

## LETTERS TO THE EDITORS

### *Testing the Heterogeneity of $F$ Values*

NEI and MARUYAMA and ROBERTSON have quite correctly called attention to a serious difficulty in testing the heterogeneity of  $F$  values in structured populations by what was come to be called the "Lewontin and Krakauer" test. We discussed this problem in our original paper (LEWONTIN and KRAKAUER, 1973, pp. 187-188), but tried to make it go away by a wave of our hands. Obviously, we were wrong in doing so, as shown by NEI and MARUYAMA's simulation and by ROBERTSON's algebra. We must also apologize for an excessive delay in the publication of these objections that has resulted from the inability of one of us (R.C.L.) to comprehend the point being made.

Unfortunately, a superficial reading of the discussion of NEI and MARUYAMA and of ROBERTSON may further confuse the potential user of our test, because neither discussion makes a clear distinction between *universes* and *samples*. Thus, the unwary reader may not realize that although populations in the universe may be correlated, populations in a random sample need not be. In order to finally clarify the issue, we list the following "do's" and "don'ts" for testing the heterogeneity of  $F$  values.

1) Our test must *not* be used if there is a hierarchical relationship among the populations of the species, *and* if the same populations appear over and over in the sample for different genes. Thus, human populations are grouped by history and migration patterns into tribes, nations, geographical races and so on, and data on these populations is taken by choosing a few populations and measuring the gene frequencies at all the loci in these same populations.

2) Our test *can* be used, even if the populations in the universe are hierarchically related, if for each locus studied, a new random sample of populations, completely independent of the previous sample, is taken *and* if the method of sampling populations is at random with respect to the hierarchical structure. That is equivalent to putting all the names of all the populations in a hat and drawing a sample out with replacement for each locus to be studied.

3) Our test is correct if there is no structure to the migration pattern among populations corresponding to the "island model" of migration. In this case, the same population *can* be sampled over and over for all the loci.

4) Our test is correct for *temporal* variation in gene frequencies within populations, as it was applied to the data of KRIMBAS and TSAKAS (*Evolution* **25**: 454-462, 1971) in the original paper.

5) Our test should *not* be used if there is reason to suppose that the underlying distribution of gene frequencies is extremely skew, as, for example, a J shaped distribution, or a U shaped distribution with one tail much higher than the other.

6) We assume that the underlying distributions of gene frequencies do not themselves give evidence on selection, but this may be false.

7) The  $\chi^2$  test for the equality of observed and expected variance may be inaccurate because the sample distribution of  $F$  is not exactly normal.

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