Appendix

We wish to derive an expression for the curvature of the adaptive landscape, *H*. Phillips and Arnold (1989) reported the multivariate result given in (6), but without derivation. The following derivation is for the univariate case (i.e., selection acts on a single phenotypic trait). The first part follows Lande (1976). Let the mean value of a phenotypic trait, *z*, before selection be

$$\bar{z} = \int z p(z) dz, \tag{A1}$$

where p(*z*) is the phenotypic distribution before selection. Let *W(z)* be the fitness of an individual with phenotype *z*, so that the average fitness in the population is

$$\overline{W} = \int p(z) W(z) dz. \tag{A2}$$

The individual selection function *W(z)* will shift the mean and variance P ($=\sigma^2$) of the trait, so that after selection the trait mean is

$$\bar{z}^* = \frac{1}{\overline{W}} \int z p(z) W(z) dz, \tag{A3}$$

and the trait variance is

$$P^* = \frac{1}{\overline{W}} \int (z - \bar{z})^2 p(z) W(z) dz. \tag{A4}$$

The shift in the mean is called the directional selection differential, $s = \bar{z}^* - \bar{z}$.

If the trait is normally distributed before selection, then

$$p(z) = \frac{1}{\sqrt{2\pi P}} \exp\{\frac{-(z - \bar{z})^2}{2P}\}. \tag{A5}$$

Later we shall need the first derivative of this trait distribution with respect to the mean before selection, namely

$$\frac{\partial p(z)}{\partial \bar{z}} = p(z)(z-\bar{z})/P. \quad \text{(A6)}$$

As a first step in solving for the directional selection gradient, *β*, we take the first derivative of $\overline{W}$ with respect to the trait mean and obtain, using (A6),

$$\frac{\partial \overline{W}}{\partial \bar{z}} = \int \frac{\partial p(z)}{\partial \bar{z}} W(z)dz = \int \{p(z)(z-\bar{z})/P\} W(z)dz = \overline{W}(\bar{z}^{*}-\bar{z})/P \quad \text{(A7)}$$

(Lande 1976). Dividing both sides of the preceding equation by mean fitness, we obtain the standard expression for the directional selection gradient (Lande and Arnold 1983)

$$\frac{\partial \overline{W}}{\overline{W}\partial \bar{z}} = \frac{\partial \ln \overline{W}}{\partial \bar{z}} = s/P = \beta. \quad \text{(A8)}$$

To obtain an expression for the curvature of the adaptive landscape, we first differentiate (A7) with respect to the trait mean and obtain

$$\frac{\partial^2 \overline{W}}{\partial \bar{z}^2} = \frac{1}{P}\int p(z)(z-\bar{z})^2 W(z)P^{-1} - p(z)W(z)dz = (\overline{W}P^{*}/P^2) - (\overline{W}/P). \quad \text{(A9)}$$

Recalling the definition of the nonlinear selection gradient (Lande and Arnold 1983), $\gamma = (P^{*} - P + s^2)/P^2$, and dividing both sides of (A9) by mean fitness, we obtain the following expression for the curvature of the adaptive landscape,

$$H = \frac{\partial^2 \overline{W}}{\overline{W}\partial \bar{z}^2} = \frac{\partial^2 \ln \overline{W}}{\partial \bar{z}^2} = (P^{*} - P)/P^2 = \gamma - \beta^2. \quad \text{(A10)}$$

In deriving this expression we assumed that the trait distribution before selection was Gaussian. Our only assumptions with respect to selection were that the individual selection function, *W(z)*, is twice differentiable with respect to the trait mean. Our expression (A10) does not assume that the adaptive landscape is quadratic or symmetrical. In the case of multiple traits, the curvature of the adaptive landscape is $\gamma - \beta\beta^T$, where γ is a symmetric matrix, β is a column vector, and T denotes transpose (Phillips and Arnold 1989).