C. R. Henderson: Contributions to the Dairy Industry[1]

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ABSTRACT

Through C. R. Henderson's position and the application of his knowledge, he had a major influence on genetic improvement in dairy cattle beginning in the 1950s. He developed herdmate comparisons in the United States. The first extensive program using pedigree selection and progeny testing of sires for use in AI was because of his suggestion. This program established the direction of dairy cattle improvement that still continues. He developed BLUP and discovered how to write the inverse of an additive genetic relationship matrix, A^{-1}, without inverting the matrix. These accomplishments had a major impact on evaluation methods of dairy cattle and other livestock species. Use of BLUP and A^{-1} are standards for evaluation of breeding values all over the world. His pioneering work in estimation of components of variance and analyses of unbalanced data were also of primary importance for animal evaluation and many other applications. Henderson made a major contribution to mankind.
(**Key words**: Henderson, C. R.; legacy; dairy industry)

Abbreviation key: MCC = Modified Contemporary Comparison, MT = multiple trait, NEAISC = Northeast AI Sire Comparison, NYABC = New York Artificial Breeding Cooperative.

INTRODUCTION

C. R. Henderson has made unparalleled contributions to the livestock industry, particularly for dairy cattle. His major contributions have been developments in statistical theory related to prediction of random variables from mixed linear models, estimation of variance components, and analyses of unbalanced data. This paper will not elaborate on methodology, but instead covers his contribution to the dairy industry with emphasis on his earlier work. Much of his earlier work relating his contributions to genetic improvement of dairy cattle was not published; regrettably, then, this history must be incomplete. Material on his graduate work and recruitment by Cornell University is included because it gives some insight into how early leaders in the field saw the need for change and how they evaluated Henderson as the person to effect change.

RECRUITMENT OF HENDERSON

K. L. Turk (16), Head of the Department of Animal Science at Cornell University, stated that when the Department was looking for a replacement for G. W. Salisbury, they decided to get more balance in the department by recruiting a specialist in animal genetics or statistical genetics to fill the position. Turk further states that Henderson had unusually good background and experience:

> He was raised on an Iowa crops and livestock farm, earned a B.S. in agriculture and an M.S. in nutrition at Iowa State College, spent 5 years in county agent work in Iowa, had 2 years of college teaching and management of livestock herds at Ohio University, and 4 years in nutrition and statistics research as an officer in the Sanitary Corps, US Army, during World War II. For the Ph.D. at Iowa State College, his major field was animal breeding with minors in genetics and statistics.

Henderson was proud of his Iowa heritage.

The outcome of the recruiting of Henderson is obvious, but had Henderson accepted an offer of employment by the National Research Council before earning his Ph.D. degree, the science of animal breeding might well have been delayed.

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THE THESIS

L. N. Hazel was the chairman of Henderson's graduate committee. For his final examination, Kempthorne was substituted for Mood. The other committee members were J. L. Lush, G. F. Sprague, W. A. Craft, and J. W. Gowen. His committee was indicative of his latter interests and work. Henderson wrote to Hazel (October 27, 1948) concerning his Ph.D. dissertation. Henderson stated,

> I am disturbed by the potential length of the thesis, but see no way to reduce it much and still give enough detail to enable anyone else to carry out a similar analysis without having to go through the pain of working out the methods. It is rather apparent methods are going to appear, from the standpoint of the number of pages, to be much more important than the experimental results.

It was clear at this stage that Henderson's primary interest was in statistical methods relating to animal evaluation.

Part of Lush's correspondence (November 13, 1948) to Henderson about his thesis follows:

> Tentatively my most vivid general impression is that the pigs are very far away! I appreciate that what I have seen is the section dealing with methods, rather than findings, and, hence, that your present treatment may be perfectly appropriate. But, I hope that the remainder of the thesis will show mainly the biological and physical aspects of the problem, with the statistical methods being merely a means for elucidating those rather than the primary objective themselves. I appreciate that your improved and more powerful methodology *may* be a much bigger contribution eventually than any of your findings about the abilities of these specific lines. If so, more power to you. But at the moment and viewing only this incomplete part of the thesis, it looks as if your major would more appropriately have been in statistical methods with the animal data being chosen only to illustrate those!

Henderson's intense interest in statistical methods, particularly as applied to livestock improvement, was clearly the underlying reason he contributed so much to practical livestock improvement. The reason that most of his work, especially the early work, was with dairy cattle was because dairying was a large part of the rural New York economy. Although most of his early work applied to dairy cattle, his interest was much more general than any single application.

STATUS OF SIRE EVALUATION IN THE LATE 1940s AND EARLY 1950s

To discuss Henderson's contribution to the early dairy industry requires some understanding of the state of genetic improvement in dairy cattle when he began his research career. Undoubtedly, owners of cattle have practiced some selection for centuries, but little is published of these efforts. Van Vleck and Pollak (17) reviewed published methods of sire evaluation. The following are summarized from their review. Among the first methods that relate to the science of animal breeding was the daughter-dam difference used in Denmark in 1902. This was followed 11 yr later by the daughter-herdmate difference (Peters) and the equal parent index (Hansson), and in the 1920s by the intermediate index (Woodward), the American index (Tapp), percentage of contemporaries (von Paton), and the Modified Mount Hope index (Goodale). These indexes were not used extensively, but Graves seems to be the first credited for use of the daughter-dam difference in the United States. In 1935, the USDA Bureau of Dairy Industry and State Extension Service adopted the daughter-dam difference.

Henderson was employed as an associate on September 16, 1948 at Cornell University (16). Henderson (7) stated that at the time he joined the Cornell faculty, the "accepted" method for sire evaluation was the daughter-dam comparison, either by the equal parent index or by the daughter average minus the dam average.

Most bulls selected for use by AI in 1948 were selected on their natural service progeny, usually in one herd, and often with as few as five daughters (7). Artificial insemination was not a new technique in 1948. The Arab horsemen are reported to have used AI in the 14th century, and several scientific studies were conducted in private herds at the University of Minnesota in 1937 and 1938 before commercial AI started (10). The first AI cooperative was in 1938 in New Jersey. Development of AI was slow until after World War II, but in 1948, when Henderson went to Cornell, the New York Artificial Breeding Cooperative (NYABC) was actively breeding cows. Also, DHIA was well in place.

By that time, then, most of the essential tools were in place for Henderson's major impact on the industry. There were reliable DHI records and paternal half sisters nearly randomly distributed across herds because all semen was unfrozen. But the other essential tool, computers, was at an early stage of development.

ASSOCIATES

The application of Henderson's work was intimately intertwined with personnel and programs at NYABC and with the faculty at Cornell. Among these were Wilmot Carter, Stanley Brownell, Ray Albrectsen, Bob Bratton, Dale Van Vleck, Bob Everett, and Shayle Searle at Cornell; and Elmer Clapp, Roger Hoyt, Morris Johnson, Charlie Krumm, Jim Mellinger, and Jeff Keown at NYABC and Eastern Artificial Insemination Cooperative. The latter was formed by a merger of NYABC with the New England Cooperatives. Henderson (7) and Turk (16) acknowledged the importance of grant funds, especially from NYABC, to the success of Henderson's early work. Also, many of the practical problems were called to his attention by people like Wilmot Carter and Elmer Clapp. Clapp (1989, personal communication) states:

> He responded effectively when he recognized the practical importance of a problem. To this end, dairymen (e.g., our sire committee men) were influential in his recognizing the need for particular research and helping with the application.

Henderson's long-time associate, Wilmot Carter, was probably the person most responsible for teaching Henderson's concepts to practical dairy producers. If dairy producers did not accept and use the new genetic tools, new developments would have had little impact on the industry.

J. M. Elliot (1989, personal communication) stated:

> Charles Henderson joined our department in 1948 and I think it would be accurate to say that it was never quite the same thereafter. Chuck started what I have chosen to call a quiet revolution in methods that were applied to selection of dairy cattle in a revolution that was soon to spread through the state, the nation and, eventually, the world.

YOUNG SIRE SAMPLING

In December 1949, soon after Henderson's arrival, the Department of Animal Science held a 2-d seminar on dairy cattle breeding (H. W. Carter, 1989, personal communication). The seminar covered selection on cow families, which were shown to have been overemphasized; natural service proofs of sires selected for milk production, which were shown to have a very low correlation with later AI proofs; prediction of sires' AI proofs from pedigree, which were at least as good as from natural service proofs; and 80% of the pedigree selected bulls were alive when progeny tested compared with 20% of the naturally proven bulls. Weighting factors for number of daughters in a sire proof for natural service and AI proofs also were presented by Henderson. Faculty members S. J. Brownell, R. Albrectsen, Wilmot Carter, C. R. Henderson, and G. W. Trimberger, and graduate student Robert Dunbar attended. Henderson stated that the results of his early work evaluating the results of natural service sires used in AI were so discouraging that he did not publish them (7). The results from this seminar literally pulled the foundation from under the existing sire selection program and led to the establishment of a much sounder foundation.

After this seminar, Henderson recommended that NYABC implement two-stage selection of young sires that were initially chosen on pedigree, then the best of these were to be selected based on a multiherd progeny test for extensive AI usage. He also recommended that the sires should be as young as possible (H. W. Carter, 1989, personal communication). Henderson reported the amount of progress expected by selecting one sire for extensive use from various numbers sampled. He suggested using 1 out of 10 to nearly maximize genetic progress but indicated 1 out of 8 would be more economical (H. W. Carter, 1989, personal communication). In 1954, the young sire sampling program was initiated by NYABC (4). Colantha, a son of Dean, was the first young sire to go into the sampling program (E. Clapp, 1989, personal communication).

Henderson spent a sabbatical leave in New Zealand in 1955 and 1956. His association with S. R. Searle resulted in improved matrix algebra skills and was a time of professional growth. He also had a strong influence in adoption of a young sire sampling program in New Zealand.

HERDMATE COMPARISONS

In the late 1940s and early 1950s, daughter averages of age-corrected production and daughter-dam comparisons with first and all records were used to evaluate sires. Some daughter-dam comparisons were within the same time period but with parent and offspring of different parities.

The next major contribution of Henderson and his students was development of the herdmate comparison. Although Johansson and Robertson (11) described contemporary comparisons for the United Kingdom in 1952, the herdmate comparison described in 1954 by Henderson et al. (8) differed in several ways.

Finding that herd-year-season effects accounted for nearly 50% of the total variance in production (1) and that most of these effects were environmental in nature led Henderson to develop the herdmate comparison. The latter compared a sire's daughters to their herdmates in the same herd, year, and season (8). Herdmate comparisons were computed at Cornell under Henderson's direction and used by NYABC in 1954. The herdmate comparison was improved in 1959 by regressing the daughter-herdmate difference for number of progeny, and this difference was published for evaluated sires (3). Although herdmate comparisons may seem now to be mundane, the use of this technology was a major step at the time, and it was not immediately accepted by the industry. Another major development of national significance was the computing of season-age-adjustment factors by Miller and Henderson (12,13). This was one of the first applications of maximum likelihood procedures to very large sets of dairy production data.

It is difficult to put a monetary value on research, but Turk (16) stated,

> We made a calculation in 1961 showing that every dollar spent on research in dairy cattle breeding was returning more than $240 to New York's dairy farmers.

The herdmate comparison replaced the daughter-dam difference as the official USDA-ARS sire evaluation procedure in 1962 (14). Although the USDA herdmate comparison used the same basic concepts as those developed at Cornell, it also differed in some aspects. It was revised in 1965 to subtract the breed average from the Predicted Average to obtain what was called Predicted Difference, and, in 1967, to add Repeatability (2).

In the mid-1960s, a competing bull stud advertised that daughters of their sires produced more milk than those from NYABC. The genetic personnel at NYABC "just knew that this could not be true" (E. Clapp, 1989, personal communication), but analyses by Henderson and Carter confirmed this allegation (H. W. Carter, 1989, personal communication). The general manager of NYABC asked why Henderson's recommendations were not producing the expected results. Subsequent analyses indicated that slightly less than three sires were sampled per bull selected compared with the 8 to 1 recommended. The number of sires sampled was soon increased to 40 per year with more emphasis put on production and less on popularity and type (E. Clapp, 1989, personal communication). No more natural service sires were purchased. Henderson's recommendation of sampling large numbers of sires set the tone for the United States AI industry. Eventually all AI studs in the United States started viable young sire programs. Among the first was American Breeders Service guided by Robert Walton.

DEVELOPMENT AND USE OF BEST LINEAR UNBIASED PREDICTORS

As the AI industry matured, it became clear that because genetic progress in the population was made using the herdmate comparison, it was no longer adequate for accurate sire evaluation. The theory for improved sire and cow evaluation had been developed and published in 1959 (9) and further elaborated in 1963 (5), but it was not yet called BLUP. As computers with larger memory and storage became available, more efficient algorithms were developed for sire and cow evaluation. The strategy for computing BLUP was developed in 1966 and tested by Paul D. Miller, Henderson, and other associates. This resulted in the Northeast AI

Sire Comparison (NEAISC), and sires were evaluated by using BLUP in 1970. The NEAISC was published with a 1968 base (4), which was the first time cattle were ranked relative to a fixed base. Henderson was directly involved in production of the NEAISC at this time, which was called a direct comparison. The development and application of BLUP theory is unquestionably a major landmark in improvement of dairy cattle and, in fact, all livestock. This was the first procedure with clearly defined theory and known and desirable statistical properties used to evaluate livestock. In 1972, Robert Everett took responsibility for sire and cow evaluation in the Northeast.

The USDA-DHIA Modified Contemporary Comparison (MCC) was implemented in 1974. This was a major improvement over the herdmate comparison. Several new concepts were incorporated, which included weighting for accuracy of information, herd × sire interaction, sires of herdmates, and grouping concepts (14). The USDA personnel developed the MCC procedures, but they used several concepts developed by Henderson, his associates, and students. So Henderson's influence was felt by dairy producers on a national basis through the PD. The USDA began publishing BLUP proofs for protein and solids-not-fat for breeds other than Holstein in fall 1977 (15). The USDA did not have large enough computers to implement mixed model procedures in the 1970s for milk and fat yields because they were committed to evaluating all sires with reasonable numbers of daughters and to using all lactations (14).

Predicted Difference was available nationally and was the primary means of evaluating AI sires on a national basis. Sires entering AI were from the registered population, so when breed associations and breeders of registered cattle gradually accepted and used improved genetic tools, primarily PD and cow indexes, the rate of genetic gain in production accelerated. The rate of genetic gain in milk production has continued to accelerate (18).

This discussion has centered on Henderson's contribution to the dairy industry as related to only production traits. Although Henderson worked very little with nonproduction traits, his students and their students have made contributions using his methods. For example, BLUP procedures have been used to evaluate sires and cows for type traits. The US Holstein Association used BLUP to evaluate type traits in 1988. Other breed associations began using BLUP in 1979. The BLUP procedures are used by AI personnel for type evaluation. Also, the first calving ease analysis published by the National Association of Animal Breeders evaluated sires with BLUP. Sires were evaluated for calving ease using BLUP from 1977 through 1987. Sires are now evaluated for calving ease using an ordered categorical analysis, which has some similarities to BLUP. It is apparent that Henderson's influence on the dairy industry has gone beyond just production traits.

Genetic evaluations by BLUP using models relevant to the design and nature of the data under varying conditions have been used throughout the world. This is a demonstration of the adaptability of Henderson's work. In recent years, there have been large exports of semen, embryos, and dairy cattle to both developed and developing countries of the world. Henderson's work has influenced both the physical and scientific well-being of a large part of the world.

USE OF THE RELATIONSHIP MATRIX

Another landmark in genetic evaluation was Henderson's discovery of how to write the inverse of a relationship matrix without actually inverting the matrix (6). Dairy breeders had long alleged that outstanding cow families were not being given enough emphasis in sire and cow evaluation. Now all additive relations could, for the first time, be included in both sire and cow evaluations at a quite reasonable cost.

In 1975, the inverse of the relationship matrix within herds was used in the NE A^{-1} ETA to evaluate cows. The next year, A^{-1} among bulls was added to produce the NEAISC A^{-1}. In 1980, maternal grandsires of the daughters were added to the NEAISC A^{-1} to correct for nonrandom mates, and the base year was changed to 1978 (4). In 1984, Everett used a multiple trait (MT) MT-NEAISC A^{-1}. This involved many changes and was much more computationally intense. In 1989, Everett started using a multiple-trait animal model

(NE-AI-MT-CASE) to evaluate cattle in the Northeast.

The last major change in evaluation procedures for USDA is the use of a single-trait animal model applied to dairy evaluation over all the United States by the USDA-ARS Animal Improvement Programs Laboratory (18). The use of A^{-1} allowed major improvements in accuracy of evaluation. This, like many other products of Henderson's efforts, improved the well-being of producers and allowed cheaper production of food. However, few of the recipients of these efforts outside the organizations working in the dairy industry knew that these improvements were the product of Henderson's work.

C. R. Henderson officially retired from Cornell University in September 1976, but his contributions to the livestock industry and to science in general continued unabatedly. He published about 50 papers after retirement. The most recent major improvements in sire and cow evaluations, the USDA-ARS-Animal Improvement Programs Laboratory animal model, and the NE-AI-MT-CASE, were not produced by Henderson. Even so, they relied very heavily on his work. It is clear why this symposium was held in his honor.

I would be remiss not to mention some of Henderson's contributions to those not directly related to the dairy industry. Indicative are 1) helping Urie Bronfenbrenner in Human Ecology at Cornell and others analyze unbalanced data, 2) providing statistical advice for many graduate students and faculty in the Animal Science Department at Cornell, 3) conducting departmental seminars with his students on data analyses, 4) giving seminars and short courses over much of the developed world, 5) providing a large number of short contacts or communications that could have seemed trivial to him, but were not, and were a great help to others, and 6) contributing to the monograph published by the American Society of Animal Science.

One way to relate Henderson's contribution to the applied livestock industry is by the awards they have presented to him. These include the Eastern Artificial Insemination Cooperative Award of Merit, 1968; the National Association of Animal Breeders Award of the American Dairy Science Association, 1977; and the Pioneer Award, Beef Improvement Federation, 1986.

In addition, he received major scientific recognition for his work: Borden Award of the American Dairy Science Association, 1964; Animal Breeding and Genetics Award of the American Society of Animal Science, 1964; Fellow of the American Statistical Association, 1969; Morrison Award of the American Society of Animal Science, 1971; Herman von Nathusius-Medaille of the German Society of Animal Production, 1981; Fellow, American Society of Animal Science, 1981; Jay L. Lush Award of the American Dairy Science Association, 1982; election to the National Academy of Science, 1985; Alumni Research Award, Iowa State University, 1984; and the Henry A. Wallace Award, Iowa State University, 1984.

Turk (14) stated that after Henderson joined the faculty of the Animal Science Department, he soon demonstrated he was the "right man" for the "right job" at the "right time". May I echo that this phrase characterized his entire productive life.

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