Controversy abounds in mathematical population genetics. Some statements like GRIGELIN’S (1972) are sweepingly naive: «The trouble with theoretical population genetics, now as always, is that so many of its basic premises are false.» Others reflect the vitality, creativity and arguments of an active science. EDWARDS (1971) would erect a grand tombstone to the concept of an adaptive surface. A «gene-less» population genetics is proposed by LEWONTIN (1970). LEIGH (1970) refers to population geneticists as «defenders of the Pope’s demography» and exhorts them to place populations in ecological context. Indeed the latter and much more is occurring. Classical population genetics is being transformed and a new theoretical population biology is emerging reflected by the work of MAc ARTHUR (1972), LEVINS (1968), MAY (1973), and collective efforts with editors LEWONTIN (1967), MOORHEAD and KAPLAN (1967), WADDINGTON (1968, 1969, 1970), KOJIMA (1970), and GREVILLE (1972) to mention a few.

Is this population biology related to the quantitative genetic theory of agricultural selection? Historically, the studies of SEWALL WRIGHT (1921), J. B. S. HALDANE (1932) and Sir Ronald FISHER’s (1918) paper on the correlations between relatives are the genetic cornerstones of both disciplines; indeed, FISHER’s paper is basic to many of our present statistical techniques. There is a rich tradition of communication between these disciplines. More distant, perhaps, is mathematical ecology defined by VITO VOLterra (1926) and A. J. LOTKA (1925). They did not use methods founded on the calculus of probability but rather on the formulation...
of differential equations and the central problem was not intra-species variability but rather competition, predation or, more generally, the biological association among species.

Historically, animal breeding and population biology have much in common. But, how is this tradition of intellectual interchange being maintained? I want to suggest that the use of laboratory animals and, in particular the Tribolium model, serves as an important interface between the theorists and the animal breeders. This interface is critical. We need only recall C. P. Snow's Rede Lecture of 1959 and another «Two Cultures»: literary intellectuals and scientists. He wrote, «This polarization is sheer loss to us all, to us as a people, and to our society. It is at the same time practical and intellectual and creative loss, and I repeat that it is false to imagine that those three considerations are clearly separable».

A «Tribolium» SELECTION EXPERIMENT

The flour beetle, Tribolium castaneum Herbst, is an excellent laboratory organism (Sokoloff, 1972) and has been used in many types of research (King and Dawson, 1972) including quantitative genetic selection experiments (Bell, 1969). Rather than attempt to review all of this work, I want to focus attention on a particular Tribolium selection experiment.

The mating and selection procedure in this experiment (Yamada and Bell, 1969) were as follows: The population consisted of 40 single pair matings. Each pair was placed in standard medium for a 48-hour egg collection, followed by four consecutive 24-hour egg collection intervals made alternately in two different culturing media. Thirteen-day larval weights were recorded for progeny reared on both diets; however, the eight families that had the smallest mean progeny weights in one of the two diets were selected for reproduction. This procedure was repeated for 30 generations.

Selection was effective in changing mean thirteen-day larval weight; indeed, the mean weight was altered from 2222 micrograms to 283 micrograms in twelve generations. What was the genetic basis of this selection response? Our objective was to more precisely define genotypes and genotypic differences.

Subsequent investigations by Costantino, et al. (1966, 1967, 1968, 1970 and 1972) revealed that the biological basis of selection was a genetic system responsive to a specific nutritional component of the media. The selection experiment yielded a population of beetles unable to utilize unsaturated fatty acids. Furthermore, this sensitivity is inherited as an autosomal recessive gene. Clearly, continuous variation can be effectively explored by non-biometrical techniques.

The measurement thirteen-day larval weight is a known function of the particular population of Tribolium examined (as defined by the sensitive allele frequency), the concentration and degree of unsaturation of the fatty acid in the culturing medium and the relative humidity of the growing environment. A laboratory animal is now available to explore the biochemistry of fatty acid metabolism. At the other end of the biological spectrum, a model is available to obtain a perspective on the dynamics of population structure. How can this empirical data be used to study population dynamics? We will consider three possibilities.
First, for a large random mating population in which one diallelic autosomal locus is segregating and differential reproduction of the genotypes exists we can write the following equation:

$$\Delta P = P(1-P) / 2\bar{W} (d\bar{W} / dP).$$

The rate at which the frequency of the sensitive allele changes in the population is proportional to the product of the allele frequencies divided by twice the mean fitness value, times the differential of $\bar{W}$ with respect to $P$. In this case, we can predict that clinal variation in the nutrient concentration of fatty acid yields populations moving toward homozygosity for the normal allele but at different rates. Shifts of relative humidity will not alter this directional selection pattern, but will influence the rate of allele frequency change (Scully and Costantino, 1973).

Another aspect of population dynamics is how long a population is able to exist. How is the mean survival time of a population influenced by its genotypic array? The relationship between the frequency of the sensitive allele and the population's mean survival time is complex (Scully and Costantino, 1974). The maximum frequency of heterozygotes, in a randomly mating population, occurs when the sensitive allele frequency is one-half and under laboratory conditions this is the first population to go extinct. The proportion of beetles surviving to pupation is the same for the normal and heterozygote genotypes, however, time to pupation is one day less for the heterozygotes (Costantino, Rogler and Bell, 1968). This may account for the shorter survival time.

A third biological consequence of the presence of unsaturated fatty acids in the culturing medium is the delayed sexual maturity of the recessive homozygote. In a genetically segregating population, neglecting the viability data, the recessive individuals would simply not participate in the mating routine of the other two genotypes. An index of this population subdivision is the cumulative frequency of isolated recessive homozygotes after $n$ generations. In the form of an equation,

$$S(n) = n Q(o) Q(n-1)$$

where $Q(n) = Q(o)/1 + nQ(o)$, Costantino (1973). Some genetic consequences of this subdivision emerge by noting that the limit of $S(n)$ is $Q(o)$. However, several interesting questions arise: How many generations does the barrier to genetic exchange between these groups have to be maintained to have a population genetic impact? Is the delayed sexual maturity sufficient to maintain the barrier to gene exchange? What environmental shifts (dietary unsaturated fatty acids and/or relative humidity) can yield subpopulation fusion? What are the population dynamics of this partial or complete subpopulation fusion?

Yes, many question remain. But the results of this Tribolium experiment designed to study the effectiveness of selection for growth in different environments serve to demonstrate the intellectual unity of animal breeding and population biology.

**Genotypic value**

In quantitative genetic theory a population is specified by genotypic frequencies and genotypic values. The genotypic values are numbers assigned to the geno-
types under discussion and the subsequent analysis of the population examines the variation of these values (Fisher, 1918).

Kempthorne (1957) commented that in the absence of linkage the loci are statistically independent, the covariance between the genotypic values of each locus is zero and the formulas for the single locus case may be extended to an arbitrary number of loci. Does it follow then, that if this covariance is zero the two loci are unlinked?

To pursue this discussion, consider the gametes GH, Gh, gH, gh with frequencies $X_1$, $X_2$, $X_3$ and $X_4$, respectively. Random union of these gametes yields the genotypic array.

Numerical values are assigned such that the genotypic value of an individual is $y = a + b$. The variance of this linear combination is $V(y) = V(a) + V(b) + 2 \text{Cov}(a, b)$.

The two locus problems has been studied utilizing the determinant of the $2 \times 2$ gametic matrix, namely, $D = (X_1 X_4 - X_2 X_3)$. It may be informative, therefore, to examine,

$$\text{Cov}(a, b) = f \{(1 - RTD(o)}.$$  

Where $R = \text{recombination fraction between the G and H loci}$, $D(o) = \text{the initial gametic phase disequilibrium and } k = \text{the generation}$. The equilibrium state is $D = 0$ for both linked and unlinked loci. To answer the earlier question, it does not follow that if $\text{Cov}(a, b)$ is zero then the loci are unlinked. It is not necessary to assume the absence of linkage but only that the loci are in gametic phase equilibrium.

Is it valid then, to say that if a population is randommated that eventually all of the genetic material will be distributed at random, both within and between loci? More specifically, does the D-value always approach zero? The two locus selection problem has not been solved in its most general form, however, the symmetric viability model involving two loci with two alleles at each locus has been studied extensively. Many paper including Wright (1952), Kimura (1956), Lewontin and Kojima (1960), Bodmer and Parsons (1962), Moran (1964, 1968) and Karlin and Feldman (1970) show that non-trivial stable equilibria do exist. Permanent non-zero D-values may exist and hence the $\text{Cov}(a, b)$ will not be zero. Finite population size may also cause gametic phase disequilibrium (Hill and Robertson, 1968, and Littler, 1973).

Of course, a population grown under agricultural conditions may negate these factors. However, as research on two, three and eventually the N-locus problem proceeds permanent gametic phase disequilibrium may be important in evaluating the expected genetic gains from agricultural selection programs.

Another aspect of the concept of genotypic value can be closely associated with growth in Tribolium. As a first approximation, von Bertalanffy (1960) suggested that the rate of physiological processes can be expressed as a power function of body weight,

$$\frac{dW}{dt} = mw' - nw'.$$

Assuming metabolic rate is proportional to body mass, $r = s = 1$, the equation becomes $\frac{dW}{dt} = w(m - n) = wb$. Integration yields the body weight of an animal at a given time as $lnw = ln(a + bt)$. For discussion, we can place this in the context
of the two locus model just presented and see that the variance of the genotypic values $Inw$ is $V(\ln w) = V(\ln a) + V(b) + 2\text{Cov}(\ln a, b)$. Note that a covariance term is present which, of course, may be negative and also that the variance is a function of developmental time. The genotypic covariance between relatives, the components of variance and heritability estimation in this model have been probed by Costantino (1968, 1969). Work on this model is continuing in our laboratory.

**SUMMARY**

Classical population genetics is being transformed into a new theoretical population biology. Is this population biology related to animal breeding? How is the rich tradition of communication between these disciplines being maintained? These questions are probed. The results from a *Tribolium* selection experiment are used to obtain a perspective on the dynamics of population structure. Gametic phase equilibrium and developmental time are considered in terms of the genotypic value concept. The intellectual unity of animal breeding and population biology is emphasized.

**RESUMEN**

La clásica genética de poblaciones se está transformando en una nueva biología de poblaciones teórica. ¿Se encuentra esta nueva biología de poblaciones en relación con la cría animal? ¿Qué podrá hacerse para mantener la rica tradición de comunicaciones entre estas disciplinas? Este trabajo trata de determinarlo. Los resultados de un experimento de selección en *Tribolium* han sido empleados para obtener una perspectiva sobre la dinámica estructural de la población. El equilibrio de la fase gamética y el tiempo de desarrollo se consideran en términos del concepto sobre el valor genotípico. La unidad intelectual entre la cría animal y la biología de poblaciones se contemplan especialmente.

**RESUME**

La génétique classique de populations est en train de devenir une nouvelle biologie de populations théorique. Cette nouvelle biologie de populations, est rapportée à l'élevage animal? Qu'est-ce qu'on pourrait faire pour maintenir la riche tradition de communications entre celles-ci? Ce travail essaie de la déterminer. Les résultats d'une expérience de sélection en *Tribolium* ont été employés pour obtenir une perspective sur la dynamique se rapportant à la structure de la population. L'équilibre de la phase gamétique et le temps de développement sont considérés comme concept sur la valeur génotypique. L'unité intellectuelle entre l'élevage animal et la biologie de populations est spécialement considérée.

**REFERENCES**


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