

# Response to Natural Selection on a Quantitative Character

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November 26, 2025

## 1 Introduction

Lande and Arnold [5] rewrote the classical “breeder’s equation” [1, Eqn. 11.2] of quantitative genetics in a form that is more useful within evolutionary biology. Rather than assuming that selection acts by truncation, as the classical theory did, they allow for a continuum of fitness values. Their treatment was multivariate; this note provides a univariate summary.

## 2 Truncation selection

The classical theory deals with the case in which a breeder wishes to increase the value of some character,  $z$ . Individuals are selected for breeding only if their character value exceeds some threshold. Thus, the mean character value of parents exceeds that of the general population, and the difference,  $S$ , is called the *selection differential*.

If the character is heritable, then its mean value among offspring will also exceed that of the parental generation before selection. This excess, written either as  $R$  or as  $\Delta z$ , is called the *response to selection* and obeys what is called the “breeder’s equation” [1, Eqn. 11.2]:

$$\Delta z = h^2 S \tag{1}$$

where  $h^2$  is called the heritability and equals the ratio,  $V_A/V_P$ , of additive genetic variance to phenotypic variance. The response tends to be smaller than the selection differential, because characters are seldom perfectly heritable.

This equation is useful not only to breeders of livestock, but also to ecologists. The two groups, however, use it in different ways. The breeder asks such questions as “how large is  $S$  likely to be if I select the upper 20% of my population for breeding?” This question would be of little interest to an ecologist, because natural selection does not work by truncation—fitness is more likely to vary continuously as a function of character value. To deal with natural selection, we need a different way to calculate the selection differential.

## 3 Response to univariate selection

Let  $f(z)$  represent the probability density function of a quantitative character. In other words,  $f(z)dz$  is approximately the probability that a random individual has a value in the interval between  $z$  and  $z + dz$ , where  $dz$  is some small number. The population mean is

$$\bar{z} = \int z f(z) dz$$

where the integral runs over all possible character values, and I am using an overbar to represent the expected value.

An individual with character value  $z$  survives to reproduce with probability  $W(z)$ , which is called the *absolute fitness* of that individual. Under truncation selection,  $W(z) = 1$  for the individuals who are selected and equals 0 for the others. In a natural population, however,  $W$  may take a wide range of values. The mean fitness in the population is

$$\bar{W} = \int W(z)f(z)dz \quad (2)$$

The density of  $z$  among selected parents must be proportional to  $W(z)f(z)$ , because  $f(z)$  is the density of individuals with character value  $z$ , and  $W(z)$  is the fraction of those that survive to become parents. However,  $W(z)f(z)$  is not a proper density, because its integral isn't 1; it's  $\bar{W}$  (Eqn. 2). The density among selected parents is  $w(z)f(z)$ , where  $w(z) = W(z)/\bar{W}$  is the *relative fitness* of individuals with character value  $z$ . Note that mean relative fitness equals unity:

$$\bar{w} = \int w(z)f(z)dz = \frac{\int W(z)f(z)dz}{\bar{W}} = 1 \quad (3)$$

The mean character value,  $\bar{z}^*$ , of selected parents is

$$\bar{z}^* = \int zw(z)f(z)dz$$

which equals  $E[zw]$ , the expected product of  $z$  and  $w(z)$ . The selection differential is

$$\begin{aligned} S &= \bar{z}^* - \bar{z} \\ &= E[zw] - \bar{z} \\ &= E[zw] - \bar{z}\bar{w} \\ &= C_{wz} \end{aligned} \quad (4)$$

where the third line uses the fact that  $\bar{w} = 1$  (Eqn. 3). Here,  $C_{wz}$  is the covariance between character value and relative fitness. This relationship between selection and covariance was described by Price [6].

Equation 4 expresses the selection differential in general terms. It is consistent with but is not limited to truncation selection. We can use this formulation no matter how fitness varies among individuals. Let us now plug it into the breeder's equation. Eqn. 1 becomes

$$\begin{aligned} \Delta z &= h^2 C_{wz} \\ &= V_A C_{wz} / V_P \\ &= V_A \beta_{wz} \end{aligned} \quad (5)$$

where  $\beta_{wz} = C_{wz}/V_P$  is the regression of relative fitness on character value. (To convince yourself of this, look up the formula for linear regression, and remember that  $V_P$  is the variance of  $z$ .) Equation 5 implies that we can study selection in nature by doing a linear regression of fitness (perhaps measured as the number of surviving offspring) against character value.

If the relative fitness function,  $w(z)$ , is a straight line,  $\beta_{wz}$  should approximate the slope of that line. It is more likely however that  $w(z)$  has curvature, perhaps rising to a peak and then declining. In such circumstances, Lande and Arnold [5] show that  $\beta_{wz}$  measures the average derivative of  $w(z)$ :

$$\beta_{wz} = \int w'(z)f(z)dz$$

where  $w'$  is the derivative of  $w$ .

## 4 Response to multivariate selection

When there are  $K$  quantitative characters,  $z$  becomes a vector,

$$z = \begin{pmatrix} z_1 \\ z_2 \\ \vdots \\ z_K \end{pmatrix}$$

and Eqn. 5 becomes

$$\Delta z = GP^{-1}s = G\beta \tag{6}$$

where  $G$  is the additive genetic covariance matrix,  $P$  is the phenotypic covariance matrix,  $s$  is a vector of selection differentials, and  $\beta = P^{-1}s$  is a vector of partial regression coefficients of relative fitness on each of the  $K$  characters [5, p. 1212]. This vector is called the *selection gradient* and describes the direction in which selection is pushing. The response to selection may however go in a somewhat different direction, if that other direction has more additive variance.

Lande used this framework to explore a variety of issues within evolutionary ecology. One study dealt with allometry between brain size and body size [2]. Another considered male and female versions of the same character as separate characters in order to build an evolutionary theory of sexual dimorphism [3, 7]. In another, he treated as separate characters the same character in different environments. This yielded an evolutionary theory of phenotypic plasticity [8]. In another, he treated as separate characters the same character at different ages. This yielded an evolutionary theory of life histories [4]. All in all, Eqn. 6 has been remarkably productive within evolutionary ecology.

## References

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