

Letters

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tained also that the social sciences by their very nature are bound to be a mixture of humanistic studies, derived from the knowledge which man has of himself through being a man, and "scientific" studies, derived from careful observation, sampling of the social universe, measurement, indexing, and testable theories. I do not think, for instance, that all of economics is contained in econometrics, but I think we owe a great deal to those who pioneered in the measurement of economic variables, and our capacity to control depressions, for instance, has been substantially increased by our ability to measure at least the gross variables of the economic system. Nor do I think that political science is encompassed in the nascent discipline of politico-metrics. Historically, however, the weight in political science has been wholly on the humanistic side of the study, and important contributions are still to be made on the other side. I believe this to be especially true in the conduct of international systems where

the absence of accurate and well-sampled quantitative information is a serious handicap.

I agree entirely with Gomberg that there is room for both traditions. Where, however, as in the case of political science, the introspective and philosophical tradition has been pursued almost to the exclusion of the other, it is surely legitimate to call attention to this imbalance.

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Feedback and Nonfeedback

This is a comment on a comment [Moment, *Science* **136**, 1056 (1962)] on a comment [Li, *ibid.* **136**, 1055 (1962)] on a comment [Moment, *ibid.* **136**, 262 (1962)]. Moment considers that the "nonfeedback model" suggested by Li to account for the high degrees of polymorphism in species such as the brittlestar *Ophiolis aculeata* "assumes a stable diversity already in existence which does not change, while the pro-

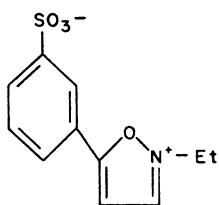
posed theory of protective variation assumes that any mutation producing a new pattern would enter the system with a selective advantage *which would decline as the frequency of the responsible gene increased*" (italics mine). On this basis, he visualizes the testability of the merits of the reflexive selection (feedback) model and the balancing selection (nonfeedback) model.

The two models may indeed yield testably different predictions, but in neither case is the selective value of a newly introduced allele unchanged as the allele increases in frequency.

In a randomly crossbreeding species, with heterozygote superiority at a locus (one form of "balancing selection"), a heterotic allele newly introduced, whether by mutation or immigration, will be present first in heterozygous condition and will remain so until its frequency, relative to population size, is high enough to create an appreciable probability that heterozygote-carriers will mate. From then on, its selective value will decrease from its initial maximum to the value determined by the equilibrium ratio of homozygotes to heterozygotes for the introduced allele, which value in turn will depend on the

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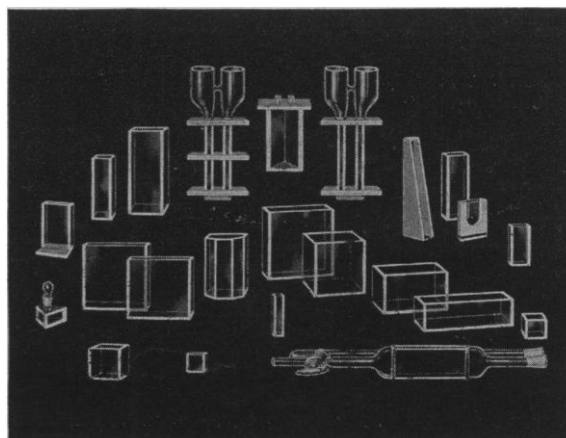
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selective value of the homozygote. In the simplest form of heterozygote superiority, let us consider a locus with multiple alleles with heterozygotes of equal selective value, arbitrarily set at 1, and homozygotes assigned selective values of less than 1 by an amount s_i , which may be different for each allele. The equilibrium frequency \hat{p}_i of any one allele A_i is given by the formula presented by Li, initially derived by Wright [in *Genetics, Paleontology and Evolution*, Jepsen, Mayr, Simpson, Eds. (1949), pp. 365-386]:

$$\hat{p}_i = 1/[s_i \cdot \Sigma(1/s_i)]$$

and the proportion of zygotes homozygous for an allele to those heterozygous for it is

$$\hat{p}_i^2/2\hat{p}_i(1 - \hat{p}_i) = 1/2[s_i \cdot \Sigma(1/s_i) - 1]$$

a value which decreases with increase in the number of alleles and in the selective disadvantage of the homozygote. Until the new allele reaches its own equilibrium frequency, it will be selectively favored, vis à vis earlier alleles already present in equilibrium proportions in both homozygous and heterozygous conditions.

Furthermore, the whole population's net fitness (\bar{W}) will be increased by the acquisition of a new heterotic allele at the locus. The early improvement in fitness will be less than the ultimate equilibrium level, due to the temporary excess of homozygotes, for the preexisting alleles. The equilibrium fitness of the population is given by

$$\bar{W} = 1 - \Sigma s_i \cdot \hat{p}_i^2 = 1 - 1/\Sigma(1/s_i)$$

where the value of each \hat{p}_i is substituted according to the earlier formula. Regardless of the value of s of the newly introduced allele, adding its reciprocal to the preexisting $\Sigma(1/s_i)$ will increase the value of the sum, decreasing the value of the fraction which is to be subtracted from 1; in other words, acquisition of a new allele at a heterotic locus makes the fitness of a population approximate more closely that of an ideal population composed solely of heterozygotes.

This increase in population fitness is similar to that arising from the addition of an allele to a system in which rarity is favored. Again employing the simplest example of this type from Li, let us consider a locus with n alleles each with frequency p_i and genotype selective values $1 - c \cdot f$, where f is the zygotic frequency of the genotype (p_i^2 for $A_i A_i$, and so on). At equilibrium, $p_i = p_1 = \dots = p_n = 1/n$. The fitness of the population attributable to this locus will be

$$\bar{W} = 1 - 5c/n^2$$

This again will increase as n increases.

Thus, the particular possibility for testing envisioned by Moment does not exist, both selective mechanisms (i) giving persistent genotypic diversity, (ii) serving to improve population fitness as the number of alleles increases, and, more importantly, (iii) giving the maximum selective advantage to the newly introduced, hence rare, allele. Only careful measurement of the change in proportions of (known) homozygotes to (known) heterozygotes in successive generations of populations initiated with arbitrary proportions will permit discrimination of the two models in any situation.

This is not intended to derogate the possibly, even probably, significant role of the selective value, to individuals and to populations, of visible diversity as such.

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