This Week's Citation Classic®

Wright S. The genetical structure of populations. *Ann. Eugenics* 15:323-54, 1951.
[University of Chicago, IL]

The effectiveness of Wright's shifting balance theory of evolution depends on a structured population. This paper, based on the Galton Lecture at University College London, summarizes the ways in which population structure can lead to random gene-frequency changes, both in domestic livestock and in natural populations. [The *SCI*® indicates that this paper has been cited in over 455 publications.]

Wright's Theory of Evolution

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This is Sewall Wright's second most-cited paper. The most-cited one, already mentioned as a *Citation Classic* on March 9, 1981, is his "Evolution in Mendelian populations,"[1] the first full presentation of Wright's shifting-balance theory of evolution. The current *Classic* develops the theory of population structure in more detail and is important because of the central role that population structure plays in Wright's theory. The paper develops his F-statistics, which can be used to describe either breed structure in livestock or geographical structure of natural populations. Especially useful is an appendix that develops Wright's method of path analysis and its applications in population genetics.

The origins of Wright's theory are found in his experiences with laboratory animals and livestock. After graduating from Harvard in 1915, Wright was employed as chief animal husbandman in the US Department of Agriculture (USDA). His evolutionary views, like those of Darwin before him, were strongly influenced by the experience of breeders. Four observations were especially influential:[2] (1) Castle's experiments with selection for the amount of white in hooded rats showed that quantitative variability is ubiquitous and important. (2) Studies of guinea pig coat colors argued that gene interaction and pleiotropy are the rule. (3) Longtime inbreeding experiments at the USDA, again with guinea pigs, demonstrated that individual inbred lines differentiate, leading to greatly increased variation between lines. (4) Wright's studies of the history of domestic livestock, especially Shorthorn cattle, where the records were most complete, suggested that improvement of the breed did not come mainly from selection within herds. Rather, at any one time there were one or more herds that happened to be of outstanding quality, and the breed as a whole was upgraded by bulls exported from these herds.

Wright's shifting balance theory asserts that in a large subdivided population, with the proper relationship between population size and migration rates, random drift will sometimes lead to favorable gene combinations in one or more subpopulations. Then, by migration, these combinations spread through the species as a whole, and the process starts over. The influence of the Shorthorn cattle model is clear.

Wright never deviated from his view that such a population structure offers the best opportunity for rapid, sustained evolutionary progress. His later papers refined the theory, particularly by making mathematical improvements, but the basic idea remained the same. Although he wrote extensively in other areas, especially developmental genetics and statistics, Wright's most-cited papers are all in evolutionary genetics. The earliest paper that is still extensively cited is his 1922 paper in which he presented his now-standard algorithm for computing inbreeding coefficients.[3] Wright's last paper was published two months before his death.[4] This is an interval of 66 years!

In 1955, at age 65, Wright moved to the University of Wisconsin, where he continued his research and writing for more than 30 years. He died on March 3, 1988, at the age of 98. Still in robust health, he was taking his regular long walk and slipped on an icy spot. He died from complications of a broken hip. He had lived through the entire history of Mendelian genetics. That his influence continues is shown by the fact that his work is cited about 500 times in the 1988 *Science Citation Index*®.

1. **Wright S.** Evolution in Mendelian populations. *Genetics* 16:97-159, 1931. (Cited 830 times since 1945.) [See also: **Wright S.** Citation Classic. (Barrett J T, comp.) *Contemporary classics in plant, animal, and environmental sciences.* Philadelphia: ISI Press, 1986. p. 322.]
2. ————. The relation of livestock breeding to theories of evolution. *J. Anim. Sci.* 46:1192-200, 1978. (Cited 10 times.)
3. ————. Coefficients of inbreeding and relationship. *Amer. Naturalist* 56:330-8, 1922. (Cited 285 times since 1945.)
4. ————. Surfaces of selective value revisited. *Amer. Naturalist* 131:115-23, 1988.

