

TABLE 1

Estimated error rates for bootstrap confidence limits on mean, from analysis of 3000 data sets of size $n = 30$; bootstrap applied with $B = 499$. [Source: Chapman (1985).]

Method	Error rates %		
	Left	Right	Total
Bootstrap $\bar{x} - \mu$	11	3	14
$(\bar{x} - \mu)/s$	6	5	11
\bar{x}/μ	6	6	12
Efron's percentile method	9	5	14
Exact	5	5	10

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The resampling procedures discussed by Professor Wu provide an important solution to several problems of current interest to population geneticists. Measuring natural selection in wild populations of plants and animals has long been

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an important goal in evolutionary genetics. Biologists have often used regression analysis to examine how phenotypic traits (such as body size) may influence components of fitness (such as the number of offspring produced). Recent advances in genetic theory (Lande and Arnold (1983); Arnold and Wade (1984)) advocate the use of multiple regression analysis to unravel multivariate patterns of association among characters. Most importantly, the partial regression coefficients, $\hat{\beta}$, can be directly related to the fundamental concepts of population genetic theory (see Lande and Arnold (1983)). Thus, analysis of natural selection in wild populations can be reduced to a straightforward problem in multiple regression.

In order to preserve the genetic interpretation of $\hat{\beta}$, it is required that fitness (or some component of fitness, such as survival or number of offspring) be measured on its original scale (Lande and Arnold (1983)), without any transformation to improve the behavior of residuals. While least-squares estimation of $\hat{\beta}$ does not entail distributional assumptions, most tests of significance on $\hat{\beta}$ require that the residuals conform to the assumptions of normal theory (Seber (1977)). Since transformation of the response variable is inappropriate for genetic reasons, many data sets will be confronted with heteroscedasticity or other problems with residuals (e.g., Ellstrand and Antonovics (1985); Grant (1985); Mitchell-Olds and Waller (1985); Schluter and Smith (1986)). The jackknife methods of inference proposed by Professor Wu provide a robust solution to this problem.

In my analysis of natural selection in wild populations of jewelweed (*Impatiens capensis*, a common wildflower), I have examined how variation in adult plant size (an important component of fitness) depends on several characters expressed early in the life cycle (Table 1). Since residuals in this analysis are heteroscedastic, jackknife estimates of $\text{Var}(\hat{\beta})$ permit tests of significance on the original scale of measurement, as is required for accurate prediction of evolutionary response to natural selection. I used a delete-one jackknife following Wu's Equation (4.1), due to its generally good performance and computational simplicity.

TABLE 1

Determinants of fitness in Impatiens capensis. Regression of fitness on seed weight and germination date. Predictor variables are log transformed, and the index of relative fitness is final plant dry weight, rescaled to have mean = 1.0, but otherwise untransformed. Dry weight is highly correlated with fecundity ($r = +0.96$). Standard errors and t -values are from a delete-one jackknife (Wu's equation (4.1)). Residuals are heteroscedastic; their variance increases with greater seed weight. $N = 455$, coefficient of determination = 0.179. Inclusion of more traits in the life cycle would increase R^2 . A more complete analysis will be presented elsewhere.

Variable	Coeff.	Std. err.	Std. coeff.	T^*
Constant	1.140	0.239		4.767
Seed wt.	0.350	0.098	0.144	3.580
Germ. date	-0.408	0.049	-0.395	-8.334

* $p < 0.001$.

This analysis shows that plants with more starting capital (larger seeds) or an earlier start on life (early germination date) attain larger final size, in accord with data from other plant species (Harper (1977)). Without a procedure such as Wu's resampling approach, formal analysis would have been far more difficult.

Estimation of natural selection gradients is a straightforward problem in multiple regression, but significance testing is complicated by constraints on transformations necessary for preservation of genetic interpretation and the relationship to population genetic theory. Resampling techniques provide a useful solution to this problem that is accessible to many biological practitioners.

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Professor Wu's paper raises many interesting points, only a few of which are touched upon in these comments.

If the bootstrap mentality is that the bootstrap sample bears approximately the same relationship to the empirical distribution of the data that the data bear to the distribution from which they were drawn, and if, in addition, the bootstrap process is to sample (x, y) pairs of residuals as if they were iid, then the deterministic predictor regression model studied here is not one for which bootstrap ideas ought to work well. Since the x_i 's of (2.1) may be stratified, perhaps any resampling plan should reflect this stratification. In particular,