

## LETTERS TO THE EDITORS

### *Remarks on the LEWONTIN-KRAKAUER test*

LEWONTIN and KRAKAUER (*Genetics* **74**: 175–195, 1973) have argued that, if natural selection is important at polymorphic loci, the value of the inbreeding coefficient,  $F$ , as calculated from the variance in gene frequency over populations within a species, should be the same for all loci. The expected variance of  $F$  over loci on the assumption of neutrality plays an important part in their argument. They suggest that a conservative value for this variance, when  $F$  is estimated from  $n$  populations is  $2 \bar{F}^2 / (n-1)$ , where  $\bar{F}$  is the average  $F$  value. They consider the consequences of a structure of relationship between different populations but conclude that this has a negligible effect on the variance of  $F$ . I contend in this note that their formula may be a serious underestimate, as for instance in the treatment of human populations. A similar point has been made by NEI and MARUYAMA in the accompanying letter.

Population relationships within a species, which may arise from common origins or from migration, can be described in terms of the correlations between the gene frequencies in them. I assume that the matrix of correlation coefficients between pairs of populations is exactly known. The sampling of gene frequencies at a set of loci, each in the same  $n$  populations, is, if  $\bar{F}$  is small, equivalent to sampling a normally distributed metric character in such a way that there is a correlation between items within a sample but not between items in different samples. If  $\bar{V}_w$  is the expected variance within samples, the expected variance of  $\bar{V}_w$  is then  $2 \bar{V}_w^2 \{ (n-1)^{-1} + V_{r'} \}$ , where  $V_{r'}$  is the variance of the correlation coefficients, the expected mean of these being supposed zero. In expectation,  $V_{r'}$  equals the squared coefficient of variation of genetic distances between populations, but the two will not be equal for any set of data.

Simulation of a species, similar in structure to man, shows that information from as much as 50 loci may be necessary to get an estimate of  $V_{r'}$  valid for this purpose. Available data would suggest a value of 0.01 for the human species. For a sample of 60 populations, as used by LEWONTIN and KRAKAUER, this would give a value for the sampling variance about six times the value given by their formula. As the observed variance between loci was ten times their expectation for the sampling variance, this would throw some doubt on their claim to have shown "highly significant heterogeneity in  $F$  values for human polymorphic genes over the world."

I would stress that this increased variance is a consequence of the genetic history of the species and cannot be overcome by any sophistication of sampling at the present time.

ALAN ROBERTSON  
Institute of Animal Genetics  
West Mains Road  
Edinburgh 9, Scotland

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