

**Limits on Stabilizing, Disruptive, and Correlational Selection Set by the Opportunity for Selection**



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## LIMITS ON STABILIZING, DISRUPTIVE, AND CORRELATIONAL SELECTION SET BY THE OPPORTUNITY FOR SELECTION

Crow (1958) showed that the phenotypic variance in relative fitness places a limit on the evolution of fitness. O'Donald (1970) independently determined the same relationship, stressing the use of the relative variance in fitness as a measure of the intensity or opportunity for selection. (The variance in relative fitness or the opportunity for selection is conveniently computed by dividing the variance in absolute fitness by its squared mean. Fitness on the new scale is relative in the sense that the mean is one and the variance is equal to the squared coefficient of variation on the absolute scale.) Wade (1979) and Wade and Arnold (1980) showed that there is often a simple relationship between fitness variances in the two sexes and stressed the use of variance in relative mating success in measuring the opportunity for sexual selection in males. Arnold and Wade (1984) pointed out that the opportunity for selection sets a limit on the strength of directional selection that can act on any character because the absolute value of the standardized directional selection differential (the shift in mean induced by selection measured in units of phenotypic standard deviation) must be less than the standard deviation in relative fitness.

I intend to show that the selection opportunity also sets a limit on stabilizing, disruptive, and correlational selection. Stabilizing and disruptive selection can be measured, respectively, by an increase or decrease within a generation in the variance of an age-invariant character, after a correction has been made for the effect of directional selection on the variance. Likewise, correlational selection refers to a change in the phenotypic covariance between two such characters, after a correction has been made for the effect of directional selection on the covariance (Lande and Arnold 1983).

The results can be applied when a preliminary study yields an estimate of the selection opportunity but no characters have been measured, and so phenotypic selection has not been estimated. In this situation, the selection opportunity can indicate the maximum value of stabilizing selection that can be detected on any particular character; it may thus be useful in deciding whether to embark on a more detailed investigation of selection.

The stabilizing selection differential is by definition equal to the covariance between relative fitness and quadratic deviations of the character,  $z$ , from its mean,  $\bar{z}$ ,

$$C = \text{cov}(w, \bar{z}^2), \quad (1)$$

where  $\tilde{z} = z - \bar{z}$  (Lande and Arnold 1983).

Because the squared correlation between relative fitness and quadratic deviations cannot exceed one, we have

$$C^2 \leq \sigma_w^2 \sigma_{\tilde{z}^2}^2. \quad (2)$$

The opportunity for selection,  $I$ , equals the variance in relative fitness,  $\sigma_w^2$ . The variance of quadratic deviations,  $\sigma_{\tilde{z}^2}^2$ , equals the fourth moment minus the square of the second moment. If  $z$  is normally distributed, the fourth moment equals three times the square of the second moment, and thus,  $\sigma_{\tilde{z}^2}^2 = 2P^2$ , where  $P$  is the variance of  $z$  before selection.

Substituting these equalities into equation (2) and taking square roots,

$$|C|/P \leq \sqrt{2I}. \quad (3)$$

Furthermore,  $C = P^* - P + s^2$ , where  $P^*$  is the variance in the character after selection,  $s$  is the directional selection differential, and  $s^2$  is the correction for change in variance caused by directional selection (Lande and Arnold 1983). Consequently, when the character is normally distributed before selection, the absolute value of the proportional change in variance caused by stabilizing selection must be less than the square root of twice the opportunity for selection.

A similar relationship holds for the correlational selection differential,

$$C_{ij} = \text{cov}(w, \tilde{z}_i \tilde{z}_j) \quad (4)$$

(Lande and Arnold 1983), when the distribution of the two characters is bivariate normal. Using equation (41.97) from Kendall and Stuart (1976),

$$C_{ij}^2 \leq I(P_{ij}^2 + P_i P_j), \quad (5)$$

where  $P_{ij}$  is the covariance between the characters before selection. Since  $P_{ij}^2 \leq P_i P_j$ ,

$$C_{ij}^2 \leq 2P_i P_j I. \quad (6)$$

Taking square roots and dividing both sides by  $P_{ij}$ , we get

$$|C_{ij}|/P_{ij} \leq \sqrt{2I}|r|, \quad (7)$$

where  $r$  is the correlation between the two characters before selection.

Thus, if the two characters show a bivariate normal distribution before selection, the absolute value of the proportional change in covariance caused by correlational selection cannot exceed the square root of twice the opportunity for selection divided by the absolute value of the correlation before selection.

Table 1 indicates the extent to which particular values for the selection opportunity,  $I$ , limit directional, stabilizing, and correlational selection. The selection opportunity does not place an informative limit on stabilizing selection unless  $I$  is less than one-half (which, in the case of viability selection, corresponds to a mortality rate of less than one-third), because the variance in a character obviously cannot be reduced by more than 100%. Likewise, an  $I$  of more than about one-third does not place a useful limit on negative correlational selection when the correlation before selection is 0.8.

TABLE 1  
SELECTION LIMITS AS A FUNCTION OF THE SELECTION OPPORTUNITY,  $I$

| Mortality Rate, $d^*$ | Opportunity for Selection, $I^\dagger$ | Maximum Value of Directional Selection:                               | Maximum Value of Stabilizing or Disruptive Selection: | Maximum Value of Correlational Selection:                   |          |          |
|-----------------------|--|---|---|---|----------|----------|
|                       |  | % Shift in Mean in Units of Standard Deviation, $100 \times \sqrt{I}$ | % Change in Variance, $100 \times \sqrt{2I}$          | % Change in Covariance, $100 \times \sqrt{2I}/ r ^\ddagger$ |          |          |
|                       |  |   |   | $r = .2$  | $r = .5$ | $r = .8$ |
| .001                  | .001                                   | 3   | 4   | 22  | 9        | 6        |
| .01                   | .01                                    | 10  | 14  | 71  | 28       | 18       |
| .09                   | .1                                     | 32  | 45  | 224   | 89       | 59       |
| .50                   | 1                                      | 100   | 141   | 707   | 283      | 177      |
| .91                   | 10                                     | 316   | 447   | 2236  | 894      | 559      |

\* Mortality rate corresponding to each selection opportunity.

† Following Crow (1958), opportunity for selection  $I = d/s$ , where  $d + s = 1$ .

‡  $r$  is the phenotypic correlation between characters before selection.

A current empirical challenge is to measure lifetime variance in fitness and lifetime selection in natural populations (Clutton-Brock 1983). Although relatively few studies have succeeded at this task (e.g., Fincke 1982; Clutton-Brock et al. 1982), a larger number of investigators have succeeded in measuring variance in reproductive success in a single season. Kluge (1981), for example, has summarized anuran studies of seasonal reproductive success. Generally, the relative variance in male progeny counts ranged from about 0.5 to 6.0; the corresponding female selection opportunity ranged from about 0.1 to 0.4. If lifetime estimates reveal a similar range in anurans and other groups, then  $I$  will be a useful indicator of selection limits for directional and stabilizing selection. Selection opportunities in this range probably do not place useful limits on correlational selection.

Houck et al. (1985) estimated the seasonal opportunity for sexual selection in male salamanders (*Desmognathus ochrophaeus*) as 0.063, on the basis of the among-male component of variance in insemination success. From that selection opportunity we estimate that directional sexual selection can shift the mean of any character by no more than about 25% of a standard deviation, that stabilizing sexual selection can reduce the variance of a normally distributed trait by no more than about 35%, and that correlational sexual selection can change the covariance of two bivariate, normally distributed traits by no more than 71% if the two traits are moderately correlated before selection ( $r = 0.5$ ).

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