Perspective

Was Wright Right?

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Among untested biological theories, one of the most popular has been Sewall Wright's "shifting balance" theory of evolution. First presented in 1931 (*1*), it has been influential, but controversial ever since. In this issue, Wade and Goodnight (*2*) provide experimental support.

Wright thought that evolution in a sexual species suffers a major defect, the inability to shift from one well-adapted state to a better one if this requires passing through less fit intermediates. A structured population offers a solution. With a large number of partially isolated subpopulations a happy gene combination may arise by chance in one of them and diffuse through the whole population by migration.

The initial phase of Wright's process, random gene-frequency drift within subpopulations, has been the subject of both mathematical and experimental work, and the appropriate levels of population size, selection intensities, and migration rates are well understood. The second phase, increase of the favored gene combination once it has arrived at a threshold frequency, is simply well-understood mass selection. The third phase—the spread of favorable gene combinations throughout the population—has been less studied. Several, including Haldane (*3*), have regarded this as the weakest part of Wright's theory, because recombination could uncouple favorable combinations before they become established. Nevertheless, mathematical and numerical studies (*4*) have demonstrated that quite small rates of emigration from the favored group are sufficient to overcome the dissipative effects of recombination and to upgrade the surrounding groups, as Wright argued.

Wade and Goodnight simulated the Wright process experimentally. They started with a series of small subpopulations of flour beetles, all derived from a common base population. The mean fitness of each group was measured by the number of progeny it produced. Those groups that produced an excess contributed to a migrant pool in proportion to this excess. Those that produced fewer than the average received enough from the pool to make up for the deficiency. Thus migrants went from the fitter groups to the less fit. After 24 generations, mean productivity had increased substantially. No such change occurred in a control population with random migration. This elegantly simple, carefully planned, and meticulously executed experiment clearly shows that when the proper conditions are met the Wright process works.

The theoretical paper (*4*) suggested a model in which the rate of emigration from a favored group is proportional to the excess of fitness of this group over the population average, the model used by Wade and Goodnight. Barton (*5*) has argued that this model may exaggerate the influence of migration, which may be more nearly proportional to fitness itself, rather than to fitness excess. This calls for further study.

Wade and Goodnight's experiments have shown that under the appropriate circumstances, the Wright process *can* work. But Wright's theory requires the right population structure, with appropriate subpopulation sizes and migration rates; such populations may be rare. Furthermore, as Fisher (*6*) argued, in a panmictic population each allele can be tested in a variety of combinations and those that work best in all combinations will prevail. Gene interactions slow the process, but Fisher doubted that in a changing environment a population is ever in a position such that no gene frequency change can improve its fitness. Thus the Wright process may be unnecessary.

How would Wright have regarded these experiments? I think he may have reacted as Einstein is reported to have viewed the famous Eddington eclipse experiments supporting his theory. Einstein was sure the theory was correct, with or without the experiments. Wright never showed much interest in experimental tests of his theory; his arguments were based on plausibility and analogy. He thought that much of evolution, the steady improvement of adaptation, could happen by mass selection acting on the additive component of the genetic variance, as Fisher said. But he thought that evolutionary creativity demanded something more. This might not happen often, and hence would be difficult to test in nature, but would be important when it did happen. In much of the debate, which became quite vehement, Wright and Fisher were talking past each other (*7*). Fisher was interested in the steady improvement of fitness; Wright, in the occasional incorporation of novel gene complexes.

In his later years, Wright's views became less adamant. In his last paper (*8*), published in his 99th year, he said, "Kimura's 'neutral' theory dealt with the exceedingly slow accumulation of neutral biochemical changes from accidents of sampling in the species as a whole. Fisher's 'fundamental theory of natural selection' was concerned with the total combined effects of alleles at multiple loci under the assumption of panmixia. . . . Haldane gave the most exhaustive mathematical treatment of the case in which the effects of a pair of alleles are independent of the rest of the genome. . . . I attempted to account for occasional exceedingly rapid evolution on the basis of intergroup selection (differential diffusion) among local populations that have differentiated at random. . . . All four are valid."

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REFERENCES AND NOTES

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