

POPULATION DIFFERENCES IN QUANTITATIVE CHARACTERS
AS OPPOSED TO GENE FREQUENCIES

In a recent paper, Lewontin (1984) argued that no useful purpose can be served by comparing the variation of gene frequencies of local groups with variation of quantitative characters. He compared (a) the statistical significance of population differences in a quantitative character with (b) the significance of gene-frequency differences at individual loci contributing to variance in the quantitative character and showed that significance in one does not necessarily imply significance in the other. In view of this, Lewontin concluded that comparisons of these types of data serve no useful purpose. I argue here that this conclusion does not follow from his argument.

Lewontin was able to construct examples in which significant differences in a quantitative character occur without significant gene-frequency differences (or the converse). The relevance of such examples depends on the frequency with which they occur in nature, that is, the frequency with which they are produced by evolution. Lewontin, however, took population differences in gene frequencies as givens rather than as random variables. Since his analysis proceeds from assumptions about the outcome of evolution, it tells nothing about the frequency with which such outcomes are produced by evolution. For example, it does not exclude the possibility that the examples he chose are events of negligible probability. Consequently, it provides no basis for conclusions concerning the value of comparing differences in gene frequencies with those in quantitative characters.

What, then, are the prospects for using such comparisons to test hypotheses about evolution? Inference is possible provided only that the results of such comparisons can be expected to differ under different evolutionary models. As I discuss below, models of genetic drift and migration seem particularly useful as a basis for generating testable hypotheses.

Wright (1943, 1951) showed, using a model of additive gene effects at a single locus, that variation among populations in the value of a selectively neutral quantitative character is, in expectation, $\sigma_B^2 = 2F_{ST} \sigma_0^2$, where σ_0^2 is the genetic variance expected under panmixia with the same gene frequencies, and F_{ST} is the correlation among uniting gametes relative to the total population. Here, F_{ST} is a parameter of the evolutionary process (not a statistic) and depends on individual mobility and the sizes of local populations. Since it is nearly independent of the mean gene frequency for loci that are not near fixation (Rogers 1982), F_{ST} can be estimated from any sample of neutral loci. It is also possible to estimate σ_0^2 using standard methods of quantitative genetics. Thus, the right-hand side of this equation can be estimated from genetic data, if some set of genetic markers is

assumed to be neutral. Wright's result is easily extended to multiple loci if one is willing to assume that linkage disequilibrium is absent (Falconer 1960). Thus, using a model that assumes both gene frequencies and the quantitative character to be selectively neutral, one can predict variation among populations in the quantitative character from variation in gene frequencies.

Comparison of observed variation with such predictions is still an idle exercise unless one has some idea of the amount by which σ_B^2 is likely to differ from its expectation. Rogers and Harpending (1983) showed that Wright's formula holds in expectation even when the assumption of linkage equilibrium is relaxed, and obtained a formula for the standard error of σ_B^2 . The standard error does not depend on the number of loci contributing to variance in the character, and its value can be estimated from gene frequencies and data on mobility among populations. Although the standard error is usually relatively large, observed variation sometimes exceeds its expectation by many standard errors. In these cases, one can infer either that observed variation reflects something other than the effects of migration and drift on a polygenic character with an additive genetic basis or that the loci used for estimating F_{ST} are not selectively neutral. Unfortunately, as Lewontin (pers. comm.) has pointed out, it is generally impossible to distinguish the one from the other. Nonetheless, some information has been gained. This example shows that hypotheses about evolution can be tested by comparing genetic differences with those of quantitative characters. Such comparisons are one source of information concerning the forces that maintain variation among natural populations.

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LITERATURE CITED

- Falconer, D. S. 1960. Introduction to quantitative genetics. Ronald, New York.
- Lewontin, R. C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. *Am. Nat.* 123:115–124.
- Rogers, A. R. 1982. Variation of neutral characters in subdivided populations. Ph.D. diss. University of New Mexico, Albuquerque.
- Rogers, A. R., and H. C. Harpending. 1983. Population structure and quantitative characters. *Genetics* 105:985–1002.
- Wright, S. 1943. An analysis of local variability of flower color in *Linanthus parryae*. *Genetics* 28:139–156.
- . 1951. The genetical structure of populations. *Ann. Eugen.* 15:323–354.

ALAN R. ROGERS

DEPARTMENT OF ANTHROPOLOGY
UNIVERSITY OF PITTSBURGH
PITTSBURGH, PENNSYLVANIA 15260

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