta_A = \beta_E = 0$ and Equation 4.58a reduces to $S = \sigma_z^2 \beta_z$, implying $\beta_z = S/\sigma_z^2$. Substituting into Equation 4.58b gives the response as

$$R = \beta_z [\sigma_z^2 + \sigma(E, A)] = \left(h^2 + \frac{\sigma(E, A)}{\sigma_z^2} \right) S \quad (4.61a)$$

which (as expected) reduces to the breeders' equation when there is no genotype-environment correlation. Under artificial selection, it is generally assumed (to a first approximation) that individual fitness is entirely based on the phenotype of the character of interest, specifically those phenotypes chosen by the breeder. In this case, the partial regression coefficients of fitness on genotype and environmental values are zero (again, as first approximation), as phenotype entirely determines fitness. In natural populations, we do not have this luxury and another possibility is that there is no natural selection of the character of interest (its phenotype, by itself has no effect on fitness), but rather selection occurs on characters genetically correlated with the one we are following. If these characters under selection are only connected to the character we are following through genetic value (i.e., no environmental correlation between characters), then $\beta_A \neq 0$ while $\beta_z = \beta_E = 0$. In this case response becomes

$$R = \beta_A \sigma_A^2 = S \frac{\sigma_A^2}{\sigma_A^2 + \sigma(E, A)} \quad (4.61b)$$

which reduces to $R = S$ in the absence of genotype-environment correlations. Another possibility is that the only correlation between characters under selection and our character is through shared environmental effects, giving $\beta_E \neq 0$ while $\beta_A = \beta_z = 0$, in which case the response becomes

$$R = \beta_E \sigma(E, A) = S \frac{\sigma(E, A)}{\sigma_E^2 + \sigma(E, A)} \quad (4.61c)$$

which equals zero unless a genotype-environment correlation exists.