

# Perspectives

## Anecdotal, Historical And Critical Commentaries on Genetics

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### SEWALL WRIGHT'S "Systems of Mating"

**William G. Hill**

*Institute of Cell, Animal and Population Biology, University of Edinburgh, Edinburgh EH9 3JT, Scotland*

NINETEEN ninety-six marks the 75th anniversary of the publication in this journal of the series of five papers by SEWALL WRIGHT (1921a–e) on "Systems of Mating." The definitions, methods, and results he presented in these and two other papers published at about the same time (WRIGHT 1920, 1922) have had a major and lasting effect on the theory and application of population genetics. My aim in this paper is to review the work in these papers and to consider their influence mostly, but not exclusively, on animal improvement, but without being comprehensive in either topics or references. Indeed, were I to cite only WRIGHT's works that developed ideas from his 1921 papers, there would be a long bibliography, and it is easy to see why the reference lists in WRIGHT's own papers looked so ego-centric. PROVINE's (1986) excellent biography provides a full review of WRIGHT's role in genetics and evolutionary biology, while WRIGHT's (1968–1978) four-volume treatise describes much of his work and views.

**Background:** WRIGHT had a broad training in biology and came into genetics as a graduate student of Castle at the Bussey Institute of Harvard University. He worked mainly on coat color patterns in guinea pigs for his Ph.D., which stimulated among other things his interest in multilocus inheritance and interactions. His first job, from 1915, was as Senior Animal Husbandman at the U.S. Department of Agriculture in Washington, with a particular remit to analyze extensive data on traits such as color and body weight collected by ROMMEL on inbred lines of guinea pigs to test the value, or otherwise, of using inbreeding in animal improvement programs. WRIGHT also undertook a substantial amount of biometrical work and a widespread correspondence on animal breeding. It was, therefore, important that he could interpret data on quantitative traits from both inbred lines and livestock populations. These and other problems he tackled in the "Systems of Mating" series while still with the U.S. Department of Agriculture.

The Mendelian theory of inheritance had become

widely accepted for discrete characters, but controversy remained as to the basis of variation in continuous traits (PROVINE 1971). WEINBERG (1910), FISHER (1918), and WRIGHT (ignorant of the work of the other two) set what became the accepted framework. WRIGHT also successfully addressed the problem of how genotype frequencies change in populations as a result of nonrandom mating based on relationship or performance. Previous analysis of, for example, full-sib mating had involved the laborious evaluation of genotype probabilities, whereas WRIGHT's methods were computationally simple and general. They were then and are still not easy to understand, partly because of his use of path coefficients with analysis in terms of continuous variables rather than genotypes and partly because critical points were dealt with very tersely.

WRIGHT had invented and used path coefficients before the 1921 papers. The initial steps in their development, to describe general and specific size factors influencing bone size of rabbits, had been taken while he was a graduate student. He had computed all partial correlations, but found that such an analysis provided no understanding of causation. By computing the path coefficients, which in statistical terms are standardized partial regression coefficients, he aimed to describe the effect of causal components. In 1918 WRIGHT published his first version of the method of path coefficients (although not calling them such), partitioning variation in length of an individual bone to independent hereditary causes including general size, length of leg bones, length of hind limbs, and an independent term.

In the first paper in which he undertook a genetic analysis of a quantitative trait, WRIGHT (1920) used path coefficients to analyze data on the proportion of white color in spotted guinea pigs, and attributed variation to three principal causes: heredity ( $h$ ), environment common to litter mates ( $e$ ), and other factors, largely "ontogenic irregularity" or developmental noise ( $d$ ). The quantity  $h$  is the path coefficient from genotype to phenotype and equals the correlation between them. WRIGHT shows that  $h^2$  is the proportion of variance attributable to heredity; this is, of course, the heritability,

*Address for correspondence:* William G. Hill, Institute of Cell, Animal and Population Biology, University of Edinburgh, West Mains Rd., Edinburgh EH9 3JT, Scotland. E-mail: w.g.hill@ed.ac.uk

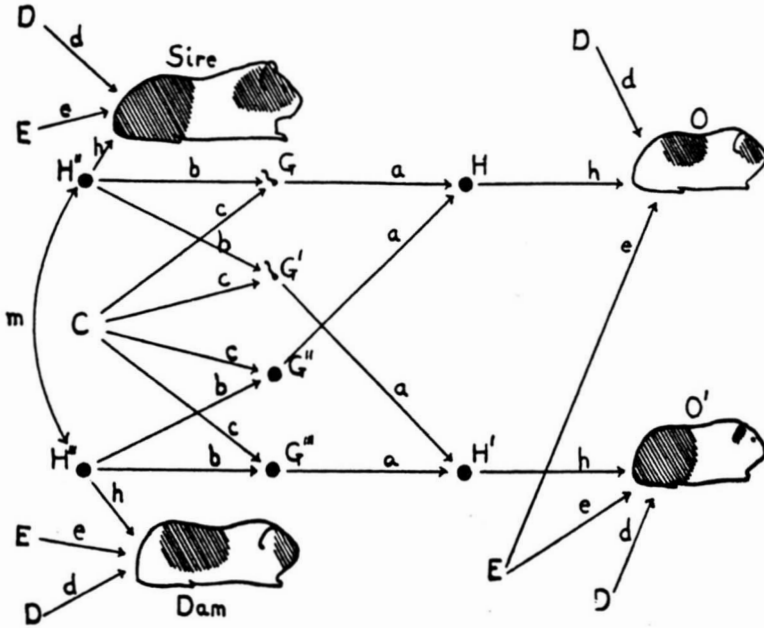


FIGURE 1.—WRIGHT'S famous diagram from his 1921 papers. The original legend is included.

FIGURE 2.—A diagram illustrating the relations between two mated individuals and their progeny.  $H, H', H''$  and  $H'''$  are the genetic constitutions of the four individuals.  $G, G', G''$  and  $G'''$  are four germ-cells.  $E$  and  $D$  represent tangible external conditions and chance irregularities as factors in development.  $C$  represents chance at segregation as a factor in determining the composition of the germ-cells. Path coefficients are represented by small letters.

a term that he did not coin (see BELL 1977 for a discussion). In his partition of variation, WRIGHT had a term for common environment of sibs but not dominance, whereas FISHER (1918) had one for dominance but not common environment. WEINBERG (1910) had already included both (see translation by MEYER in HILL 1984), but had been ignored!

**The "Systems of Mating" series:** Although the path diagram for coat color in guinea pigs first appears in the 1920 paper, it returns in part I of the better known "Systems of Mating" the following year with one significant change, which took WRIGHT beyond the work of WEINBERG and FISHER, the addition of a term ( $m$ ) describing the correlation of the parents, which enabled him to analyze the effects of nonrandom mating. The figure from WRIGHT (1921a), surely one of the best known diagrams in biological science, is reproduced here (Figure 1). Important definitions in the 1921 paper are indeed obscure. He introduced and defined  $f$  (called the inbreeding coefficient in a later paper) as follows (p. 118):

If there is assortative mating from any cause, there will be some correlation between the gametes which unite. Represent this correlation by  $f$ .

Later (p. 119) he introduces  $m$ :

The correlation between the egg and the sperm depends on that between the parental formulae which we will represent by  $m$ . . . . The correlation between the parents is greater or less than that between their genetic constitutions, depending on whether the assortative mating is based on somatic resemblance or consanguinity.

For these two cases he gives formulas relating  $f$  to  $m$ ,

thereby setting the basic framework for the analysis of the effects of inbreeding and assortative mating on the correlation among relatives. In particular, WRIGHT computes how, for a locus with two equally frequent alleles, the frequency with which  $A$  alleles unite with  $A$ ,  $a$  with  $a$ , and  $A$  with  $a$  depends on the correlation  $f$  and shows that the percentage of heterozygosity is  $p = (1 - f)/2$ . The result is then used to show how  $h^2$  depends on heterozygosity and thus  $f$ . WRIGHT thereby made the critical transitions from a correlation  $f$  of continuous variables to a function  $p$  of frequencies of discrete genotypes and back to another quantitative measure  $h^2$ .

Subsequently (p. 121), WRIGHT defines  $m$  more explicitly as "the correlation between the genetic constitutions of the parents" and provides many formulas, including that for the correlation between full sibs when there is nonrandom mating, *i.e.*,  $m \neq 0$ . [Unfortunately, his results for dominance were incorrect and were corrected subsequently (WRIGHT 1931 and by hand on the reprinted copy of the 1921 papers issued by Iowa State College Press). FISHER (1918) had given the right formulas for the dominance contribution to the sib correlation.] WRIGHT also points out that if an expression can be provided for  $m$ , the correlations and path coefficients in each generation can be expressed in terms of those in the previous generation.

This he does in the second paper (WRIGHT 1921b), initially deriving results for repeated brother-sister matings: "As the reader may feel some doubt as to the validity of the method of analysis used here, it will be well to begin with a case in which the results have already been determined by direct methods. . . . In this

case the correlation between mates is simply that between a brother and sister, produced by the preceding generation." He gives a recurrence formula for  $m$ , which he shows can be written in terms of  $f$  in preceding generations ( $f'$  and  $f''$ ) as the now familiar result  $f = (1 + 2f' + f'')/4$ . WRIGHT provided such recurrence formulas for a range of repeated mating systems and thereby essentially solved the problem of computing the consequences on genotype frequencies for mating systems based on consanguinity.

The third paper deals with assortative mating based on phenotype, in which WRIGHT (1921c) showed that, in contrast to mating of relatives, the consequences depend on the number of loci affecting the trait. Although there may be little increase in homozygosity when the nonrandom mating is continued, the variance in the population can increase greatly with very strong positive assortative mating. The fourth paper is on selection; although the mathematical results have had less influence than those in the first three papers, significant conclusions are drawn. For example, he introduces the idea of selecting for an intermediate fixed phenotype and shows this does not lead to a substantial reduction in variability of the trait, just as for perfect negative assortative mating, even if the trait is completely heritable (WRIGHT 1921d). The final paper comprises a review and a summary (WRIGHT 1921e, pp. 177–178) of the series:

It will be seen that all of the systems of mating have their advantages and disadvantages. Close inbreeding automatically brings about fixation of type and prepotency. Intermediate types are fixed as readily as extremes. It is the only method of bringing to light hereditary differences in characters which are determined largely by factors other than heredity. On the other hand, close inbreeding is likely to lead toward reduced fertility, size and vigor.

Matings between relatives more remote than first cousins have little significance as inbreeding, except in so far as there is continued breeding within a population of small size.

Assortative mating and selection can lead to fixation of extreme types only and are not very efficient in this respect. Selection, however, is the only means of permanently changing the relative proportions of the various genes present in the original stock. It is an essential adjunct of the other systems as means of improvement.

Assortative mating leads to the greatest diversification of the population as a whole, and thus is practically always accompanied by selection either in nature or in live-stock breeding. Under conditions such that all progeny are to be saved for breeding, this diversification of the population is a disadvantage. Disassortative mating is the method which best holds the whole population together, pending the fixation of the average type by close inbreeding.

**Inbreeding and relationship:** In the following year, WRIGHT (1922) formally defined the correlation of uniting gametes,  $f$ , as the inbreeding coefficient and extended the ideas to relationship, defining the coeffi-

cient of relationship of two individuals as the correlation between them. He is not explicit as to what measure on the individuals is being taken, but the formulas imply it is the sum of values of the gametes, regarded as quantitative traits, of an individual. Hence the relationship is referred to by LUSH (1948) as the correlation of genic values. The relationship  $r_{sd}$  between sire ( $S$ ) and dam ( $D$ ) in terms of their own and their offspring's ( $O$ ) inbreeding coefficient is given by

$$r_{sd} = 2f_o / \sqrt{(1 + f_s)(1 + f_d)}$$

and the numerator of the expression (to which we shall return) is the covariance of genic values. WRIGHT (1922) showed how to compute the inbreeding coefficient of  $O$  from a general pedigree by the now famous formula

$$f_o = \sum (1/2)^{n+n'+1} (1 + f_a)$$

where summation is over all paths, of length  $n$  and  $n'$  from the parents of  $O$  to the common ancestor  $A$  with inbreeding coefficient  $f_a$ . [Subsequently, WRIGHT (1951) changed the algorithm but not the result by simply counting the total number,  $n + n' + 1$ , of *zygotes* in the path, a form that can also be applied to sex-linked loci.] These formulas are sufficient to enable inbreeding and relationship to be computed for all pedigrees, and in the 1922 paper WRIGHT used them to compute the inbreeding coefficients for animals of the Shorthorn breed, finding one bull, Comet, with an inbreeding coefficient of 0.47. The impact that high values such as this had on WRIGHT's ideas on both animal breeding and evolution is discussed later. WRIGHT subsequently contributed further both to methods of calculating the inbreeding coefficient, showing how it could be estimated by sampling rather than taking all paths back in the pedigree (WRIGHT and MCPHEE 1925), which was useful in analysis of livestock breeds, and to its prediction for specified mating systems.

In the "Systems of Mating" and associated papers, WRIGHT had made major advances: he had introduced the ideas of path coefficients and of the inbreeding coefficient, given a formal definition to relationship, shown how to compute changes in inbreeding and heterozygosity, quantified the effects of assortative mating, and more. These are fundamental to any modern population genetics course and were a great achievement. WRIGHT's inbreeding coefficient, both as a concept and, as he showed, an easily computed quantity, is arguably his most important, widely used, and lasting single technical contribution to population genetics, even though alternative definitions and derivations were obtained subsequently and FISHER (1949) wrote a whole book on *The Theory of Inbreeding* without citing WRIGHT. Further, the inbreeding coefficient was noncontroversial, in contrast to some of WRIGHT's later ideas such as the shifting balance theory.

**Influences on animal breeding:** I now take up some threads from the papers. I shall deal mainly with implications for animal improvement, where his ideas and methods had ready application, and in some circumstances WRIGHT's definitions led to more natural application than others. Further, his work on animal breeding also had an impact on his views on evolutionary biology, on which he concentrated after his appointment to the University of Chicago in 1926. The photograph of WRIGHT (Figure 2) was taken in 1928, shortly after his move.

Although WRIGHT never had a significant research group, he greatly influenced JAY L. LUSH of Iowa State College (later University) who became the leading figure in the genetics of livestock improvement and perhaps WRIGHT's most important disciple. LUSH had previously corresponded with WRIGHT and then attended his classes in Chicago immediately after moving to Iowa in 1930. LUSH established a major school at Ames, where he and colleagues trained many who were to become influential in animal breeding in the United States and abroad. LUSH's book *Animal Breeding Plans* (1937 and later editions) was nontechnical but had a big impact on thinking. He prefaced it, "The ideas in this book have been drawn freely from the published works of many persons, I wish to acknowledge especially my indebtedness to Sewall Wright for many published and unpublished ideas upon which I have drawn, and for his friendly counsel." LUSH's (1948) mimeograph *The Genetics of Populations*, which was widely read but unpublished until recently (1994), included a formal exposition of much of WRIGHT's work, particularly that relating to animal improvement. "Systems of Mating" and other important papers were reprinted in 1949 and 1958 by Iowa State College Press with a preface by LUSH and some handwritten corrections by WRIGHT.

The quantitative genetics and animal breeding group in Edinburgh were also influenced directly by WRIGHT (see FALCONER 1993). ALAN ROBERTSON spent some time with him in 1947 while converting from chemist to geneticist. Subsequently WRIGHT visited Edinburgh for a year (1949–1950) and taught a course, much of it summarized in a review paper (WRIGHT 1952) that was a forerunner to his treatise published later.

The method of path coefficients was used almost exclusively by LUSH, but now is little used in animal breeding research. It was developed at almost the same time as FISHER (1918) invented the analysis of variance to partition variability between hereditary and nonhereditary causes. The path diagram provides a nice picture of the model and many quantitative problems can be solved with the method, and it is featured in LI's (1955) text on population genetics. Unless people were schooled in path coefficients to the exclusion of variance/covariance methods, however, they generally used the latter. Indeed, at Ames, applied statistics was taught by SNEDECOR from his book, and the more fun-



FIGURE 2.—SEWALL WRIGHT in 1928, shortly after moving to the University of Chicago.

damental genetic statistics by KEMPTHORNE, both of whom were very much committed to use of the analysis of variance. KEMPTHORNE (1957) included, however, an expository chapter on path coefficients in *An Introduction to Genetic Statistics*. Path coefficient methods did not feature significantly in the 1940s to 1960s in other centers of quantitative genetics and animal breeding research and teaching: Berkeley (LERNER, DEMPSTER), Birmingham (MATHER, JINKS), Edinburgh (ROBERTSON, FALCONER, REEVE), Ithaca (HENDERSON), Raleigh (COMSTOCK, ROBINSON, COCKERHAM). In what is probably the most widely used text on quantitative genetics, FALCONER (1960 *et seq.*) makes no use of path coefficients.

**Definitions of inbreeding and relationship:** WRIGHT's definition of inbreeding coefficient (variously  $f$  or  $F$ ) in terms of a correlation is obscure to population geneticists not used to thinking in terms of quantitative traits. What he did was to attach implicit values to each gamete, which are sums of the effects of the genes on some arbitrary trait, essentially assuming what has become known as the infinitesimal model (BULMER 1980) or, alternatively, attaching to an arbitrary locus assigned allelic values of 1 and 0. For this reason, MALÉCOT's (1948) definition of inbreeding as probability of identity by descent is less

opaque to population geneticists or students. Both alternatives have specific useful features, however: WRIGHT's can naturally take negative values, for example, when parents are less related than random, which leads on to his partition of the correlation of uniting gametes using his  $F$  statistics (WRIGHT 1951). MALÉCOT's but not WRIGHT's is readily extended to include mutation, for example, to compute heterozygosity for infinite alleles (KIMURA and CROW 1964), and to more than one locus, for example, the probability that alleles are identical by descent at both of a pair of loci. This is important in computing covariances among relatives in which contributions from epistasis (see KEMPTHORNE 1957) are included. Similarly, such higher-order terms are essential when computing probabilities of identity and correlations among inbred relatives (COCKERHAM and WEIR 1972).

**Prediction of breeding value:** There are various threads to developments in animal breeding that date back to or rely heavily on the "Systems of Matings" papers. Perhaps that of greatest current utilization is in breeding value prediction, to which WRIGHT's definitions of inbreeding and relationship in terms of covariances and correlations transfer directly. In livestock improvement, the objective is to select animals expected to have the highest performing offspring, so that accurate prediction of breeding value is of fundamental importance. The problem is, however, that selection may have to be practiced among animals that are not directly comparable on performance either in space or time and have different amounts of information available on them or their relatives. In dairy cattle, bulls are used in artificial insemination unequally over many herds, and cows to rear the next generation of bulls have to be chosen among herds. Furthermore, it is necessary to combine information on several traits of different economic importance. These problems were seen by LUSH (see 1937, 1948 for details) among others. He showed how records from different individuals, *e.g.*, the animal itself, its sibs and progeny, differed in their information content and how a progeny mean should be regressed to allow for different numbers of records. His colleague HAZEL (1943) showed how information on multiple traits should be combined into a selection index, basing his arguments on a path coefficient approach to multiple traits.

The problem of comparisons of dairy sires having daughters distributed unequally over many herds required both statistical and computational input. This was first provided through the contemporary comparison (ROBERTSON 1953), in which environmental effects were eliminated in a cross-classified structure by assuming that sires of contemporaries were randomly sampled. The problem of simultaneously estimating the breeding value of all animals to take account of nonrandom usage became more important as progeny test results became used by breeders. The principles of mod-

ern procedures are due to HENDERSON, initially in his 1949 Ph.D. thesis while a student of LUSH at Ames, where he saw how to simultaneously estimate fixed effects (*e.g.*, environmental groups) and predict random effects (*e.g.*, breeding values); he elaborated later in the context of dairy cattle (HENDERSON 1974). The method, which he called best linear unbiased prediction (BLUP), became applied to dairy sire evaluation in the 1970s, but with computing kept to a minimum by predicting breeding values only of sires and ignoring other relationships.

The additive genetic contribution to the variances and covariance of all animals in a population can be described by the numerator term in WRIGHT's definition of relationship. This could be readily evaluated in a sequential manner to construct a table or matrix. (In 1963 I attended LUSH's course at Ames based on *The Genetics of Populations*, in which he illustrates the computation of the genic covariance. He described the construction of a "covariance chart," which he used extensively, for one is so labeled in my handwritten notes and there is a separate mention that it is a covariance matrix.) It is more commonly described, to follow HENDERSON's usage, as the *numerator relationship matrix*. For example, the covariance of records of a pair of half sibs, otherwise unrelated, is  $V_A/4$ , and the variance of inbred individuals is  $(1 + f)V_A$ , where  $V_A$  is the additive genetic (or genic) variance. In general, using, as is the animal breeding custom,  $\mathbf{A}$  to denote the matrix and  $a_{ij}$  its elements, the (co)variance of the performance of two individuals is  $a_{ij}V_A$ . [The numerator relationship is twice the *coefficient de parenté* of MALÉCOT (1948).] HENDERSON showed how this covariance matrix featured in a simple way in generalizations of his mixed model or BLUP equations. Evaluation of the equations requires the inverse of the numerator relationship matrix, which needs major computation to get from  $\mathbf{A}$  if many animals are being evaluated. HENDERSON (1976) found, however, that the elements of  $\mathbf{A}^{-1}$  could be evaluated by simple steps directly from the pedigree. This enabled the computations for the so-called animal model, which includes an equation for each animal, to be undertaken with all the data, even for dairy populations of millions of animals. The methodology is widespread and standard for breeding programs of most species of livestock and has spread into improvement of trees. Thus, WRIGHT's concept of relationship and inbreeding in quantitative genetic terms corresponds directly to the animal model BLUP framework, and the pedigree of the method was undoubtedly from WRIGHT to LUSH to HENDERSON.

Current methods of estimating genetic variance components, heritabilities and correlations are based on maximum likelihood, specifically on restricted maximum likelihood (REML) developed primarily by THOMPSON (1973 *et seq.*) for quantitative genetic application, although there is increasing use of Bayesian ideas. In these meth-

ods, general data structures including information on animals of different generations are handled by using the numerator relationship matrix to specify the covariance between all observations. Critically, as for the development of BLUP, increased computing power has facilitated the utilization of theoretical developments.

**Population size:** WRIGHT had a great interest in the importance of the size and mating structure within populations on the opportunities for and rates of genetic improvement by artificial selection and the beneficial and harmful effects inbreeding might have. In the "Systems of Mating" series (1921b), he computed rates of inbreeding for different fixed mating structures in closed populations and subsequently used his methods to estimate levels and rates of inbreeding in livestock populations, an activity that persists to this day. The schemes he computed, such as quadruple second cousin matings, are what have become known as maximum avoidance schemes, in that inbreeding is delayed for as many generations as possible but at the expense of higher long-term rates of loss of heterozygosity when family sizes are equal (KIMURA and CROW 1963; CABALLERO 1994).

WRIGHT later (1931 *et seq.*) developed the idea of effective population size ( $N_e$ ) and showed how to compute it for a range of breeding structures. WRIGHT's  $N_e$  has, like his  $f$  (or  $F$ ), become a standard for comparison among breeding programs. While WRIGHT found very high levels of inbreeding in some of the breeds he studied, there was concern among breeders in the 1950s and subsequently that the concentration of genes possible with the introduction of artificial insemination would lead to an increase in rates. This did not happen initially because a wider pool of breeding stock was tested in artificial insemination than in traditional pedigree programs; but as selection has become more intense and international movement of livestock more common, rates of increase in average relationship are rising in the world's major breeds of dairy cattle, with inbreeding lagging by avoidance of mating relatives. In particular, the high weight given to family information in modern breeding programs through the use of selection indices or BLUP means that rates of inbreeding are likely to be much higher than with selection on individual phenotype. ROBERTSON (1961) initially identified the effects of selection on rates of inbreeding, and formulas have been developed recently by WRAY, THOMPSON, WOOLLIAMS, and colleagues to give more precise answers and to allow for selection using combinations of individual and relatives' performance (see CABALLERO 1994 for a review). There is a conflict in that maximizing rates of short-term response leads to increasing rates of inbreeding and loss of heterozygosity, thereby reducing long-term improvement from within population selection.

**Breeding structure and shifting balance:** The analyses of breeding structure that WRIGHT conducted while

working for the Department of Agriculture had a very significant influence on his views not only on animal improvement but also on the evolutionary process, for the shifting balance theory was developed before he moved to Chicago and published "Evolution in Mendelian Populations" (WRIGHT 1931). Many years later, WRIGHT (1978) recalled that he was impressed by four observations: the large responses obtained by CASTLE to high and low selection for extent of color in the coats of hooded rats, which showed the power of mass selection but also revealed unfavorable correlated responses in mortality and fecundity; the results of his Ph.D. thesis on the interaction among genes for color and pattern in the coat of guinea pigs, which indicated that an organism must be viewed as a vast network of interacting systems; the great variation found for many traits among inbred strains of guinea pigs, which showed the effectiveness of simple genetic sampling in creating diversity; and the high levels of inbreeding and high relationship to particular animals found in the Shorthorn breed of cattle, which "yielded the proper balance between the extreme plasticity of the original heterogeneous Shorthorn stock and the more complete fixation of the characters which would have resulted from closer inbreeding." These observations led him to suggest both the shifting balance theory of adaptive evolution and the way to improve livestock breeds. Improvement would occur most rapidly in small populations, where favorable new epistatic combinations of genes would arise, and these would spread by migration or between-line selection. For further discussion, see HILL (1989) and CROW (1990).

In animal improvement programs, there are many cases in which a subset of a population has improved rapidly and others have caught up by introgression. For example, North American Holstein cattle originated from Europe 100 years or so ago, but underwent more rapid improvement for milk production than the European populations and have, over the last two decades, largely replaced the latter. There is little or no evidence that this or any other example is conferring benefits through epistatic interactions; what is striking is the almost complete lack of detectable interactions among, for example, sire families when tested in the United States or abroad in different populations and environments, so that there is a major international trade in dairy cattle semen.

There have been a number of laboratory experiments to evaluate improvement programs by use of WRIGHT's ideas on population structure. These have not usually been effective, in that simple mass selection in a large population has typically outperformed a program of selection in small lines with subsequent between-line selection, at least partly because the experiments have used mainly additive traits (see HILL and CABALLERO 1992 for review). Direct experimental evaluation of the shifting balance theory by interdemec selection and mi-

gration has, however, revealed some response indicative of nonadditive effects (WADE and GOODNIGHT 1991).

There was much interest in the 1940s and 1950s in inbreeding and crossbreeding programs in animals to utilize heterosis following their success in hybrid maize, with the most obvious potential application being in poultry breeding for table egg production. The low reproductive rate of even this species compared with maize and the long number of generations required to obtain high levels of inbreeding implied that each round of selection was slow and expensive, and selection intensities were low. While there is extensive use of crossbreeding to utilize heterosis and different properties of breeds, *e.g.*, specialized sire and dam lines with high performance for traits of growth and reproduction, respectively, there is not much use of inbreeding and between-line selection in animal improvement programs.

Thus, it is the case that, for one reason or another, animal improvement has been in recent decades and still is very much based on additive genetic change. Consider, for example, broiler chickens, where intense selection on juvenile growth has been practiced for many decades. In a recent comparison of "1957" broilers, available as an unselected control stock, and 1992 broilers, HAVENSTEIN *et al.* (1994) found that at 8 weeks of age the modern strain was almost four times heavier. Nor is there evidence that levels of heritability are declining appreciably because of selection and inbreeding. Therefore, the ideas of WRIGHT's shifting balance theory, which he elucidated at least in part to explain the apparent success of breeding programs, have, as far as I know, had little impact on livestock improvement as practiced by professional geneticists and the companies they advise (but, of course, details of programs in commercial companies are not public). Furthermore, I have surmised (HILL 1989) that had WRIGHT known of the effectiveness of direct selection in large populations of livestock, he would not have arrived at and championed the shifting balance theory.

**Concluding remarks:** Even if WRIGHT had done nothing else in his long research career, his standing would be recognized for the major technical impact he made in his series on "Systems of Mating." Who cannot have wished to invent something so simple and important as the inbreeding coefficient? No doubt someone else would have developed it later, but he was first.

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