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COMMENT

Selection may be strongest when resources are scarce: a comment on Wilson

Wilson (1995) posed a little studied but interesting question regarding the strength of selection at different resource levels. The strength of natural selection on traits used to acquire resources should vary with resource abundance. Wilson (1995) used a graphical model to argue that selection should be strongest at intermediate resource levels (Fig. 1). Absolute fitness was presented as a function of resource levels using what Wilson (1995) termed 'resource value' functions. These functions characterized how the ability of a phenotype to use the resources at some given level translated into absolute fitness. Using these functions, he noted that the difference in absolute fitness between the best and the worst phenotypes should be low when resources are very scarce and again when resources are very abundant. In the first case, resources are so scarce that no individuals can obtain any, regardless of the phenotype. In the second case, resources are so abundant that all individuals can obtain them, again regardless of phenotype. He argued that selection should therefore be strongest at intermediate levels because it is at this point that the difference in absolute fitness is maximal. Wilson (1995) tested this idea using artificial character variation for petal size in *Drosera tracyi*. The results showed that differences in pollination success were indeed maximal at intermediate pollination levels, in apparent agreement with his hypothesis.

Here we argue that Wilson's (1995) hypothesis is flawed in one fundamental respect: the difference in absolute fitness between phenotypes is not a measure of the intensity of natural selection. Rather, selection intensity is a function of differences in relative fitness. We use quantitative selection theory to show that Wilson's (1995) graphical scenario of 'resource value' functions actually predicts selection should be strongest at low resource levels. We reanalyse a portion of his field data and find that they, too, do not support the hypothesis of strongest selection at intermediate resource levels.

Intensity of natural selection

The intensity of natural selection on a single phenotypic trait is usually measured as the selection differential (s), which is the covariance between relative fitness (w) and the trait (z):

$$s = \mathrm{Cov}[w, z] \tag{1}$$

(Price, 1970; Lande and Arnold, 1983; Arnold and Wade, 1984). The relative fitness (w) is the absolute fitness divided by the mean fitness, $W/\bar{W}$. This measure is related to the selection gradient, ß, which is the slope of the regression of relative fitness (w) on the single trait (z), as follows:

$$\beta = \frac{\mathrm{Cov}[w, z]}{\mathrm{Var}[z]} \tag{2}$$

(Lande, 1979; Lande and Arnold, 1983; Arnold and Wade, 1984). These and not the difference in absolute fitness are the relevant measures of the intensity of natural selection because they are

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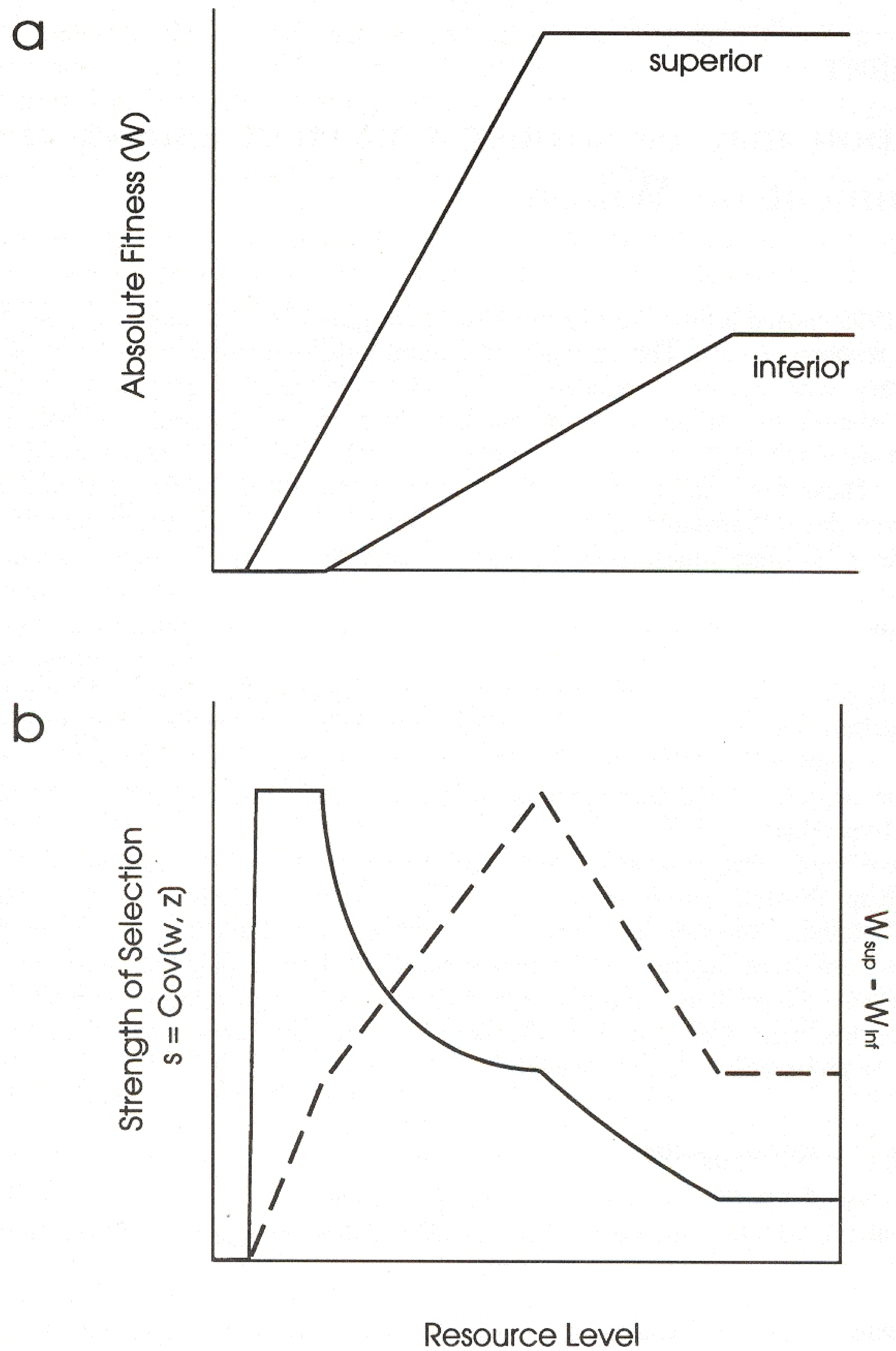

Figure 1. (a) The resource value functions assumed for a superior (W_{sup}) and an inferior phenotype (W_{inf}), as presented in Wilson (1995). The superior phenotype begins to gain fitness at a lower resource level than the inferior phenotype, rises with a greater slope and has a higher point at which additional resources do not result in a fitness gain. (b) The strength of selection at various resource levels. The broken line represents Wilson's (1995) surrogate for the strength of selection, the difference in the absolute fitness of the two phenotypes (note, the scales of the *y*-axes are not equal). The selection differential (s) is presented as the best measure of selection intensity (solid line). The scales of the two measures are arbitrary and the focus is thus on the shape of the curves.

the measures that directly predict evolutionary change. For a single character, the evolutionary response (r) across a generation is predicted by $r = h^2 s$, where h^2 is the heritability of the character trait. For multivariate selection, the change in the mean of each phenotypic character across a generation ($\Delta\bar{z}$) is predicted by $\Delta\bar{z} = G\beta$, where G is the additive genetic variance–covariance matrix for the characters (Lande, 1979; Lande and Arnold, 1983; Arnold and Wade, 1984).

We applied this measure of selection intensity (s) to Wilson's (1995) graphical model (Fig. 1a). We assumed that the inferior and superior phenotypes were equally abundant and we assigned values of 0 and 1, respectively, as measures of the phenotypic trait (z); the choice of the values of z had no effect on the results. In contrast to Wilson (1995), the selection intensity does not peak at intermediate resource levels. Instead, under his scenario, selection is highest at lowest resource levels and declines as resource levels increase (Fig. 1b). The decline is a result of the decreasing variance in the relative fitness. As resource levels increase, the mean fitness increases. With increasing mean fitness, the relative fitness of the superior phenotype decreases, while that of the inferior increases. The result is a decreasing variance in relative fitness and thus the covariance between the relative fitness and the trait.

Reanalysis of *D. tracyi* experiments

Whether or not selection in the wild is most intense at low resource levels remains an open question. We reanalysed Wilson's (1995) field data concerning both pollen removal and deposition at various pollinator (resource) densities (Fig. 5 in Wilson, 1995). The conclusions from the two were similar and thus we present only the results for pollen deposition.

Wilson (1995) created artificial character variation in *D. tracyi* by trimming the flower petals to approximately one-half the normal diameter in one of each of a pair of flowers (the inferior phenotype). The other flower was left unaltered (the superior phenotype). Two pairs of these flowers were then placed at 15 stations in the field for approximately 4 h. This was repeated over 7 days. The absolute fitness was measured as the proportion of pollen removed from a flower. The difference between the proportion removed from the normal and trimmed flowers ($W_{sup} - W_{inf}$) was taken as a measure of the strength of selection on the flower diameter. The resource levels were not measured directly; instead, Wilson (1995) used the sum of the proportion of pollen removed from the normal and the trimmed flowers ($W_{sup} + W_{inf}$). This procedure was repeated for the 105 pairs of flowers representing each station-day.

Wilson's (1995) plots of the difference in the absolute fitness at different resource levels are constrained as the x-axis was not an independent measure of the resource levels (Fig. 5 in Wilson, 1995). This constraint allowed us to recalculate the absolute fitness of every flower from the individual points in his Fig. 5. A few points which lay outside the mathematically possible parameter space (Fig. 5 in Wilson, 1995) were omitted. The phenotypic character, flower size (z), was assigned values of 0 and 1 for the trimmed and normal flowers, respectively. The selection differential was then calculated using Equation 1.

In contrast to Wilson (1995), we found that selection was not most intense at intermediate resource levels. Instead, the selection intensity changed little between the resource levels 0 and 1 and then declined at higher resource levels (Fig. 2). The possible range of selection intensities is severely constrained for these data. This is because Wilson's (1995) resource level was the sum of the absolute fitness values of the two phenotypes and because the maximum difference in absolute fitness was 1 for the two equally frequent phenotypes. The maximum selection intensity (s) is 0.5 between resource levels 0 and 1. Between resource levels 1 and 2, the maximum s has the form:

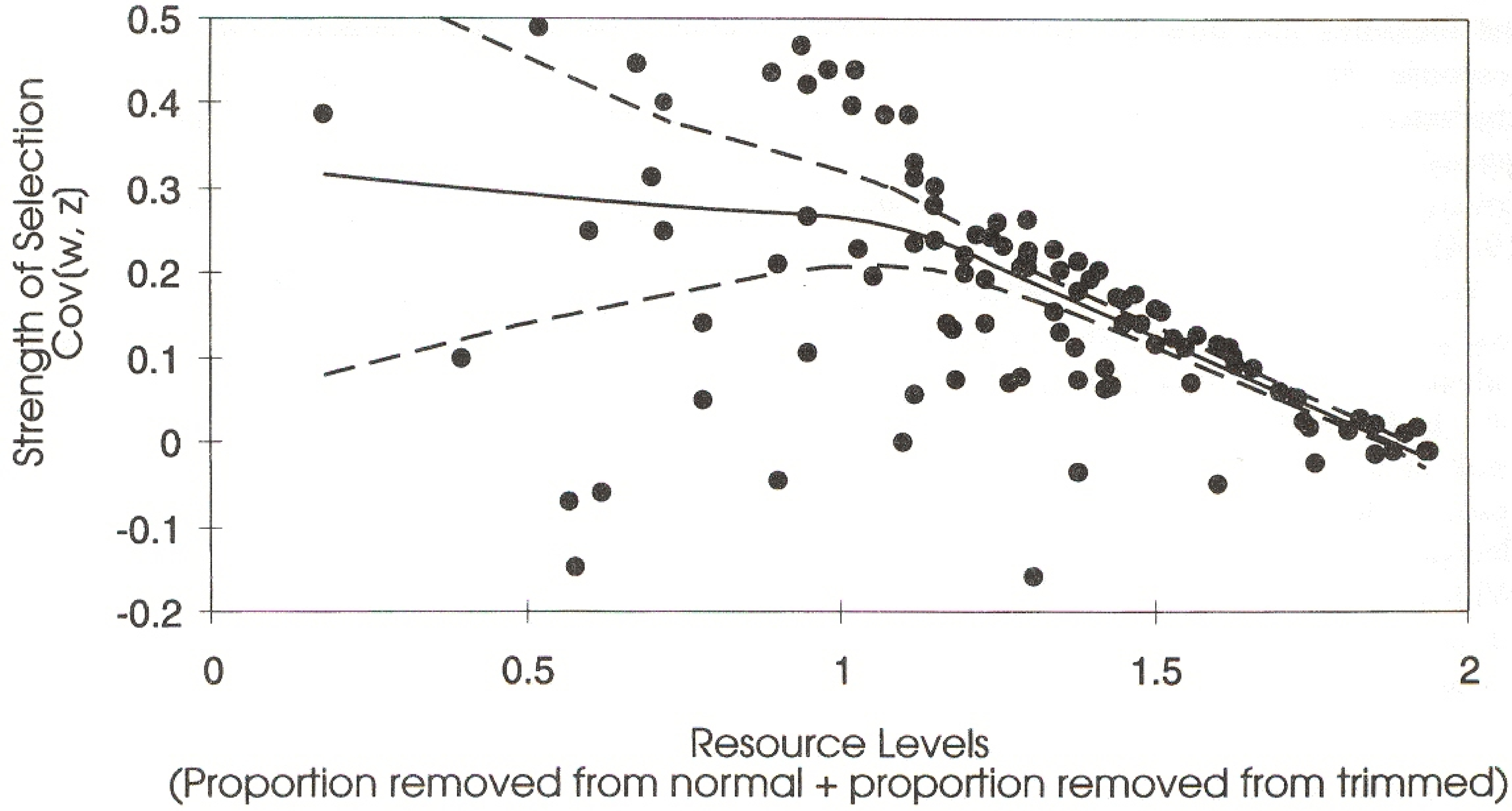

Figure 2. Variation in the strength of selection for pollen removal on artificial character variation. The strength of selection is measured as the selection differential (s). The resource levels are measured as the sum of the proportion of pollen removed from normal and trimmed flowers. The solid line represents a Lowess smoothing function applied to the points (Statistical Sciences Inc., 1993). The broken lines indicate ±2 SE of the predicted values determined from 200 bootstrap replicates using a procedure as outlined in Schluter (1988), with the exceptions that the line was a Lowess smooth and the variances were determined locally.

$$\mathrm{Max}(s) = 1 - (\text{resource level}/2) \tag{3}$$

Although the results show a decreasing trend as predicted by our reanalysis of Wilson's (1995) graphical scenario, the lack of data points at low resources, in combination with the variability in the data, result in wide confidence limits at low resources (Fig. 2, broken lines). These results are inconclusive and further research is needed to determine the realized relationship in nature.

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