From Bakewell to BLUP
Modern Livestock Breeding's Short History

By Richard Gilbert

The history of livestock breeding reveals two surprising facts: scientific selective selection is a relatively recent development in the long centuries of breed formation; and quantum leaps in genetic progress have been made even more recently and by a mere handful of men.

Many have heard of Robert Bakewell, a farmer known as the father of selective breeding. Bakewell (1725–1795) became famous for transforming his region's sheep. Paintings of him show a portly man with cool eyes set in a pudgy face. From Dishley in central England, Bakewell came to epitomize breeding success primarily because of his New Leicester sheep.

He also improved the native English Longhorn cattle and created the Shire horse, a large, black breed with notable strength and stamina, from a traditional Dutch type. And he helped introduce English farmers to turnips and other root crops for feeding ruminants.

At one time, sheep drove selective breeding progress, attracting ingenious, independent thinkers like Bakewell. This is because, by the 1400s, wool was wealth, Roger J. Wood and Víteslav Orel explain in Genetic Prehistory in Selective Breeding: A Prelude to Mendel.

"Of all domestic species, sheep had revealed the most to Bakewell," Wood and Orel write. "The idea of learning from sheep was at the same time an in-joke and a shared revelation within the circle to which the secret was being revealed."

Bakewell's farm, Dishley Grange, consisted of 450 fertile acres, and he was the third generation of Robert Bakewell on the land, which was leased. The Bakewells were self-described graziers who fattened sheep and cattle for city meat markets (Dishley is about one-hundred miles north of London).

Bakewell began to manage the farm at an early age and grew into a bold, competitive man. He expanded the farm's irrigation infrastructure and could flood much of it. Unconstrained by precipitation, he could take four hay crops a year and bragged he could cut hay until Christmas. He divided the farm into ten-acre paddocks he could further subdivide for efficient grazing.

Dishley Grange's productivity permitted the master to become the first English farmer to specialize in selective breeding. Bakewell sought to increase growth rates and maturity (sheep were then being slaughtered at three- to four-years of age); to increase the muscling; and to produce sheep with the least amount of feed. Bakewell reportedly called his New Leicester sheep "machines for turning herbage...into money."

How did Bakewell do it?

To compare growth rates and efficiency of an animal in converting feed into flesh, he fed individuals the same amount of feed and weighed them. He fed out twenty to forty top ram lambs a year and recorded their growth rates. He also looked for beauty (important for sales) and the texture of flesh. In one experiment cited by Wood and Orel, he bought a number of ram lambs from different sources and fed them for almost twelve months to ascertain growth rates, feed efficiency, and consequent differences in income when sold.

Bakewell's methods were both mysterious and controversial. To begin with, he learned that a change in location didn't necessarily change animals. He believed that an animal's nature functioned independently from the external world and had no qualms about bringing to his farm sheep from different regions. This was heresy in a time when most people believed that the environment produced different types of animals.

Under the prevailing beliefs, there was no point in importing fine-wooled Merino sheep from Spain to improve Great Britain's woolens, because the English climate would convert the animals into typical English coarse-wooled sheep. In fact, while the damp weather might challenge Merinos, which had been selected in a dry climate, the effect of the weather on the wool they grew would be negligible.

Of course, Bakewell was concerned with meat production. He was astonishingly interested in wool—another heresy. A Southdown breeder marveled that Bakewell told him "he wishes to breed a sort of sheep that produces no wool, a sort of doctrine I could not understand."

But the coarse wool from typical English longwool sheep wasn't valuable even in Bakewell's day.

Bakewell did experiment with a Merino ram in the 1780s and may have considered creating a dual-purpose sheep at one time. But he concluded that scenario was inefficient, saying, according to a 1794 book, General View of the Agriculture of Lincoln, cited by Wood and Orel, "it is impossible for sheep to produce mutton and wool in equal ratio; by a strict attention to the one, you must in great degree let go the other."

In addition to practicing rigorous selection, Bakewell inbred, and this was the most upsetting rumor of all. Bakewell learned, probably from cockfighters and pigeon fanciers, but perhaps also from racehorse breeders, that inbreeding could fix characteristics. If his best animals were closely related, he bred them to each other regardless of how close that relationship was.

An inbred animal was more likely to be prepotent, which meant that it would stamp its characteristics on its progeny. Bakewell's sheep looked alike, and performed differently from other sheep, to an astonishing degree. But the inbreeding of mammals violated ancient incest taboos that had arisen from experience with both humans and animals. Inbreeding led to weaknesses and deformities.

How did Bakewell get away with it?
First, he started with a diverse population; breeds, as we know them, didn't exist. In the late 1740s, he bought what he considered the best sheep in the region and rigorously selected for fifteen years. He judged a sheep by its performance—and, most importantly of all, by the performance of its offspring. That remains a difficult concept even today. Many a handsome, purple-ribboned ram of noble pedigree sires mediocre offspring.

Bakewell's lesson often is reduced to "he inbred," but Genetic Prehistory in Selective Breeding reveals his rigorous selection for performance, conformation and constitution. Contrary to legend, a cornerstone of Bakewell's work apparently was extensive outcrossing as well. Jay L. Lush, in his classic textbook Animal Breeding Plans, writes, "There is also more than a hint that he kept his operations secret because of certain extreme outbreeding he was practicing which, if known, might have injured the commercial reputation of his stock. Thus, there were rumors of a mysterious black ram used in his sheep breeding which visitors were never permitted to see and whose existence he would never admit."
During the 1760s, Bakewell pioneered the practice of leasing his top rams, rather than selling them, so he could evaluate their breeding worth on the ewes of other shepherds. “His annual auctions, or ram-lettings, attracted great attention and were a distinct financial success,” writes Lush. “He is said to have received as much as 1,200 guineas for one year’s use of a ram. By this practice of ram-letting, the best sires came back to him each year and any whose progeny had proved them much better than the others could be kept for use in his own flocks or herds.”

Bakewell also brought in rams sired by his best rams that he had leased—more new genes. And Lush speculates that Bakewell occasionally took back for his own use a ram that he had thought somewhat flawed but that was seen to have sired superior lambs in a customer’s flock.

A breeders’ club, the Dishley Society, established in 1789 with Bakewell as its first president, was important in uniting superior sheep and limiting inbreeding. The society shared similar goals, and this was a historic shift away from the previous pattern of breeders having vastly different ideals. Members had first choice of one another’s rams, with Bakewell’s being favored.

“This early version of the progeny test, designed to assess a male’s breeding value, was acknowledged by later breeders as a highly significant step in technique,” write Wood and Orel. “Bakewell had privileged access to all the flocks of the Dishley members on which to test his rams. From the point of view of progeny testing, the Dishley agreement was equivalent to his possessing an enormous herd.”

Bakewell’s goal was a useful number of above-average animals, not merely a few superior individuals that couldn’t perpetuate themselves. This “population thinking” was another breakthrough, according to Wood and Orel. They report that Bakewell’s first publicist, Arthur Young, secretary to the Board of Agriculture in London, quoted Bakewell as saying, “The merits of a breed cannot be supposed to depend on a few individuals of singular beauty: it is the larger number that must stamp their character on the whole mass: if the breed, by means of that greater number, is not able to establish itself, most assuredly it cannot be established by a few specimens.”

The principle of comparing a large numbers of animals of the same type and with common relationships—population genetics—would become a cornerstone of modern livestock breeding theory 150 years later. As computer technology and genetic knowledge advanced, the impact of population genetics mushroomed: a staggering number of animals could be compared on separate farms and assigned estimates of breeding value. Bakewell was considered secretive, but more likely he merely was busy and unwilling to waste his words on the uninitiated or on those who needed to be convinced, despite the living, breathing evidence. He talked with disciples, a handful of progressive breeders who practiced and who published his methods, but he wasn’t inclined to leave a written roadmap himself. The inner circle appears to have shared information freely but was cautious about sharing ideas with those bound by convention.

George Culley (1735–1813), who wrote a book based on Bakewell’s methods, referred to their practices humorously as Bakewell’s “sheepish doctrine.” These breeders ignored irrelevant controversy. For instance, by emphasizing early maturity, Bakewell reduced internal fat, which upset butchers who made money by selling tallow.

As for specific technique, apparently Bakewell kept parallel, unrelated lines within his flock and could “cross” them when relationships became too close or performance suffered. He outcrossed to sheep that also had been selected rigorously for growth rate and conformation.

“Such matings within a stock already strongly selected, brought substantial benefit with a manageable degree of risk, and it set the pattern for other breeders to follow,” observe Wood and Orel. “A grazer’s skill in distinguishing intrinsically fast and slow fattening animals opened the possibility of producing fast fattening breeds. Only a committed experimentalist like Bakewell was prepared to take this route, which was unacceptable to the majority of farmers because of loss of income in the short term.”

The corollary of Bakewell’s realization that inherent qualities didn’t alter merely because an animal was moved was that improvements didn’t hold constant, either, but had to be fought for in each generation. Rigorous selection would be relentless and never-ending.

The Dishley Society was also ahead of its time in realizing that accurate comparison could be confounded by different management practices. An important rule of the society was that rams being evaluated wouldn’t be fed grain, according to Genetic Prehistory in Selective Breeding. “Bakewell and his friends clearly appreciated that extravagant feeding on some farms, but not on others, would confuse the genetic picture. Their willingness to cooperate represented a radical departure from the traditional practice of ‘making up’ [heavy feeding and fattening].”

Again, the science of livestock breeding would codify this 200 years later in “contemporary groups”: animals being compared should be managed similarly. The effect of this principle is now much more powerful, because computers can calculate relative performance: a fifty-pound, pasture-raised lamb on one farm can be compared with a seventy-five-pound, grain-fed lamb on another; they’re first compared with their contemporary group and then their growth rate (not raw weight) can be assessed.

The Dishley breeders’ passion and excitement were unaffected by the fact that their traffic in rams was laughed at outside their circle as a “visionary romance.” While neighbors scoffed, however, the world was literally beating a path to Bakewell’s door as word of his achievements spread. Visitors came to Dishley Grange from across England, from France, from the outer reaches of the Austrian monarchy, from Poland, and even from Russia. On the way to Bakewell’s farm, they braved hazardous seas, roads that were muddy quagmires, language barriers, and crude roadhouses.

Bakewell’s maiden sister, Hannah, received visitors, and sometimes she and her staff hosted them for weeks until her brother returned from a trip. He was generous with these pilgrims, conducting what was, in effect, a school of agriculture. Bakewell’s irrigated farm was an innovative showplace for animal breeding and feeding—he even had developed his own strain of forage cabbages.

Two Russian youths who apprenticed themselves to him, and who struggled to learn English for that purpose, saw whole carcasses preserved in salt and hung side-by-side in the Dishley slaughter-
Breeders of livestock, and of sheep in particular, created an interest in heredity and left an important legacy to science, according to Genetic Prehistory in Selective Breeding. Breeders’ pressing practical problems raised the most interesting theoretical questions—many of which would be illuminated by a monk who began crossing peas in a monastery garden 61 years after Bakewell’s death.

If Robert Bakewell is the father of selective livestock breeding, an Iowa farm boy named Jay Lush became the founder of modern scientific breeding. The field has a surprisingly short history, and only a handful of great thinkers separate the eighteenth-century Englishman and the twentieth-century American.

The monk Gregor Mendel (1822–1884) is the most significant bridge between them. Mendel illuminat- ed mysteries of inheritance by cross-breeding peas in a walled monastery garden in Brünn, Moravia (now part of the Czech Republic), between 1856 and 1863. There, he discovered heredity’s basic unit, the gene.

Shepherds can take pride in the linking of Mendel with sheep breeders by Roger J. Wood and Viteslav Orel in their book Genetic Prehistory in Selective Breeding: A Prelude to Mendel: “Intimately involved in the continuing discussions about heredity, which arose from efforts to improve wool quality, were a number of experts destined to have a direct influence on Mendel’s career and intellectual development. Our analysis... has convinced us of the significance of Moravian sheep breeding in the progress of ideas about heredity.”

Fine wool was a mainstay of the Brünn (now Brno) economy, dependent upon clothing manufacture, and wool was the most profitable crop on the monastery’s farms. A local society of shepherds had begun to discuss the need for scientific principles to guide them, as did a group of plantmen. Mendel’s chief patron, monastery Abbot C.F. Napp, was Mendel’s link to these practical breeders.

Napp was fascinated by the methods used to create Moravia’s fine-wooled sheep. He took particular interest in reports from England of animal and plant crossbreeding. Johann Nestler, a professor of natural history and agriculture at a Moravian university, also influenced Napp. Keenly interested in sheep breeding, Nestler used the word “heredity” in a speech to the sheep society decades ahead of its common usage.

“Only in rare cases will the breeder know the Mendelian formula for more than a few genes in his animals,” notes Lush in Animal Breeding Plans. “He will never see the genes but can judge whether or not they are present only by the effects they produce, either in his animal itself or in some of its close relatives.”

Lush moved the field of livestock improvement to a new level by applying the quantitative methods and population genetics theories laid down by three men who built on Mendel’s work: British statistician Ronald Fisher; American zoologist Sewell Wright; and British evolutionary biologist J.B.S. Haldane. These pioneers explained change in populations mathematically.

“Fisher, Wright and Haldane showed theoretically how evolution in nature could be explained by selection, mutation, drift and systems of mating, without the need for other hypotheses,” writes Louis Olliver in his paper “Scientific Challenges to Animal Breeding and Genetics.”

Wright, for example, quantified inbreeding depression based on studies with guinea pigs as he sought to explain the optimum population structure for evolution. Lush, in turn, clarified the uses of both linebreeding and hybrid vigor for livestock improvement and established the practical applications of population-change theory.

Achieving consistency through linebreeding and taking advantage of vigor from heterosis remain of great interest to practical breeders, and Lush’s writing remains an excellent guide. Building on Bakewell’s work in Tudor England, Lush published in 1933 a famous bulletin on linebreeding that advocated the subdivision of a flock or herd into many lines, each mildly linebred to outstanding ancestors, with continuous pressure to discover exceptional animals and eliminate inferior ones.

Some research stations adopted Lush’s plan, but it was complicated and expen-
sive. Individual breeders have emphasized linebreeding (mild inbreeding) and use Lush’s method. But those who make a fetish of linebreeding would do well to ponder Lush’s reporting that every animal carries eight to ten defective genes.

The oldest breeds are young, with genetic defects fixed by the inbreeding used to create them. Even such “pure” breeds cannot truly be purified. Consider this caution from late in Lush’s life:

“[M]ost of us far underestimated the number of loci; it was already near 1920 when Muller rocked most of us to our heels by estimating that Drosophila [fruit flies] had something more than 2,000 loci. Most of us acted as if we thought that the pure breeds of livestock were nearly homozygous [pure]. With those two ideas in our mental background, the certain goal of genetics seemed clearly to be that we should compile a catalogue of the genes which each breed had. The rest would be easy!”

Biology and genetics have since moved into the molecular era and are mapping genes. The useable results for farmers, however, may be a long way off. In the meantime, Lush’s Animal Breeding Plans is the high water mark of twentieth-century thought and practice and a roadmap of the basics into the twenty-first century.

Jay Laurence Lush (1896–1982) was born in a log house in southwestern Iowa of English and Scotch-Irish stock, according to the autobiographical sketch he wrote for his induction into the National Academy of Sciences. He majored in animal husbandry at Kansas State Agricultural College, where he found mathematics easy but not intriguing, and was active in debating.

After receiving his bachelors degree in 1916, Lush taught in a Kansas high school for a year and then returned to Kansas State to earn his master’s degree. After nine months in the Army Air Corps and a brief stint in another Kansas high school, in 1919 Lush entered the doctoral program in genetics at the University of Wisconsin. Upon finishing in 1922, he went to the Texas Agricultural Experiment Station, where he worked for more than eight years on the genetics of Brahman cattle and Karakul sheep and on dairying issues.

Reflecting in a 1969 paper on his formative studying cattle and sheep in Texas, Lush revealed much about his mindset in advancing animal breeding. “I think my general attitude was that I respected immensely what the breeders of livestock had accomplished (without necessarily believing that all of this was really worth accomplishing) but I had an
almost religious faith that these breeders could have done still more, or have done it more easily, if they had known genetics,” Lush wrote.

“For the most part,” he added. “I didn’t try to tell them what their goal should be, but only to find better methods of approaching that goal, whatever it was. I tried to visit ranches and farms where anything unusual about breeding was said to be happening.”

Having no papers to grade or class rolls to call, he listened—to the animals, he reflected in a 1973 paper. “Usually the animals were saying something like: ‘Most of the things you think you know may be true in principle but you have many of them out of all proportion to their actual importance.’ I was always needing to be surer of how the various factors interacted in any whole operation we might be considering.”

In short, Lush came up against the problem of measurement. The differences between the humped Asian cattle and other breeds were apparent to him on horseback from a quarter of a mile away. But as he tried to measure and quantify differences, within-breed variations became apparent. And many qualities that could be measured had no practical importance.

Colleagues and friends in chemical engineering, statistics, and mathematics helped Lush adjust for such variables as the effects of weather on the day he weighed animals. Yet he was hindered by the difficulty in analyzing large data sets. The Texas research apprenticeship ended in 1930 when he left for Iowa State College. By then, Lush had struggled with so many analyses on so many topics that he was, he said, “peculiarly ripe to learn.”

At Iowa, he audited Sewell Wright’s class on statistical genetics, traveling to the University of Chicago. This prepared him for instruction by statistician Ronald Fisher, who guest-lectured for five weeks at Iowa. As Lush refined his understanding, he began a famous career of teaching graduate students. One wrote of him, “He was a warm and friendly person with a tremendous respect and tolerance for students.”

By the late 1940s, Animal Breeding Plans, first published in 1937, had been translated into Spanish, Polish, Portuguese, and Rumanian. Lush’s emphasis on breeding based not on the appearance of an animal but on its performance and genetic makeup had enormous influence. He considered his single most important paper his 1947 study on how much attention should be paid to the strengths and weaknesses of littermates when choosing swine for breeding stock.

“The problem developed into the more general one of asking how much a population mean [average] would be changed by selection on individual performance alone versus selecting on family merit alone,” wrote one of his former graduate students, Arthur B. Chapter.

The bottom line for pig farmers was that Lush wrote equations for predicting the breeding value of an individual based on its own performance and its family average.

It was one of Lush’s doctoral students, another Iowa farm boy, C.R. Henderson, whose work would transform animal breeding around the globe by showing how to draw linear meanings from masses of performance data, missing information, and genetic relationships.

“Chuck” Henderson, born fifteen years later than Lush in the same county, showed exceptional promise from an early age. Growing up on a classic diversified farm, where horses supplied power for fieldwork, Henderson was named Iowa’s Farmer of the Year as a senior in high school. He excelled in sports and was interested in classical music.

His master’s thesis involved estimating variance in the progeny of crosses from lines of inbred swine. Endorsed by the legendary statistician Fisher and published in Biometrics in 1953, the work became a standard reference on variance.

Henderson minored in statistics during his subsequent doctoral study in animal breeding. As part of his doctoral work, he developed a method to minimize problems caused by missing data.

With his dissertation still to write, Henderson took a job in 1948 at Cornell University, where in about a year he presented his refined techniques as BLUP: Best Linear Unbiased Prediction. BLUP merged several techniques to deal with “messy, unbalanced data”—random genetic effects, environmental factors, and missing data that must be predicted. BLUP disentangles nature (genetics) from nurture (the environment). Uniting two major but formerly separate equation models, Henderson showed how millions of computations could be performed simultaneously in genetic evaluations to appropriately emphasize pieces of information. BLUP didn’t require random sampling of the population to prevent bias—this was vital, because selection of sires and dams is made on the basis of their performance, not because they are “representative” or average animals.

Henderson’s statistical technique improves its accuracy when there are genetic relationships among groups being evaluated on different farms. In a major practical application, he convinced New York State dairymen to use the semen of young bulls in many herds so that their daughters could be evaluated in several places. Although this was highly controversial, his method soon showed which sires were superior at transmitting milking ability. The experiment was a breakthrough in applied livestock breeding and resulted in the fastest genetic progress for milk production that had ever been seen.

Once computing power caught up with Henderson’s ideas in the early 1980s, the most effective and accurate way to evaluate animals was complete.

BLUP bases its estimates of breeding value on farmers’ measurements body weight or milk production and takes into account a myriad of variables: the age of dams, genetic progress and the effect of selection, the heritability of traits, effects of inbreeding, the quality of the animal’s own herd or flock, and the season of the year. Once these computations are made, animals from different farms, management systems, and even those born in different years can be compared directly.

“Lush, and later Henderson, led the profession for nearly all of the twentieth century,” wrote L. Dale Van Vleck in a brief biography of Henderson. “Lush outlined the basic principles and methods for genetic improvement. Henderson followed by developing methods first to estimate the genetic parameters needed for the application of those principles and then to predict most accurately the genetic values of animals available for selection.

“Henderson’s methods have been since the 1950s—and will be for the foreseeable future—the basis for genetic evaluations for every breed of every class of livestock in every country in the world. Millions of beef cattle, dairy cattle, pigs, sheep, and other species are evaluated annually with what are called ‘Henderson’s mixed model equations.’ These equations are also applied to sta-
tistical analyses in many other disciplines. The impact of Henderson’s discoveries is perhaps incalculable.”

In the estimation of Van Vleck—Henderson’s graduate student, friend, and colleague—Lush and Henderson “had more impact on modern animal production in the United States and the world than any other pair of scientists since the rediscovery of Mendel’s laws.”

Henderson (1911–1989) would join Jay Lush in 1985 as a member of the National Academy of Sciences, a rare honor for animal scientists. Like Lush and Sewell Wright, his chief role models, Henderson continued working until he died. He passed away after preparing slides for a scientific meeting to be held a week later.

Henderson’s work has so successfully transformed livestock that, inevitably, it has been attacked. Increasingly during early 2000s, BLUP’s expected progeny differences (EPDs) have been blamed for creating cattle and sheep that are too big, animals suited for feedlots but unfit for life on pasture.

However, single-trait selection for such things as growth rate and mature size was a problem long before EPDs. The show ring is notorious for emphasizing large size and irrelevant beauty points. But because EPDs are so effective, they can make the bad consequences of wrongheaded breeding happen much faster than any other method.

Lush is Henderson’s eloquent defender from the grave. He wrote in Animal Breeding Plans, “Considerably more needs to be done in developing practical selection indexes which will pay attention to each practically important characteristic without the risk of overemphasizing it.”

Indexes thwart the human tendency to maximize and thereby to lose biological balance. Growth rate is important, but not at the cost of losing mothering ability or other aspects of biological fitness. Among thinking livestock breeders, indexes have become vital for identifying genetics that are balanced, efficient, and optimal for the production environment.

Increasingly, EPDs and the easy distribution of breeding stock are being implicated in a lack of fitness for particular environments. Animals comfortable in extreme environments—deserts, mountains, jungles—usually must originate in those environments. A breeder of Hereford cattle in Georgia may ruin his herd’s adaptive progress to heat and humidity by using a Minnesota bull.

Again, Lush, from Animal Breeding Plans: “It seems likely that the matter of local adaptability will receive more attention in the future than it has in the past…. The ideal must often be a compromise between satisfying the market and satisfying one’s own conditions most completely.”

From this distance, Lush seems like a parent whose gently expressed cautions haven’t been heeded. He had thought about problems decades before they became issues. But sometimes the tools are blamed instead of the way they are used. It is true, as the Amish know, that tools can drive behavior. But it is also true that a balance between common sense and the use of technology is possible.

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At least, as a breeder unwilling to forget the power of EPDs, I believe so. The rigorous approach is to define goals, assemble an index that reflects them, and make measurements. But the general level of breeding knowledge among today’s stockmen appears to be low and limits them. They fall for trends and for people selling their own systems.

Most breeders don’t study Bakewell’s lessons concerning selection pressure or Lush’s explication of breeding systems or use EPDs. Henderson’s measure of breeding worth. Some intimidation may be involved—genetics quickly becomes math, which becomes statistics. But the concepts can be grasped.

Shepherds have lessons to learn from the greatest minds that have struggled with the question of how to breed better livestock.

Richard Gilbert says he’s made his share of mistakes in breeding sheep for ten years near Athens, Ohio.