

Sewall Wright (1889–1988)

SEWALL Wright, the last of the triumvirate of Fisher, Haldane and Wright who brought about the marriage of darwinism and mendelian genetics, died on 3 March of complications following a fall on the ice when walking near his home in Madison, Wisconsin. He was 98.

Today, when the union of evolution theory and population genetics is a long-established orthodoxy, it is hard to appreciate that the early mendelians engaged in a bitter debate with the darwinians about the mechanism of evolution. The latter held that evolution proceeded by the natural selection of continuously varying traits; the former that large, discrete mutations, obeying Mendel's laws, were the raw material of evolution, and that continuous variation was irrelevant.

Thanks to the work of Fisher, Haldane and Wright, carried out mainly in the period 1920–30, we now see that this argument was based on a misunderstanding. It is true both that mendelizing mutations are the raw material, and that natural selection within populations, often of continuously varying traits, is the main cause of evolution. To show this required that the behaviour of genes in populations be worked out mathematically. Wright's 1931 paper, *Evolution in Mendelian Populations*, was a major contribution to elucidating this problem.

Although it is customary to refer to the three architects of population genetics as if they were engaged in a joint enterprise, in fact they worked independently. This had its drawbacks, as it led to quarrels that may have been enjoyed by the main protagonists, but were confusing for their students. But it had the advantage that three rather different pictures of evolution emerged, each of which may be an aspect of the truth. Wright's particular contribution was to emphasize the importance of population structure. The world does not contain effectively infinite populations, in which any male can mate with any female; instead, populations are divided into many partly isolated groups, or 'demes'. Thus chance events play an important part. In contrast, Fisher held that most populations were so large that chance changes in gene frequency, so-called genetic drift, would be overwhelmed by the effects of selection. Wright displayed remarkable originality — one could almost say idiosyncrasy — in working out the consequences of the demic structure of populations.

His particular view of evolution can best be understood in the light of two features of his early career. First, attempting to apply genetics to animal breeding, he made a detailed study of inheritance in guinea pigs, and second, he studied the breeding of shorthorn cattle. The first of these enterprises persuaded him of the

importance of epistasis — that the effect of genes at one locus depends on what genes are present at other loci. From the shorthorns, he learnt the importance of group structure: in particular, he was struck by the fact that, if a particular herd achieves success, its genes could be spread (mainly by the bulls) through the breed. From these two insights, his 'shifting-balance' theory of evolution emerged.

The theory is as follows. Because of epistasis, evolutionary progress may be impossible in a large random-mating population. Suppose, for example, that the present genotype, at two loci, is *ab*, and that it would be advantageous to evolve to *AB*, but the intermediates *aB* and *Ab* are of lower fitness. A large population cannot make the jump, but the change could occur by chance in a small deme. In a species consisting of many demes, the transition has a good chance of occurring somewhere. If it does, the new genotype can spread through the species, as the

genotype of a successful herd of cattle can spread through the breed.

Wright's shifting-balance theory is still controversial. It is a legacy of the debate between Wright and Fisher that the theory is less popular in Britain than in the United States. But there is no question of the importance of his contributions to population genetics, in particular to the theory of inbreeding, of genetic similarity between relatives, and to the distribution of gene frequencies in populations. Perhaps his most enduring legacy is an image, rather than an algebraic formula, although he left us plenty of the latter. The image is of populations climbing peaks in an adaptive landscape.

Wright continued to work to the end. The last volume of his great textbook, *Evolution and the Genetics of Populations*, was published in 1968, when he was 79 years old. He had a paper in press in the *American Naturalist* when he died.

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Particle physics

New phase for an old theory?

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COLLISIONS between heavy ions with just sufficient energy to overcome their mutual electrostatic repulsion reveal a series of peculiar phenomena, involving unexplained line structures in the energy spectra of emitted positrons and correlated electron-positron and photon-photon signals. Although many have speculated about the origin of these effects, no satisfactory solution is yet in sight. The most intriguing explanation for the data, suggested recently by three groups^{1–3}, is that the phenomena are the manifestation of a new phase of the theory of electromagnetic interactions, quantum electrodynamics (QED). Because QED is a venerable theory, whose predictions are tested to eight decimal places, this suggestion has been greeted with considerable scepticism by many theorists.

Early experiments at the EPOS^{4,5} and ORANGE^{6,7} collaborations at GSI-Darmstadt revealed a sharp line structure near 350 keV, with a linewidth less than 100 keV, in positron-emission spectra of heavy-ion collisions. The line position is apparently independent of the total charge $Z = Z_1 + Z_2$ of the colliding ions. This feature has been confirmed in further experiments carried out by both collaborations. Various sharp lines appear in the sum-energy spectra, recorded at EPOS^{8,9}, of positrons and electrons emitted back-to-back with kinetic energies near 350 keV. The simplest kinematical explanation is that the correlated signals corres-

pond to the decay of neutral objects, produced at rest in the heavy-ion collision.

With this interpretation, the sum-energy peaks seen in U + Th collisions correspond to states of invariant mass of $1,823 \pm 8$; $1,782 \pm 20$ and $1,630 \pm 8$ keV. A recent experiment at EPOS revealed a line in the sum-energy spectrum of U + Ta collisions corresponding to an invariant mass of $1,770 \pm 8$ keV, and a line seen recently in U + U collisions at ORANGE corresponds to a mass of 1830 keV, agreeing with the EPOS work (Bokemeyer *et al.* and Bederman *et al.* in the *GSI scientific report*, 1987). Also, earlier single-positron spectra produced by Pb + Pb to U + U collisions at ORANGE¹⁰ include lines that seem to be essentially independent of Z at about 250, 340 and 410 keV. Finally, correlated pairs of γ -rays emitted back-to-back in U + Th collisions¹¹, correspond to the decay of an object of mass 1,062 keV. It is of particular significance that the correlated peak is extremely sharp, less than 2.5 keV wide, more than a factor of 10 sharper than the correlated electron-positron peaks.

Several aspects of the data fit nicely with the idea that some kind of phase transition has taken place. First, the peaks seem to appear only in the strong, and strongly varying, electromagnetic field of the heavy-ion collisions, as no similar phenomena have been seen in beam-dump searches¹². Second, the narrow width of the signal points to the formation