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A 100-Year Review: Methods and impact of genetic selection in dairy cattle—From daughter–dam comparisons to deep learning algorithms[1]

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ABSTRACT

In the early 1900s, breed society herdbooks had been established and milk-recording programs were in their infancy. Farmers wanted to improve the productivity of their cattle, but the foundations of population genetics, quantitative genetics, and animal breeding had not been laid. Early animal breeders struggled to identify genetically superior families using performance records that were influenced by local environmental conditions and herd-specific management practices. Daughter–dam comparisons were used for more than 30 yr and, although genetic progress was minimal, the attention given to performance recording, genetic theory, and statistical methods paid off in future years. Contemporary (herdmate) comparison methods allowed more accurate accounting for environmental factors and genetic progress began to accelerate when these methods were coupled with artificial insemination and progeny testing. Advances in computing facilitated the implementation of mixed linear models that used pedigree and performance data optimally and enabled accurate selection decisions. Sequencing of the bovine genome led to a revolution in dairy cattle breeding, and the pace of scientific discovery and genetic progress accelerated rapidly. Pedigree-based models have given way to whole-genome prediction, and Bayesian regression models and machine learning algorithms have joined mixed linear models in the toolbox of modern animal breeders. Future developments will likely include elucidation of the mechanisms of genetic inheritance and epigenetic modification in key biological pathways, and genomic data will be used with data from on-farm sensors to facilitate precision management on modern dairy farms.

Key words: genetic selection, dairy cattle, genomic selection, statistical models

THE BUILDING BLOCKS

Performance Recording

Pedigree records and performance data were the key building blocks in developing effective genetic selection programs in the pre-genomic era, as noted in Appendix Table A1. Pedigree records traced back to the origin of breed societies in the late 1800s, and widespread collection of performance data began shortly thereafter, with the encouragement of early dairy industry pioneers such as W. D. Hoard. The first statewide association for recording milk weights and analyzing butterfat samples was formed in Michigan in 1905, and by 1908, the United States Department of Agriculture (USDA) Bureau of Animal Industry began organizing local and state cow testing associations into the national Dairy Herd Improvement Association (DHIA). Responsibility for this effort was transferred to federal extension workers in 1914, and participation in milk testing grew rapidly (VanRaden and Miller, 2008), as shown in Figure 1.

Monthly DHIA testing was the norm for many decades, but now about two-thirds of dairy farms use labor-efficient a.m./p.m. testing plans, in which milk samples are taken at alternate times each month. Future strategies that focus on more frequent DHIA sampling of recently fresh cows or cows in the highest-producing pens may provide more useful data for cows that are at peak efficiency and at the greatest risk for common health disorders. Electronic measurement of data, via radiofrequency identification (RFID) sensors and inline sampling systems, has replaced manual entry of pedigree and performance data, as shown in Figure 2.

Local bull associations were common during the 1920s and 1930s, until the widespread adoption of AI in the 1940s, when dozens of regional AI cooperatives were formed. Because virtually all traits of interest in dairy cattle are sex-limited, genetic evaluation of a bull's own

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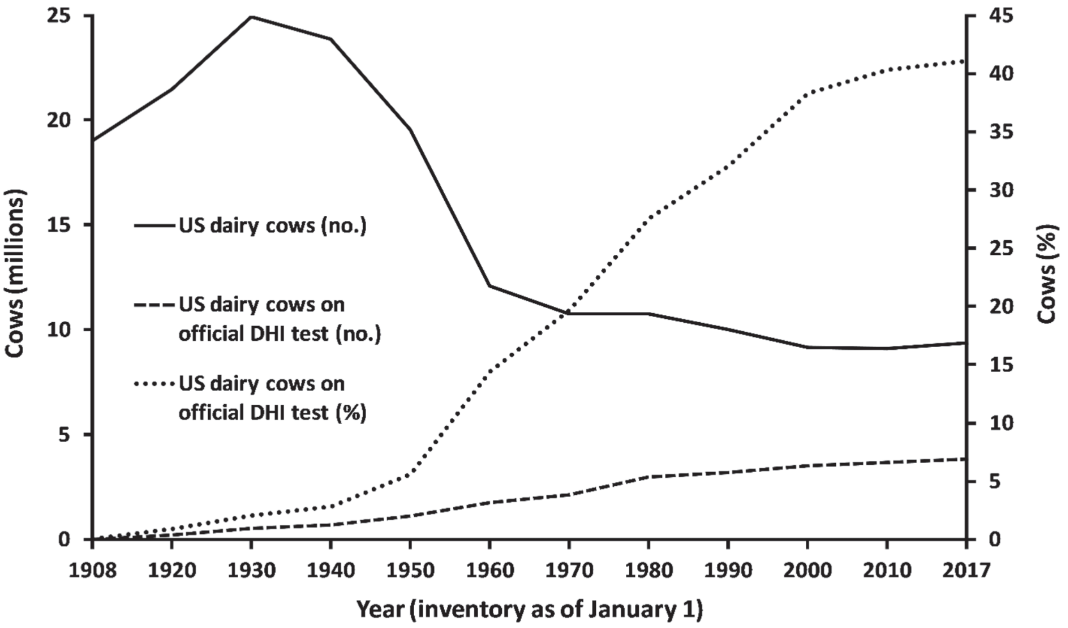
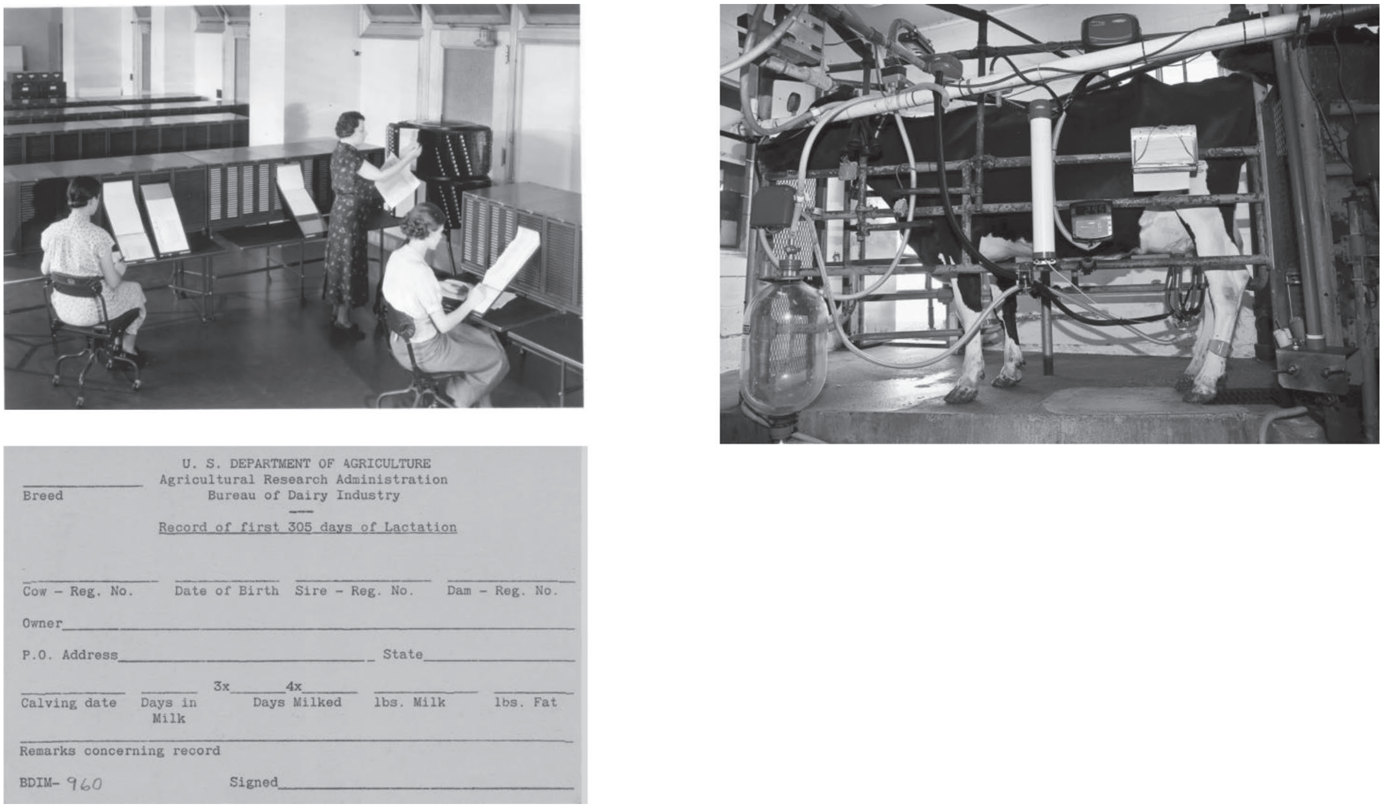


Figure 1. Participation in milk recording programs in the United States, from 1908 to 2017.



U. S. DEPARTMENT OF AGRICULTURE
Agricultural Research Administration
Bureau of Dairy Industry

Breed

Record of first 305 days of Lactation

Cow - Reg. No. Date of Birth Sire - Reg. No. Dam - Reg. No.

Owner

P.O. Address State

Calving date Days in Milk 3x 4x Days Milked lbs. Milk lbs. Fat

Remarks concerning record

BDIM- 960 Signed

Figure 2. Recording of performance data for dairy cows then (1936, left panels) and now (2017, right panel).

phenotypes is not useful, and strategies for estimating a bull's genetic superiority or inferiority based on the performance of his offspring were needed.

Pedigree Data

Despite the fact that dairy cattle breed societies assigned unique identification numbers to individual cows and bulls as early as the late 1800s, a large proportion of nonregistered animals ("grades") were not included in breed society herdbooks. An alternative identification method was needed, and USDA introduced metal ear tags with unique numbers in 1936. These evolved into the 9-digit tag series (e.g., 35ABC1234) introduced by the Animal and Plant Health Inspection Service (APHIS) and National Association of Animal Breeders (NAAB) in 1955, which are still used for many cows today. The American ID series, introduced in 1998, features a 2-character breed code, 3-character country code, and 12-digit identification number (e.g., HOUSA00035ABC1234 or HO840012345678910). This system was designed to be unique worldwide and to include both registered and grade animals, and it allows multiple identification codes for individual animals to be cross-referenced to a single unique number.

EARLY METHODS TO PREDICT BREEDING VALUES

Daughter–Dam Comparison

The lactation performance of a cow was long thought to be influenced by heredity, and early selection decisions were based simply on an individual cow's phenotype for milk or butter yield. The idea of comparing a cow's milk production with that of her dam emerged near the turn of the 20th century. Several indices were proposed for this purpose (Davidson, 1925; Graves, 1925; Yapp, 1925; Goodale, 1927; Gowen, 1930; Bonnier, 1936; Allen, 1944) and their relative accuracy was compared by Edwards (1932). In practice, the earliest known daughter–dam differences in the United States were computed by individual bull associations around 1915, based on a handful of sires with a few offspring apiece—this was the first serious attempt to improve dairy cattle by selection. By 1927, approximately 250 cooperative dairy bull associations, representing more than 6,000 farmers, provided data to the USDA and, for the next 4 decades, the USDA computed daughter–dam comparisons for dairy bulls and mailed the results to their owners. Artificial insemination became available in the late 1930s, and with it, the opportunity for superior bulls to produce hundreds or thousands of offspring in many herds. Large groups of daughters performing under a variety of management and environmental conditions greatly enhanced the accuracy of genetic predictions. During this period, the work of giants such as R. A. Fisher (1918, 1930) and J. B. S. Haldane (1932) laid the foundations of population and quantitative genetics, which allowed pioneers such as Sewall Wright (1932) and Jay Lush (1931, 1933) to develop the science of animal breeding and the statistical methodologies needed for accurate evaluation of dairy sires. Various indices based on daughter–dam comparisons were developed, including those of Wright (1932) and Lush et al. (1941).

Daughter–dam comparisons facilitated genetic evaluation of bulls that were used in multiple herds, as long as performance data were available for the dam and her daughters. This method accounted for herd-specific management practices and local environmental conditions if the dam and daughter were housed in the same herd. Changes in management or environmental conditions that occurred in the time between dam's and daughter's performance were ignored. Relationships between sires and their mates were not considered, and this assumption was sometimes violated if the bull was used in his herd of origin. Variation in the phenotypic performance of the dam, relative to her actual genetic merit, was a huge source of error in the resulting predictions. Genetic trends over time were ignored, but genetic progress was negligible in most herds at the time. An important limitation was that sire evaluations were not regressed to the mean, so bulls evaluated based on only a few daughter–dam pairs were more likely to have extremely high or low genetic predictions. During this period, methods were developed to standardize records for lactation length (305 d), milking frequency (2×), and age at calving (mature equivalent). Adjustments for season of calving were also developed, but differences in environmental conditions between years were generally ignored.

Selection Index

Hazel and Lush (1942) introduced the selection index for EBV for individual traits, and this method was used by Lush (1944) to derive weights for various sources of information in daughter–dam comparisons. The EBV of a selection candidate was predicted using multiple linear regression, where each independent variable represented individual or mean performance for a specific type of relative, such as dam, sire, maternal half-siblings, paternal half-siblings, or progeny. The regression coefficients represented index weights, which were a function of genetic relationships and the amount of information contributed by the phenotypic record or average (e.g., number of lactations or number of offspring). The amount of information from various types of relatives often differed between selection candidates, so index weights were adjusted for the number of relatives or lactations contributing to mean performance, based on heritability and repeatability parameters.

Contemporary (Herdmate) Comparisons

Contemporary comparisons represented a huge leap in the accuracy of genetic evaluations because of their ability to account for the specific management and environmental conditions under which phenotypes were expressed (Robertson et al., 1956). Robertson and Rendel (1954) are credited with introducing contemporary comparisons, and Henderson et al. (1954) formally published the herdmate comparison model in the same year. However, Searle (1964) noted that this method had been used in New Zealand before either publication. The concept of contemporaries or herdmates exposed to similar management and environmental conditions is much like that of an epidemiological "cohort," in which patients are grouped based on commonalities in demographic features (e.g., age, sex, or geographical region) and lifestyle characteristics (e.g., exercise regimen or tobacco usage). A critical consideration in designing contemporary groups is the balance between a precise definition of the cow's environmental conditions and the need for enough herdmates to provide an accurate estimate of the contemporary group effect.

Progeny testing became widespread during the era of daughter–dam comparisons. However, the introduction of contemporary comparisons allowed AI centers to fully capture the benefits of distributing the semen of young bulls to dozens or hundreds of herds with different geographical locations, environmental conditions, and management practices. Contemporary comparisons were enhanced by regressing average daughter contemporary deviations (now known as daughter yield deviations) toward zero, based on heritability and number of progeny, because mean deviations for bulls with few offspring have larger variance than mean deviations for bulls with many offspring. Some contemporary comparison models also included a herd by sire interaction adjustment to limit the effect of a single herd on a sire's EBV.

Cornell University implemented a regional sire evaluation system based on contemporary comparisons in the mid-1950s (Henderson, 1956), in which records were weighted based on the number of lactations per cow and a repeatability parameter. However, information about the number of daughters or contemporaries was not used when combining daughter contemporary deviations to compute the sire's EBV. The contemporary comparison method was applied by the USDA in 1961, replacing the daughter–dam comparison system. This model allowed the inclusion of cows for which performance records of the dam were unknown. Herd-year-season contemporary groups were based on a 5-mo moving average, and herdmate averages were adjusted for seasonal effects. As in the Cornell model, sire effects were regressed to the mean, so a bull could not rank highly unless he had a significant number of daughters. Records of cows that were culled or sold for dairy purposes were extended to 305 d, whereas longer records were truncated at 305 d.

Other adjustments were implemented at this time, including factors for extending short lactations to 305 d that were specific to breed, region, season, and parity, and records were weighted by length of lactation. A time lag between the cow's calving date and initiation of the sire summary ensured that records from culled cows with short lactations did not bias the genetic evaluations of their sires. This was an obvious limitation as regards timeliness of data entering the genetic evaluation system, at least until 1975, when records in progress became available for all cows in the herd. Estimates of sires' genetic merit were published as the predicted difference (**PD**) in performance of their daughters relative to contemporaries in a typical herd. The term "repeatability" (later "reliability") was used to denote the accuracy of a bull's PD, and it indicated the level of confidence a farmer should have when purchasing the bull's semen. This method, which was used until 1973, allowed the inclusion of more data, tended to be less biased, and provided a cow index for ranking elite females.

Several competing methods for sire evaluation were introduced during this period. Most were closely related to each other and to the weighted least-squares approaches of C. R. Henderson (1952, 1963) and Cunningham (1965), as well as simplified versions of the best linear unbiased prediction (BLUP) models described in subsequent sections (Thompson, 1976). The cumulative difference method of Bar-Anan and Sacks (1974) is essentially equivalent to the contemporary comparison method but with an adjustment for the genetic level of sires of the cow's contemporaries. The term "cumulative" recognized that performance data of a bull's daughters accumulate over time, resulting in increased accuracy of predictions, and this method was the basis of the modified cumulative difference method proposed by Dempfle (1976).

Genetic evaluations of dairy sires were unified at USDA in 1968 (Plowman and McDaniel, 1968), when dairy cattle breed associations discontinued their own sire rankings for production traits. In 1972, the USDA Division of Dairy Herd Improvement Investigations was renamed as the USDA-ARS Animal Improvement Programs Laboratory (**AIPL**)—this laboratory set the global standard for translational research on genetic evaluation of dairy cattle for the next 45 years.

Modified Contemporary Comparison

In 1974, the modified contemporary comparison (**MCC**) method was introduced (Dickinson et al., 1976; Norman et al., 1976). In this model, a bull's PD represented a weighted average of his pedigree value and the deviation in performance of his daughters from their contemporaries. In previous methods, a bull's pedigree information was generally discarded when data from milking daughters became available. The MCC method also allowed the inclusion of sire and maternal grandsire pedigrees. The genetic merit of competing sires within a given herd (i.e., sires of contemporaries) was taken into account, and this approach could better accommodate genetic trends over time (Norman et al., 1972). These features of the MCC method were increasingly important, because modern selection tools and advanced reproductive technologies now allowed some farmers to make more rapid genetic progress than their peers (McDaniel et al., 1974). In addition, positive assortative mating had become popular, as farmers "mated the best to the best" to improve their herds (Norman et al., 1987). The first 5 lactation records from a given cow were included in the MCC model, which provided a more accurate picture of an animal's genetic superiority or inferiority in lifetime productivity. Contemporary groups differed for primiparous and multiparous cows within a herd. As previously, a bull's evaluation was regressed based on heritability, number of daughters, and lactations per daughter, but regression was toward his pedigree value, rather than the population mean.

The MCC method produced results that were nearly identical to those of BLUP in a sire model, but with substantially lower computing requirements. The practice of resetting the genetic base was initiated during this time, so farmers would be reminded to raise their sire selection standards as the breed made genetic progress. However, periodic resetting of the genetic base "forgives" undesirable genetic trends that may occur as correlated responses to selection (e.g., female fertility) or biases in the perceived value of certain traits (e.g., stature). The MCC method was widely accepted by pedigree breeders and AI studs, and it led to impressive annual genetic gains of about 45 kg of milk per cow per lactation. Another innovation during this period was the incorporation of pricing data for milk, fat, and protein, so that estimates of genetic merit could be expressed as the financial gain or loss relative to an average sire of the same breed (**PD$**). Cow indices became widely used during the MCC era; these represented a weighted average of the cow's modified contemporary deviation and her sire's PD (and later her dam's cow index), with weights depending on the amount of information contributing to each component.

LINEAR MODELS

Mixed Linear Models

Henderson (1953) advocated the use of statistical models to partition genetic and environmental variance components and predict the genetic merit of dairy sires, and this led to the development of BLUP methodology. Despite its theoretical appeal, computing limitations prevented implementation of BLUP until 1972, when Cornell University implemented BLUP in a sire model; this model was later modified to include genetic relationships among sires.

A mixed linear model is expressed most succinctly in matrix notation as

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e},$$

where $\mathbf{y}$ is a vector of phenotypic measurements on a group of animals; $\mathbf{b}$ is a vector of continuous or categorical fixed effects that are known to influence the phenotype, such as age at calving or herd-year-season contemporary group, as one would encounter in a traditional least-squares analysis; $\mathbf{u}$ is a vector of random effects, such as sire breeding values; $\mathbf{X}$ and $\mathbf{Z}$ are incidence matrices that map the phenotypic observations in $\mathbf{y}$ to the fixed and random effects in $\mathbf{b}$ and $\mathbf{u}$, respectively, and $\mathbf{e}$ is a vector of random residual effects, such as temporary environmental conditions or measurement error. The variance components σ_u^2 and σ_e^2, corresponding to the random effects $\mathbf{u}$ and $\mathbf{e}$, can be estimated using a variety of methods, such as maximum likelihood (Harville, 1977).

Sire and Maternal Grandsire Models

If the vector $\mathbf{u}$ in the mixed model equations comprises the breeding values of dairy sires and $\mathbf{y}$ contains the lactation records of their daughters, the aforementioned mixed linear model would be considered as a "sire model." If we specify that $\mathbf{G} = N\left(0, \mathbf{I}\sigma_u^2\right)$, this model assumes that sires are unrelated to each other, and the resulting sire EBV are regressed toward the population mean in proportion to the magnitude of σ_u^2 relative to σ_e^2. The assumption that sires are unrelated to each other is highly unrealistic, given the widespread use of AI and embryo transfer, which lead to large families of paternal half-siblings and small families of

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