

thin film of polystyrene was removed and placed under a microscope so that areas of interest could be selected. Pieces of the replica were fixed with 'Durofix' to a specimen holder and coated with gold-palladium in a vacuum coating unit before being examined in the 'Stereoscan' microscope.

A preliminary investigation shows that quite fine detail can be resolved from the replica, as seen in the accompanying micrograph of part of the leaf surface of *Limonium vulgare*.

I thank the Cambridge Instrument Company Limited for the use of their 'Stereoscan' microscope, and Dr B. Shachar of this department for the use of the micrograph which forms part of a current project on *Limonium*.

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Received November 27, 1967.

¹ Lingappa, B. T., and Lockwood, J. L., *Phytopathol.*, **53**, 529 (1963).

GENETICS

Genetic Load of an Evolutionary Change

ACCORDING to Fisher's "Fundamental Theorem of Natural Selection"¹, the rate of change of the mean fitness of a population equals the genetic variance in fitness. If w is the fitness and V_{Gw} the genetic variance in fitness, then by Fisher's theorem

$$\Delta \bar{w} = V_{Gw}$$

Falconer² showed that if fitness varies in a way that is partially determined by variations in a character, x , then

$$\Delta \bar{x} = cov_G(x, w)$$

where $cov_G(x, w)$ is the genetic covariance of x and w . This equation Falconer calls the "Extension to Fisher's Fundamental Theorem". It will be true only if the regression of fitness and the character is linear. That is, we must have a relationship

$$w = a + bx$$

where

$$b = \frac{cov_G(x, w)}{V_{Gx}}$$

It then follows that the genetic load of any change $\Delta \bar{x}$ in the mean of the character can be calculated. We have by definition of the genetic load³

$$L = \frac{w_{\max} - \bar{w}}{w_{\max}}$$

where w_{\max} is the fitness of the most fit genotype. Now we have

$$w_{\max} = a + bx_{\max}$$

and

$$\bar{w} = a + b\bar{x} = 1 \text{ by convention}$$

It then follows directly that

$$L = \frac{cov_G(x_{\max} - \bar{x})}{V_{Gx} + cov_G(x_{\max} - \bar{x})}$$

If the change per generation in the mean of the character is known, then

$$L = \frac{\Delta \bar{x}(x_{\max} - \bar{x})}{V_{Gx} + \Delta \bar{x}(x_{\max} - \bar{x})}$$

The genetic load is an important quantity to know because it measures the intensity of natural selection. If fitness is the probability of survival, then the genetic load is the proportion of the deaths which arise from variations in fitness. Thus if L is large, a population may be in danger

of extinction. For example, suppose a continuous series of fossils shows a change to a new form. During a period of change, we can find $\Delta \bar{x}$ if we know the number of generations that has passed. x_{\max} will be the value of the character when the new form has finally become stable. \bar{x} will be the mean at some point in time in the evolutionary process. Thus we can find L at that time. Usually, evolutionary changes occur as populations adapt to new environments. In a new environment x_{\max} will have a new value. The shift of \bar{x} away from x_{\max} produces the genetic load which may be high if V_{Gx} is small. The formula for L shows why a large genetic variance helps a population to adapt to an environmental change: if V_{Gx} is low the genetic load may be high and the population may become extinct before it can adapt itself. It would therefore be interesting to compare the genetic loads in fossil populations which died out and in those that increased in numbers.

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Received November 3, 1967.

¹ Fisher, R. A., *Genetical Theory of Natural Selection* (Clarendon Press, Oxford, 1930).

² Falconer, D. S., in Meade, J. E., and Parkes, A. S., *Genetic and Environmental Factors in Human Ability* (Oliver and Boyd, Edinburgh and London, 1966).

³ Crow, J. F., and Kimura, M., *Proc. Eleventh Int. Cong. Genet.*, 495 (1964).

Rare Pseudoallelic Crossover between Two Phenotypically Identical Alleles at a Restricted Sublocus of Dumpy in *Drosophila melanogaster*

THE dumpy locus has been extensively mapped¹⁻⁴. Many of the sites within the dumpy gene have phenotypic specificity; that is, mutants of similar phenotypes map at the same restricted part of the region. A series of mutants which show an *ov* phenotype (oblique wings and thoracic vortices) were mapped to the right of *lv*¹ and to the left of *v*² (ref. 4). The *ov* mutants are viable as homozygotes and in combination with each other, except for *ov*^h, which is a facultative lethal in the homozygote but which is viable with the other *ov* alleles. The *ov*^h allele also shows a more extreme phenotype, and it is distinguishable in combination with other *ov* mutants by a more extreme phenotype. A crossover between *ov*¹ and *ov*^h was obtained by Southin⁵. The work reported here was carried out using other *ov* alleles of indistinguishable phenotype (*ov*¹ and *ov*^{52b}) in an attempt to establish critically the fine structure of the dumpy locus by obtaining crossovers between these alleles.

For the cross reported here, the virgin females used were 3-6 days old and the males were 1-7 days old. The flies were mated in groups of twenty males and twenty females and transferred to fresh medium every 3 days to establish four groups of bottles. The progeny were scored every other day, starting with the tenth day and continuing until the sixteenth day. The flies were cultured at 27°C.

Virgin females of the genotype *ed ov*¹ *cl/ov*^{52b} were mated to males *ov*^h *lv Cy*. The exceptional crossover type obtained was a female phenotypically wild type. On mating to an *ed ov*¹ *cl* male, the resulting progeny, excluding non-virginity, were six ++ *cl/ed ov cl*, and five *ov*^h *ed ov*¹ *cl*. The progeny test indicates that the genotype of the exceptional female was ++ *cl/ov*^h. It is therefore unlikely that this exceptional female arose by mutation in either of the parental chromosomes, for this occurrence would require at least two simultaneous mutational events (the probability of such an occurrence would be