

Charles Roy Henderson, 1911–1989: A Brief Biography¹

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Page County, Iowa

Two giants in the field of animal breeding and genetics were born in Page County, Iowa: first Jay L. Lush in 1896 and, on April 1, 1911, Charles Roy Henderson. This coincidence was a source of considerable pride to Henderson, who from his birth on a farm near Coin, Iowa never forgot his roots. He was active in 4-H and FFA, which honored him as State Farmer of the Year. Some later colleagues may be surprised to know that he was a member of the state championship livestock judging team. He was even more outstanding in sports. At a Page County Farm Bureau picnic, he entered and won the races for 12 and under, 14 and under, and 16 and under. The next year the races were for ages 10 to 12, 13 to 14, and 15 to 16! He later was center on the Coin High School basketball team. His track career continued at Iowa State College, which included an indoor world record in the 4 by 220 yard relay, the Iowa State field house record of 51.7 s for the 440-yard run in 1933, which stood for 30 yr, and an outdoor best of 48.6 s when the world record was only about 1 s less. This interest in sports was maintained throughout his life.

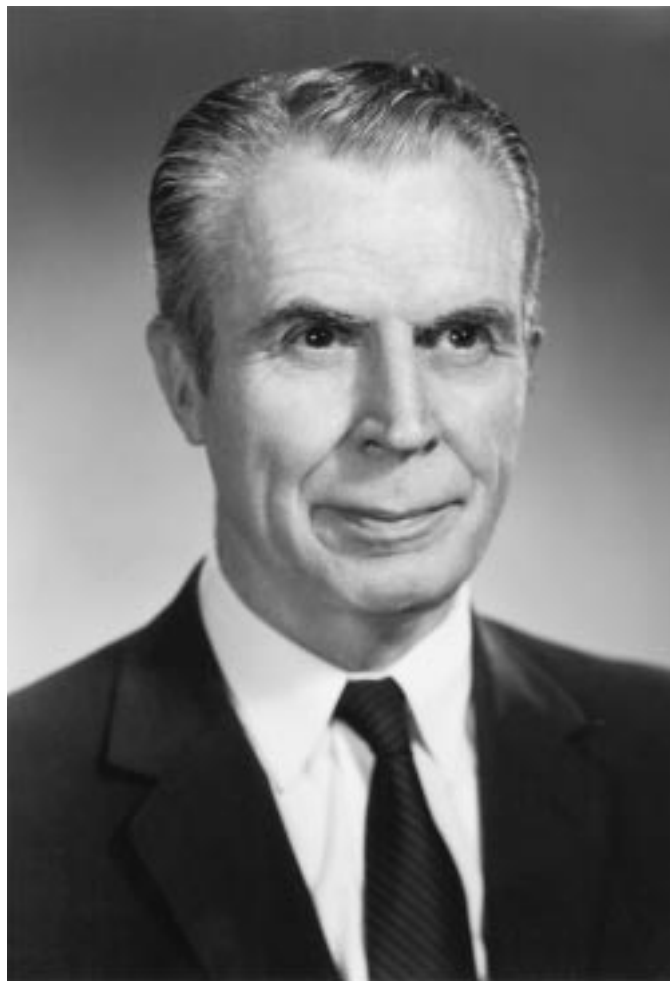
Another interest of Henderson's was music, in particular that of J. S. Bach. His wife, Marian, attributed his initial interest to a visit to his school by the County School Superintendent, who brought a wind-up phonograph and a record of the *William Tell* Overture.

Iowa State College

Henderson's academic record at Iowa State was the best in his division, surpassed at graduation in the whole college only by one engineering student. While

compiling this record, he was running track in the indoor and outdoor seasons, was a member of the livestock judging team, and worked his way through college with numerous jobs. In the year after graduation, he earned the M.S. degree in animal nutrition at Iowa State.

From 1935 to 1940, Henderson was a county agent. During this period, a fellow county agent asked whether his daughter could ride with Henderson to Ames, where Henderson was enrolled in a summer course in economics and the daughter, Marian M. Martin, for her M.S. degree. A little more than a year later they were married. Shortly after their marriage on December 21, 1940, he accepted a position at Ohio University in Athens.



¹Most of the material in this biography has been taken from papers presented at a symposium, The Legacy of C. R. Henderson, which was organized by G. E. Shook for the American Dairy Science Association at its annual meeting in 1990 at North Carolina State University (Freeman, 1991; Kennedy, 1991; Schaeffer, 1991; Searle, 1991; Van Vleck, 1991). The papers were given by five of Henderson's 32 Ph.D. and 17 M.S. students.

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In 1942, Henderson volunteered for a commission in the U.S. Army Sanitary Corps. His assignment to the Nutrition Division led to his becoming unofficial statistician for a research group toward the end of his tour of duty. That interest in statistics and data analysis surely contributed to his decision to return to Iowa State College as a graduate student with Jay L. Lush. His obvious talent during his 2 yr of study for the Ph.D. was statistics. This was at age 35, and he now had a young son, Charles, Jr. His other children, James and Elizabeth, were born in Ithaca, NY.

Scientific Contributions

In the fall of 1948, Henderson's professional career in Animal Breeding and Genetics began with his appointment as associate professor at Cornell University. That fall, he finished his thesis. His thesis had an important influence on the statistical computing package later developed by W. R. Harvey and also was a reference for several decades for graduate students at Iowa State. Nevertheless, material from his thesis does not seem to have been published. The reason, no doubt, is that shortly afterward he discovered a better method for which he was to become slowly but forever remembered: Henderson's mixed model equations (MME). The mixed model equations result from a simple modification of least squares equations. The simple modification results in best linear unbiased estimators (BLUE) of fixed effects and best linear unbiased predictors (BLUP) of random effects such as genetic values. Both BLUE and BLUP can be obtained in other far less computationally feasible ways. What Henderson did was transform a problem that was usually impossible into one that is often possible even with a large number of equations.

Along the way, Henderson learned matrix algebra while on sabbatical leave in New Zealand with the help of Shayle R. Searle, who was not only a friend but later his student and colleague. Henderson, over the years, introduced matrix algebra as a tool to a reluctant set of animal breeders. Matrix formulation made description and derivation of properties of the MME much easier.

Matrix algebra also led to Henderson's second most important discovery, one that ensured the MME would become the foundation both for genetic evaluation systems worldwide and for estimation of the necessary genetic variances and covariances. He knew that records of relatives of an animal provide information about the genetic value of that animal. The numerator relationship matrix among the animals, A , multiplied by the genetic variance is used in the MME to account for that information. The function of the numerator relationship matrix, however, that is used is its inverse, A^{-1} . The difficulty is that time to compute A^{-1} is proportional to N^3 , where N is the number of

animals. Even though rules for computing A were well known, computing A^{-1} for more than a few animals was impossible. What Henderson (1975) discovered by inspection with the help of pencil and paper after 20 yr of searching was a simple way to calculate elements of A^{-1} that required only a list of animals with sires and dams. Nearly all genetic evaluation programs in the world now make use of Henderson's MME and rules for A^{-1} applied to animal models.

Among many national and international awards, Henderson received the highest awards of the American Dairy Science Association and the American Society of Animal Science, was a member of the National Academy of Science, and was a fellow of the American Statistical Association.

Early Contributions

To the United States Henderson introduced the herdmate (stablemate, contemporary) comparison method of dairy sire evaluation in 1955. The herdmate method soon became the standard in many countries until the sire comparison based on MME was first introduced by him in 1970 in New York.

Even earlier, he proposed the then revolutionary and strongly resisted idea of young sire sampling to find the best bulls for heavy use by artificial insemination. He, with his extension colleague at Cornell, H. Wilmot Carter, convinced the directors of the New York Artificial Breeders Cooperative to use a sample of 20 young Holstein bulls per year randomly across many herds. Now nearly all bulls available through AI have proofs based on young sire sampling.

Henderson, who considered himself an animal scientist, produced a paper that became one of the most frequently cited papers in scientific literature. Searle (1991) described Henderson's (1953) paper as "a landmark in the history of estimating variance components." The paper described three methods for estimating variance components that have become known as Henderson's Methods I, II, and III. Method III remains the basis for estimation of variance components for many statistical computing packages. That paper established his reputation as a leading statistician as well as animal scientist and also stimulated much needed research into methods of estimating variance components.

Some 20 to 30 yr later, his MME became the basis for estimation of variance components with newer, more powerful, methods. In fact, he and his students showed that sums of squares of solutions to the MME with the expectations calculated from the inverse of the coefficient matrix for the MME could be used to obtain MINQUE estimates of variance components. Iterative MINQUE with normality is the same as REML. Thus, the familiar MME are used widely for variance component estimation with REML algorithms by nearly all animal breeders.

Final Contributions

Many of Henderson's discoveries, including those discussed in this biography, are summarized in his book (1984) *Applications of Linear Models in Animal Breeding*, which was reprinted in 1994 by the University of Guelph. The book also contains what Kennedy (1991) described as "the unfinished legacy" of ideas and methods that have not yet been fully utilized. Even after mandatory retirement from Cornell University at age 65 in 1976, his work continued with many academic appointments, especially at the University of Guelph (where he finished his book) and at the University of Illinois, along with professorships for shorter periods at many institutions around the world. He died on March 14, 1989, after a short illness in Champaign, Illinois, but not before preparing slides for a presentation scheduled a week later for a regional meeting of ASAS in his home state of Iowa. His wife, to whom he dedicated his book, died at home in Ithaca on April 16, 1994.

Many of us admired Henderson not only as a brilliant scientist but also as a person. We felt sure that his ideas came easily to him, yet his wife, to whom he was a devoted partner, insisted that he felt his successes were not easily achieved and were largely due to much hard work and perseverance. His work ethics, which contributed so much to his successes and which inspired his students by example,

were listed on a transparency he prepared at Kyoto University in response to a request from his sponsor:

Some Advice to Young Scientists

1. Study methods of your predecessors.
2. Work hard.
3. Do not fear to try new ideas.
4. Discuss your ideas with others freely.
5. Be quick to admit errors. Progress comes by correcting mistakes.
6. Always be optimistic. Nature is benign.
7. Enjoy your scientific work. It can be a great joy.

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