

# Theory and Method: An Analysis of European and American Animal Breeding Practices, from the Eighteenth to the Twenty-First Century

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*In the twentieth century a conflict arose between geneticists and practical breeders over which theory of heredity should direct animal breeding strategies and methods. Two different approaches existed and competed with each other over how to develop a breeding methodology for the livestock industries. This article addresses strategies on the basis of theoretical outlooks by explaining the way they arose over the eighteenth and nineteenth centuries, what brought them into conflict with each other after the rise of Mendelian genetics in 1900, and ultimately how and why the differing systems emanating from them affected animal industries over the twentieth and into the twenty-first century. Looking at methodology through the lens of its theoretical roots provides an enriched appreciation of the interrelationship between science and practice, and also shows that the intellectual disagreements between geneticists and practical breeders rested on foundations that far predated the science of genetics.*

**T**HIS ARTICLE ANALYZES THE WAY THEORY and method together shaped European and American animal breeding and, subsequently, the livestock industries that breeding supported. The article does so by reviewing and contextualizing how a twentieth-century conflict arose between geneticists and practical breeders (generally speaking specialized and nonspecialized farm animal breeders but also hobbyists) over which theory of heredity should direct animal breeding strategies and methods. Two different approaches existed and competed with each other over how to develop a breeding methodology for the livestock industries. The two strategies are addressed on the basis of their theoretical outlooks. Specifically, this article explains the way these strategies

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arose over the eighteenth and nineteenth centuries, what brought them into conflict with each other after the rise of Mendelian genetics in 1900, and ultimately how and why the differing systems emanating from them affected animal industries over the twentieth and into the twenty-first century.

Approaching methodology through the lens of its theoretical roots provides an enriched appreciation of the interrelationship between science and practice. For naturalists (later scientists), there were two competing theoretical understandings of heredity. An organism or holistic approach rested on the conviction that animal populations could be successfully changed through breeding because of the presence of a biological but unknown “force,” which did not need to be understood or identified. A genetic architecture approach took the position that the “force” should be fully explained, within the framework of cell theory, before animals could be bred properly. Under the genetic architecture point of view, change, as a result of breeding, was to be judged on the basis of individuals, not populations. There was considerable debate among naturalists and later scientists over which model should guide selection schemes. No such oscillation occurred in the thinking of most practical breeders over the centuries: they tended to adhere to variations of the first approach. This theoretical outlook dovetailed well with the desired aims of the majority of practical breeders, resulting in methods amenable to their interests. In other words, the intellectual disagreements between geneticists and practical breeders that emerged in the twentieth century rested on foundations that far predated the science of genetics.

By looking at breeding strategies in light of their theoretical roots, it is also possible to see that an interconnected triangle (breeding intent, industry structure, and methodology) helped determine practical breeders’ acceptance or rejection of geneticist breeding plans. The aims of practical breeders in artificial selection affected how the structure of livestock industries developed; industry structure in turn played a role in directing what methodology breeders would use. This article will provide not simply an appreciation of how the chain of historical events unfolded, but also a more nuanced understanding of what they mean when taken together, yielding new insight into the dynamics of animal breeding and their impact on livestock industries.

The historiography regarding agricultural breeding and genetics does not normally address practical animal breeding through the lens of theory. The tendency has been to study genetic methodology in light of its ultimate acceptance or rejection by practical breeders. Furthermore, the vast amount of scholarly work devoted to this overarching topic deals primarily with plants.<sup>1</sup>

Genetics in relation to practical animal breeding remains an understudied subject. Scholars have also examined the methodologies of practical animal breeders and geneticists through the lens of eugenics.<sup>2</sup> Patterns in the relationship of science to practice, and perhaps equally importantly the relationship of pseudo-science to both, are revealed by this combined scholarship. But rooting methodology in theory, especially significant when it comes to animals, adds more information about the science-practice connection.

Selection strategies for practical purposes received serious European attention in Roman times. The earliest principle was set out by Varro, who hinted at an important breeding tool: progeny testing. Offspring should be used to judge the breeding quality of the parents.<sup>3</sup> In the first century AD, one hundred years after Varro, Columella expanded on the subject in his twelve-volume *De Re Rustica*.<sup>4</sup> All breeding strategies set out by classical writers must be seen within the framework of their attitude toward heredity. They saw heredity as being affected by, and therefore intimately tied to, environmental factors. After the fall of Rome and until the seventeenth century, practical breeders continued to be influenced by this concept, which argued that what animals ate and the environment in which they ate it affected what the creatures became.<sup>5</sup> Generally speaking, before the eighteenth century, practical continental European and British breeders used varying breeding strategies to counteract the effects of environment on heredity in order to maintain the quality of animals rather than improve it.<sup>6</sup>

Naturalist thinking during the Enlightenment brought major shifts in attitudes toward heredity. Naturalists, a mixed group of thinkers across Europe who came from different intellectual backgrounds and training, observed the natural world. Their commonality resulted from their desire to understand the dynamics behind all aspects of nature, generally speaking by postulating and then testing theories. Before the eighteenth century the naturalist outlook toward heredity was irrevocably entangled with views concerning generation, via conception, birth, and embryology.<sup>7</sup> They began to see heredity as separate from these other phenomena, as a process or “force” in its own right, in the eighteenth century. Practical breeders translated this theory to mean that heredity, now detached from environmental factors, could be manipulated to advance human concerns. The breeding objectives of the practical breeders changed and became focused on improvement.<sup>8</sup> The conviction that quality was a maintenance issue is a highly significant concept in animal breeding and did not die after that time.<sup>9</sup> Practical breeders, however, remained interested

only in breeding results, not in the underlying dynamics behind those results.

Methods designed to bring about improvement within that theoretical framework developed quickly and rested on the conviction that good breeding could proceed with no knowledge of underlying hereditary laws. Experience taught which systems brought about the desired results because only through experience could a breeder learn which selection strategies worked best to increase the ability of chickens to lay eggs, cows to give milk, or cattle to develop good meat qualities. Two particularly important methods, both of which arose from that standpoint and aimed at creating lines that bred truly over generations, took shape in England. The two methods would play an enormously important role in practical breeding systems over the nineteenth and twentieth centuries. The first evolved from a desire to make farm animals more uniform in type and better for agricultural production. While many breeders probably contributed to the framing of the method, British tenant farmer Robert Bakewell (1725–1795) gets the credit for its popularity.<sup>10</sup> While Bakewell himself wrote little about his breeding methods, letters of the Culley brothers, reports by agriculturalist Arthur Young, and a treatise by the breeder Sir John Sebright reveal Bakewell's principles.<sup>11</sup> His system was based on three primary premises: first, inbreeding for type; second, equal emphasis on males and females, which were considered to contribute identically to the characteristics of the offspring; and third, selection for both quality and vigor on the basis of the progeny test.<sup>12</sup> Progeny testing and inbreeding were particularly important to his method.<sup>13</sup> Although he valued the input of females, Bakewell tended to emphasize progeny testing of males from his inbreeding programs. Since males provided half the hereditary input to a herd or population, Bakewell could quantify resulting changes across herds or populations more effectively.

Bakewell and his fellow farm breeders seem to have been the first to look at inheritance in terms of populations rather than individuals.<sup>14</sup> Volume was especially important to Bakewell, because he saw breeding as a tool to rapidly augment food production for Britain's growing population, a trend that worried many and that culminated in the famous 1798 treatise of Thomas Malthus, who theorized that the food supply could not keep up with population growth. Although no accurate figures existed before 1801 on the actual population of England and Wales, many individuals in the late eighteenth century were aware that the number of people was growing at a disproportionate rate. Clearly Bakewell recognized that there would be an ever larger market for food supplies, particularly meat, as this trend progressed. He was

interested in stamping type, and he aimed at creating lines that bred truly, that is “breeds,” because this process sustained greater levels of production. Bakewellianism was designed to work with assumed hereditary laws—laws that seemed evident from breeding experience—in order to achieve the objectives of breeding—namely, better, more uniform farm animals in greater volume. Bakewell recognized the value of livestock breeders working together as a group, and in 1783 he formed an organization, the Dishley Society, to advance their interests.

The second breeding method resulted from the development of the Thoroughbred horse. Like Bakewell, the horse breeders intended to breed for true-producing lines. But Thoroughbred horse breeding varied from Bakewell’s method in four critical ways. First, Thoroughbred horse breeding emphasized the input of males over females. The system was based on the crossing of Arabians on local horses—classically, Arabian stallions on local mares, although later DNA testing has shown that Arabian females played a significant role in the makeup of early Thoroughbreds.<sup>15</sup> The crosses were considered to be “thoroughly bred” and therefore labeled “Thoroughbred.” Second, ancestry breeding and emphasis on individual worth, not progeny testing and quantification of breeding results, were the main selection tools. Third, inbreeding was avoided. Fourth, public pedigree-keeping was central to ancestry breeding. The General Stud Book, established as early as 1791 by James Weatherby, recorded pedigrees for these horses. Pedigree-keeping introduced concepts of purity and status to animals.<sup>16</sup> From the beginning, the elite members of society—royalty and the nobility—were the principal breeders, and that fact meant that their class views shaped and colored horse breeding philosophy. The cultural and social impressions that arose from these associations would be significant over the years.

Both methods were designed to provide improvement by taking into account what past experience had taught breeders about the working of the hereditary force—that is, the contradictory effects that inbreeding and outcrossing breeding strategies had on the resulting progeny. As far back as Roman times, breeders understood that inbreeding could reduce the vigor and fertility of plants and animals, and that crossing inbred lines brought a return of both vigor and fertility. The outcrossed progeny of the two inbred lines were often better than either parent line, but that progeny would not breed truly to its improved state.<sup>17</sup> The new eighteenth-century methods devised more formalized approaches to working with these known complex patterns and to neutralizing the dangers that came with excessive inbreeding or out-

crossing. Bakewell's system focused on inbreeding. He planned to capitalize on the benefits it offered (namely, uniformity) and to minimize its dangers. Selection and the progeny test made it possible to identify good animals. It was the percentage of good and strong offspring over bad and weakened that defined the parent as a superior breeder. Good offspring that withstood inbreeding were often bred back to that parent. Avoidance of inbreeding by Thoroughbred horse breeders reduced the chances of encountering inbreeding difficulties, but even mild outcrossing confronted them with unpredictability. Thoroughbred horse breeders believed that this problem would be overcome by relying on ancestry breeding, particularly the past performance of specific but unrelated males recorded in pedigrees. The input of quality ancestors via their descendants might not guarantee success, but it did enhance the odds of getting good results. The challenge of working with this interplay of inbreeding and outcrossing would dominate all future breeding methodology, whether it related to practical strategies or the theories of naturalists/geneticists.

By the late eighteenth century, the evident effects that artificial selection had on animals fascinated naturalists concerned with heredity. The naturalists were not interested in the way practical breeders bred animals; instead, breeding results commanded their attention. For instance, in 1745 the French mathematician and astronomer Pierre-Louis de Maupertuis (1698–1759) noted that artificial selection had altered domestic animals and plants, and he wondered if natural selection could be powerful enough to cause the development of new species.<sup>18</sup> Encouraged by evidence of change seen in practical breeding results, naturalists began experimental breeding programs as a way to explain hereditary mechanisms. Perhaps the dynamics of hereditary factors could be revealed through breeding exercises.

In 1751 Swedish botanist Carl Linnaeus published a systematic discussion of plant hybrids, thereby founding the hybridist tradition for scientific analysis and experimental breeding.<sup>19</sup> The first person to be credited with working with this breeding method was the German travel writer, historian, and geographer J. G. Kölreuter, who published the details of his experiments in 1761.<sup>20</sup> Experimenters initially focused on plant breeding in their hybridizing work, meaning the crossing of unrelated lines. Deviation was what they were after. Breeding “like to like” did not interest them because no underlying laws would be revealed through homogeneity. Breeding methods were not tailored, therefore, to produce true breeding lines. In the nineteenth century a few naturalists began experimenting with animal breeding, and they did so along the hybridizing lines of the experimental plant breeders and for the same reason,

specifically to understand the force behind the hereditary laws that drove variation. In 1819 Hungarian nobleman Count Festetics undertook inbreeding/crossing experiments with animals and subsequently wrote a treatise entitled "Hereditary Laws of Nature."<sup>21</sup> The basic outlook of the naturalists differed from that of practical breeders in all this experimental breeding. Naturalists tended to seek deviation and/or variation through hybridizing, which resulted in progeny not intended for use in future breeding. Practical breeders looked for continuity in true breeding lines, which were designed to produce quantitative changes over generations, meaning a gradual increase in output of eggs, milk, or meat. Occasionally breeders utilized the two approaches together, attempting to find methods that would deal with both objectives (understanding hereditary dynamics and bringing about improvement). Such was the case with sheep breeding experiments near Brno, Moravia, in the 1830s.<sup>22</sup>

After the mid-nineteenth century, naturalist views concerning heredity became more complex. By 1860 notions of heredity as a kind of "force" lingered in the minds of some, but others began to conceptualize inheritance within a cell theory framework, meaning that some unknown but separate physical matter must lie behind the process of heredity.<sup>23</sup> This attitude could be described as the beginnings of a genetic architecture approach to the study of heredity. Efforts to identify certain aspects of the substance encouraged greater emphasis on experimental hybridizing. The rise of cell theory also initiated the separation of naturalists who supported the theory from practical breeders. Throughout the nineteenth and twentieth centuries, breeder views regarding heredity remained underpinned by the sense that an unknown but general force drove inheritance patterns and that this force could be manipulated and controlled.<sup>24</sup>

Over the nineteenth century, however, patterns in practical breeding shifted in significant ways within that force-dominated framework. Breeding saw the decline of Bakewellianism and the growth of purebred breeding, also established in England. Purebred breeding developed from a fusion of Bakewellianism and Thoroughbred horse breeding, and its creation can be attributed to the work of one man, the English livestock breeder Thomas Bates. About 1800 he began to acquire Shorthorn cattle, bred by the Colling brothers on the basis of Bakewellian principles. Bates then followed a new breeding strategy incorporating tenets of Thoroughbred horse breeding. He recognized that the horse breeding system had proved to be a powerful marketing tool with its emphasis on keeping publicly recorded pedigrees. Bates linked inbreeding, purity, and ancestry breeding together in the use of public pedigrees. He



championed the registry that George Coates established for Shorthorns in 1822 and argued that it provided proof of inbreeding and therefore purity in the stock.<sup>25</sup> Inbreeding and purity connoted different meanings in Bakewellianism and in Bates's method: under Bakewell they brought consistency of type, but under Bates they also meant lack of contamination, a concept derived from Thoroughbred horse breeding.

With the passage of time, many purebred breeders ceased to recognize that purebred breeding was not synonymous with Bakewellianism, or that the infiltration of Thoroughbred horse culture to farm breeding had brought about the expansion of an entirely new method, albeit one that still rested on the theoretical view that hereditary force could be manipulated without knowing what the dynamics of that force might be. When explaining the purebred method to farmers in North America, for example, editors of journals simply outlined Bakewell's principles, implying they matched those of purebred breeding. Especially noticeable was their linkage of public pedigree-keeping with the Bakewellian system.<sup>26</sup> The infusion of Thoroughbred horse culture to the Bakewell method led in turn to the spread of complicated views implying that quality in animals could be related to quality in people. Purebred breeding provided a rationale for imbuing the concept of purity with ethical and social implications. By providing evidence of purity's value, purebred breeding was used in support of eugenics, which spread throughout societies around the world.<sup>27</sup> While there is undeniable linkage between eugenics and animal breeding through this emphasis on purity, it should be noted that the underlying power of "purity" for animal breeders remained consistency of type, which in the long run meant marketing power. Bates's strategy created cattle that were in demand, indicating that the system had economic implications. It enhanced the marketability of animals bred to its standards, which drove the spread of the method's use, first in Britain, then in continental Europe and North America. By the late nineteenth century, the method had become the most favored strategy for improvement breeding throughout the western world. Structures to support purebred breeding—namely, breed associations and joint-purebred organizations—arose and effectively disseminated ideas about how breeding should ideally proceed in most livestock industries. Purebred breeders promoted the method's value on the basis of endorsement from agricultural institutions and governments. The influence of the method on breeding was profound: all attitudes toward breeding came to reflect its impact even if not all animals were purebred, and all breeding manifested the same concern purebred breeders had with producing true lines.



While the literature addressing purebred breeding and its effects on both animals and humans is vast, for the purposes of this article four factors are particularly important. First, after 1900 purebred breeding became the most important type of practical improvement breeding to confront the genetic architecture approach; second, purebred breeding brought a significant move away from the Bakewellian progeny test and quantification of breeding results; third, individual worth took precedence over population assessments; and fourth, beauty became a valued feature in animals—aesthetics mattered.

By the late nineteenth century, naturalists increasingly fell into the two divided and even opposing groups that would go on to dominate twentieth-century geneticist attitudes toward heredity and breeding. Naturalist groups now either looked at inheritance in terms of cell matter within individuals via hybridizing breeding or assessed shifts in inheritance on the basis of populations. In their attempts to explain natural selection, or population shifts under Darwinism, the second group turned to statistical means to explain hereditary patterns within populations. In 1886 the discipline of biometry was born from that standpoint. It was founded by Briton Francis Galton, a Victorian statistician, inventor, anthropologist, and eugenicist, among other endeavors, who was influenced by his cousin Charles Darwin. British mathematician and statistician Karl Pearson, associated with University College, London, elaborated on Galton's work by devising more sophisticated statistics. Biometry hypothesized that hereditary patterns should be understood in terms of generational changes within populations.<sup>28</sup> Practical breeding methods had played a role in shaping the theory behind biometry. Charles Darwin, who looked at population change in his work on evolution and who influenced the thinking of biometricians, had been very interested in practical breeding, even breeding pigeons himself. Galton had taken note of the breeding strategies of Thoroughbred horse breeders. Pearson had assessed the effects of breeding over the years on color patterns in Shorthorn cattle. The approach of this group, built to some degree on practical breeding, closely matched the basic view of practical breeders that an unknown force directed heredity. With the rediscovery of Mendel's laws and the birth of Mendelian genetics after 1900, experimental inbreeding and hybridizing drew the increased interest of naturalist/scientists.<sup>29</sup>

Gregor Mendel, a Moravian monk, had worked with the standard hybridizing inbreeding/crossing method of breeding as early as 1865. In effect he invented a controlled approach to research breeding, and it has been argued that he only intended to explain hybridizing. After 1900 his re-discoverers

saw the method as one that could be used to elucidate much more. Specifically, it could be used to explore the nature of hereditary laws in general.<sup>30</sup> Scientists quickly took Mendel's sense of immutability in cellular material driving hybridization as meaning genes generally were constant and unchangeable, thereby suggesting that mutation alone could shift their nature. The constancy factor, along with the recessive/dominant nature of genes, helped scientists in their new studies. The genetic architecture of patterns, such as the well-known phenomena of reduced fertility of inbred lines and hybrid vigor from crossbreeding, might now be explained by Mendel's two laws. As early as 1908 George H. Shull (an American plant geneticist who graduated from the University of Chicago and worked at the Carnegie Institute) questioned why the progeny of inbred lines could not sustain superiority into the next generation. He wondered as well if there was a Mendelian explanation for the hybrid vigor (which he labeled "heterosis" in 1914) of the first generation crosses.<sup>31</sup> Experimenters were convinced that their highly developed breeding methodology, now with the aid of Mendelian theory, could be used to reveal many hereditary patterns of evolution that had so eluded them in earlier times. Mendelism triggered the beginnings of what would erupt shortly into a serious divide in outlook, ultimately leading to confrontation between practical breeder and scientist.

Mendelian experimentation received the lion's share of research aid after 1900, and while plants continued to dominate the work, a number of studies were conducted on chickens, designed to assess such elements as deviations in color and leg and wing shape. Even though such research was largely funded by academic institutions in service to agriculture, it had little or nothing to do with increasing farm productivity.<sup>32</sup> The very interest of governments in funding genetic studies within agricultural institutions, however, paved the way for a future shift: from breeding in order to understanding genetic laws and/or evolution to breeding that utilized genetic laws to achieve improvement.<sup>33</sup> When naturalists (now geneticists) started in the twentieth century to more seriously address plant breeding and, subsequently, animal breeding from an improvement point of view, they confronted practical breeders over method and general outlook. Under these conditions, clashes between practical animal breeder and academic scientist became common.

A particularly good example can be seen in the 1913 debate between American biologist Raymond Pearl and practical breeder H. H. Stoddard over chicken breeding. Pearl, a scientist working at the Maine Experiment Station between 1907 and 1916, who later spent most of his working life at

Johns Hopkins University, was one of the few early researchers interested in farm animal improvement. Pearl hoped his experiments would reveal how hereditary laws governing egg laying operated and, therefore, what breeding strategies made the best sense for farmers. He believed, as did many of his time, that traits like egg-laying ability were inherited on a relatively simple gene basis. He concluded that practical breeders should avoid the “childishly simple scheme of breeding like to like.” Pearl stated that the method was counterproductive because it did not take into account (which his tests did) the importance of the male in egg-laying ability.<sup>34</sup> Stoddard, a lifelong chicken breeder and journalist, disagreed with Pearl’s approach and theories. While Stoddard accepted the idea that males were important, he argued that experience proved females “had a great deal to say about” egg-laying capacity.<sup>35</sup> Furthermore, “like to like” breeding worked, and did so because it took into account the dynamics of hereditary laws that governed the input of both male and female. The method might not result in consistently superior progeny, but it led to some offspring being as good as the parents “and some decidedly better,” Stoddard wrote.<sup>36</sup> By breeding from the “decidedly better” progeny for the next generation, improvement was possible.

The Pearl-Stoddard debate also appeared to pit scientist against practical breeder in terms of qualitative traits (either inherited or not) versus quantitative traits (always inherited and only varying by degree of expression). The two men seemed to be at odds over the complexity of trait inheritance as well. Pearl’s experimental position seemed to rest on the qualitative/simple-gene Mendelian stance, while Stoddard’s experience-oriented view led him to support a quantitative/complex-gene approach. The implications of Pearl’s comments could be unclear both generally (e.g., his assessment of relative male and female input to egg-laying ability) and for the purposes of actual breeding methodology (e.g., his emphasis on progeny testing versus ancestry breeding was not evident in his publications), thereby undermining his arguments. It remained difficult, even for scientists, to see how genetics could affect agricultural breeding of animals. William E. Castle, an American embryologist and Harvard University professor who turned to mammalian genetics after the rediscovery of Mendel’s laws, contended that, as far as animal breeding was concerned (especially the larger animals), traditional methods would prevail. Farmers “breed animals as our fathers and grandfathers did because their time-honored methods succeed and we know of no reason for changing these methods,” he wrote in a 1912 issue of the *American Breeders’ Magazine*.<sup>37</sup>

Geneticists who relied on a genetic architecture approach increasingly ar-

gued that hybrid breeding should take precedence over true line breeding in agriculture. Experiments along these lines started with plants. In 1917, while working with corn, D. F. Jones, an American agricultural plant geneticist working at the Connecticut Agricultural Experiment Station, undertook the task of making the traditional hybridizing method of breeding serve agriculture's concern with improvement. He began by trying to understand what underlay the process of heterosis. Jones reasoned that dominant/recessive gene pairs could produce heterosis—it was not necessary to have dominant/dominant pairs. Jones believed that the dominance/recessive factor also explained why inbreeding caused degeneration. Inbreeding revealed the presence of “lethal” recessives because it encouraged recessive/recessive inheritance.<sup>38</sup> Recessives cannot show their lethal effects if they are paired with a dominant half.

He hypothesized that a double-cross hybrid method of breeding would take into account the dominance/recessive factor behind heterosis and, at the same time, would overcome the problem of recessive/recessive inheritance. He planned to take two inbred lines and cross them to produce a first generation line. Two other inbred lines would be crossed for another first generation hybrid line. Next these two first generation lines would be crossed to produce the final product, which would show hybrid vigor (or heterosis). Jones postulated that he could, by the first cross of inbreds, restore the lines to the original fertility (by removing the recessive/recessive inheritance) and, by the second cross, bring out superior hybrid vigor in a dominant/recessive or dominant/dominant inheritance pattern.<sup>39</sup> In order to maintain that level of hybrid vigor over succeeding generations, seeds from the final cross would not be used for breeding. New generations demonstrating hybrid vigor would always be regenerated by stock belonging to the parent and grandparent generations. Jones had invented the double-cross hybrid corn breeding method, which was designed, not to uncover patterns of inheritance, but rather to increase corn productivity. It would become the foundation of genetics' agricultural breeding methodology.

The rise of the double-cross hybrid corn method illustrates the complete transition from Mendel's approach as explanation to its use for agricultural production. Early geneticists believed that Mendel had actually deduced general laws of heredity, and also that the Mendelian method could be used to elucidate the dynamics of gene interaction. Jones represented the new vision: proven genetic laws could be put to use and capitalized on to advance specific interests such as agricultural production. It is worth noting that the common thread through this transition was the continuation of hybridizing. There was

no deviation in breeding methodology. The transition did, however, bring about a theoretical change with respect to agricultural breeding: hybridizing should replace true breeding lines.

Companies interested in corn breeding were prepared to invest in experimenting with the new method because they recognized that it had the potential to generate guaranteed income. They could maintain economic viability by virtue of the fact that the producer would be a forced return customer. Saving seeds for next year's planting would not result in similar corn, because hybridized plants and animals will not breed truly to their quality. Effectively, companies would have a patent, which could be described as a biological lock. In spite of propaganda that suggested otherwise, it would take some years, and considerable effort and expense, before the method was more successful than traditional corn-breeding methods, which relied on selecting for lines that reproduced truly.<sup>40</sup> Geneticists researching for the companies had achieved some success by the 1920s, enough to encourage farmers to begin buying double-cross hybrid seeds. This breeding *volte-face* would bring about a complete structural change in the American corn industry. As faith in breeding true lines collapsed, corn-producing farmers stopped breeding and collecting their own seeds for next year's crop. When the company-bred hybrid corn replaced farmer-bred corn, the industry became fractured in a way that was new to any agricultural industry: farmers were separated from both breeding and control of breeding. The breeding arm of the industry fell under the control of corporate enterprise.

Success led to geneticist experimentation over the 1920s with the double-cross hybrid method on chickens, funded by the input of the corporate bodies that had revolutionized the corn industry. The cheapness of individual birds and their fast reproductive life encouraged corporate enterprise to promote the creation of good hybrid lines in order to reap the same rewards that hybrid corn had generated: repeat guaranteed customers due to the biological lock and natural patent. By the 1930s American geneticists had successfully developed hybrid chickens along the same lines, and the chicken breeding industry underwent a transformation similar to that found in the corn industry, first in the United States, and by the 1950s around the world. Farmers producing eggs no longer bred their own hens. They bought chicks from the corn/chicken breeding companies. Genetics had entered the world of farm animal breeding. Genetic breeding meant hybridizing.

There were reasons for this revolution that had little to do with science or understanding genetic architecture. The geneticist approach ultimately took

precedence over the traditional approach, not because of superior breeding knowledge, but rather because of changing industry structure at the time. Of primary significance was the fractured nature of the traditional chicken breeding world in the 1930s within the United States, where the revolution began, a situation that ultimately divided the breeding arm from the producing arm of the industry.

An escalating separation had been developing since the 1890s between breeders and chicken farmers keeping hens to produce eggs. A major underlying divisive factor in the chicken industry throughout this period related to the gender of people functioning within the two sectors: breeders were increasingly men only, while producers were overwhelmingly women. The breeders themselves encouraged a greater industry division than gendered labor would imply. Many chicken breeders worked with inbreeding and crossing inbred lines and, by following such strategies, had tended for years to separate themselves from ordinary chicken farmers, who were women. By the 1920s North American chicken breeders were also hopelessly divided themselves, a situation that in the end created a sort of breeding vacuum. The adherence of the American Poultry Association to the Standard of Perfection, which was based on phenotype, undermined attempts by some breeders to breed for utility. The resulting division in the breeding world also seemed to promote a general loss of knowledge of classic breeding methodology set out by such renowned poultry breeders as I. K. Felch and H. H. Stoddard. All of these factors made it difficult for chicken farmers to breed birds themselves. The hatchery industry—composed of commercial enterprises that bought eggs from breeders and incubated these to produce baby chicks—encouraged this trend and acted as another wedge between the breeding and producing arms of the chicken industry. Increasingly, farmers producing eggs bought stock (usually baby chicks from hatcheries) rather than replacing stock with their own breeding. Producers, separated from the process of breeding, began to demand hybrid stock when the companies made it available.<sup>41</sup> By the 1950s, successful American breeding companies joined similar ones that had arisen in Europe in dominating worldwide chicken breeding. The biological lock had been the primary corporate driver. The collapse of traditional approaches to breeding methods that emphasized the true line breeding of birds fed into the situation.<sup>42</sup>

The hybrid chicken method did not penetrate other animal breeding industries to the same degree, but not for lack of trying.<sup>43</sup> This method had little effect, for example, on either dairy or beef breeding. Inherent characteristics

of hybrid breeding and industry structure both played a role in deterring any such change. The cost of the individual animals and slow reproduction made hybrid breeding a difficult and lengthy process in cattle and therefore discouraged the involvement of corporate enterprise. Tens of thousands of chickens had been required to find superior hybrids, and since cows produce one calf a year, generating similar numbers was difficult (and cost prohibitive). Experiments on dairy cattle, however, commanded considerable attention from academic institutions. People in both Europe and the United States questioned if crossbreeding, and even inbreeding and crossing inbred lines, would improve the productivity of dairy cows. A number of crossbreeding and/or inbreeding experiments designed to find answers took place between 1906 and 1969. Results were inconclusive, providing little incentive for the dairy industry to abandon purebred breeding.<sup>44</sup> (By 1980 it was evident that no crossbreeding of Holsteins showed improved production over pure Holsteins. They exceeded crossbreds for general performance by 10 percent.<sup>45</sup>) The structure of the dairy industry also did not lend itself to the hybrid method. Ordinary dairymen were part of the breeding arm in a way that was not true of ordinary chicken producers. While dairymen made their living from the milk their cows produced, they needed to breed those cows in order to generate that milk, a situation that intimately connected them to the breeding world. Dairymen worked ever more closely with breed and government organizations in most countries of the world and supplied the data on milk yields that in turn drove their selection plans and those of the elite breeders. Purebred breeders and ordinary dairymen were also united by their focus on the production of true breeding lines. The increasing masculinization of the producing arm—milking had traditionally been women's work, while the breeding arm had tended to be male-dominated—reinforced the interconnected structure of the industry in a way that had not been true in the chicken situation.

Inbreeding/hybrid crossing techniques seemed at first glance to be amenable to beef breeding because of the role crossing of breeds played in it. One successful Canadian chicken breeder, Don Shaver, attempted to introduce the hybrid corn breeding method to the North American beef industry because of this interest with crossbreeding, but failed to do so.<sup>46</sup> The international organization of the breeding sector and of the industry generally explained why. The breeder arm of the beef industry was comprised of the elite purebred breeders and farmers, known as cow/calf operators, who kept cows to produce calves designed to be slaughtered for meat. These farmers effectively multiplied animals for the meat industry. The cow/calf operators bought from



the elite breeders and acted as breeders themselves in their multiplication work by the fact that they decided how to use stock generated by the elite breeders. Purebred breed associations—well established by this time—and government encouraged that trend by advising cow/calf operators to rely on purebreds in their programs. Final production involved “feeders.” The feeders acquired the calves from the cow/calf operations and fed the stock until it was ready for slaughter. The whole structure was tied together by the fact that the feeders decided what stock they wanted from the cow/calf operators, and the cow/calf operators decided what purebred cattle they would bring into their programs and how they would combine the genetics of those animals. From early times, cow/calf operators had tried to utilize hybrid vigor by crossing bulls of a certain breed or type on cows with a different genetic background—they normally used purebred bulls—but they resisted biological locks, which hindered their control over breeding for feeder demand.<sup>47</sup> Since both breeder sectors and the final producing arm played a role in how breeding proceeded, the breeding and producing arms were strongly linked together, a situation that discouraged corporate involvement.

The hybrid corn method’s stunning success in chicken breeding, regardless of its failure in the world of large farm animals like cattle, encouraged the geneticists’ conviction that hybridizing could eventually revolutionize agriculture, even though it was clearly apparent that industry structure had to be compatible to its introduction. Changes within the discipline of genetics itself, however, dictated that ultimately different strategies emanating from that science—strategies more akin to practical breeding outlooks—would direct dairy and beef breeding. The biometrician view that heredity should be addressed in terms of populations or groups had, over the 1920s and 1930s, fused with Mendelism to create population genetics.<sup>48</sup> The reunification of the two separate disciplines widened the lens of genetics. While the primary significance of biometry’s fusion with Mendelism related to a reevaluation of Darwinism and evolution (often bringing with it eugenic concerns), the union effectively introduced important practical animal-breeding concepts to genetics. Traits observed in animals—milk yields or egg-laying strength, for example—could be assessed quantitatively, meaning by degree of strength. Gradual change within populations was possible over time. This quantification of hereditary characteristics paved the way for a new emphasis on true breeding lines and an introduction of Bakewell’s principles—the progeny test and assessment of breeding via populations, not individuals—to genetics. Bakewellianism brought with it practical animal breeders’ views toward how

to understand heredity, although that reality remained hidden for some time.

It took Jay Lush—an American animal geneticist at Iowa State University and acknowledged founder of livestock genetics—to see that the changes introduced by the rise of population genetics lent themselves to modification of breeding strategies in the livestock industries.<sup>49</sup> Lush operated from a combined inbreeding/hybridizing and biometric/quantifying position and intended to devise breeding plans that would fit with the existing livestock industry structure, which supported true breeding lines. Lush wrote extensively about the historical background of livestock breeding within that context. In the process he removed Darwinian evolution—so embedded in biometry, early Mendelism, and population genetics—from the practical problem of heredity under artificial selection.<sup>50</sup> He was particularly concerned with quantifying the effects that inbreeding had on family groups or strains and on the predictability of results from different breeding plans within that framework.<sup>51</sup> What selection strategies worked best? Did breeding half siblings to each other, for example, bring better results than mating cousins?<sup>52</sup>

Lush drew on the views of two of the scientists concerned with evolution and credited with bringing about the rise of population genetics. One was Sewall Wright, an American geneticist who graduated from Harvard University (trained by Castle) and who worked at a number of institutions including the Bureau of Animal Industry. Wright's theories concerning inbreeding and population bottlenecking through inbreeding, as well as his path coefficient theory, which calculated the level of shared genetic material that would result from different inbreeding systems, proved highly significant to Lush.<sup>53</sup> The other scientist to inspire Lush was the British geneticist and statistician, R. A. Fisher, a graduate of the University of Cambridge who taught at public schools in London and later worked at a number of institutions, including the Rothamsted Experiment Station from 1919 to 1933. Fisher's important 1918 paper, which argued that inheritance and change resulted from the interaction of many genes over time within populations—a theory known as the infinitesimal model—proved critical to Lush's evolving ideas.<sup>54</sup> Over the 1930s and 1940s, Lush united the visions of Wright and Fisher and designed new systems to fine-tune existing practical breeder practices.<sup>55</sup> While Lush always believed he owed much to Wright's research on inbreeding, the incorporation of Fisher's infinitesimal model was equally important and perhaps in the long run more significant.<sup>56</sup> Wright and Fisher might have played a role in the development of Lush's ideas, but it was Lush himself who invented quantitative genetics from the base of population genetics. Scholars from across North

America and Europe would study under him and/or be influenced by his theories from the 1930s through the 1960s. In essence, quantitative genetics focused on alterations brought about by artificial selection, while population genetics addressed changes under natural selection. Quantitative genetic principles, however, would be useful in various disciplines.

Better statistics to evaluate strategies used in artificial selection were important to quantitative genetics from the beginning. As early as 1913, American statistician G. W. Snedecor (1881–1974) at Iowa State University began devising statistics specifically for use in agriculture.<sup>57</sup> Pearson and Fisher had been interested in applying statistics to the biological problems of evolution and human progress—namely, the results of natural selection, not artificial selection. Lush played an important role in the development of agricultural statistics, particularly those models designed by his student and colleague, American L. N. Hazel, who spent his working life as a statistician at Iowa State, and Hazel's student, American C. R. Henderson. A statistician and quantitative geneticist concerned with animal breeding, Henderson went on to Cornell University but later in life wrote his most important paper at the University of Guelph in Canada. Between the 1940s and early 1970s, Henderson focused particularly on systems that would quantify the value of breeding bulls. He developed a significant statistical way to assess that value through what is known as BLUP (best linear unbiased prediction). A mathematical model designed to predict an animal's breeding potential under environmentally neutral conditions, BLUP allowed for a more accurate estimation of a bull's superiority.<sup>58</sup> On the basis of Lush's theories and evolving statistics, as early as the 1940s, scientists turned their attention to livestock industries that supported both purebred and true line breeding, most specifically dairy cattle. They worked with (and needed) the data collected by dairymen, who kept records of their cows' milk output hoping with the use of quantitative statistics to make that data yield clearer information on the relative value of sires. Alan Robertson, a British population geneticist from the University of Cambridge, was particularly significant in efforts to improve dairy cows by focusing quantitative statistical studies on locating better daughter-producing bulls. Robertson studied principles of quantitative genetics under both Lush and Wright in the United States before starting research at the Animal Unit Research Centre at Edinburgh after the Second World War.<sup>59</sup> The advent of artificial insemination (AI), and by the 1950s the ability to freeze semen, allowed him to be more effective in statistically progeny testing males.<sup>60</sup> With the aid of international organizations like Interbull, founded in Sweden in the

1980s to collect data on milking cows from around the world, as well as the use of computers, quantitative genetics revolutionized dairy cattle breeding on a worldwide scale.<sup>61</sup> Emphasis on statistical quantification and its use to progeny test males clearly placed a non-gene-architecture approach at the center of livestock genetics. The outlook was also reminiscent of Bakewell's most noteworthy principles.

It helped that the international dairy industry's structure (specifically, the integral role of the ordinary dairy farmer in breeding good milking cows) was amenable to principles arising from the new animal science. The dairy associations were prepared to work with governments and to use new information arising from genetics. In fact, the North American purebred dairy associations had initiated data collection before the advent of genetics itself.<sup>62</sup> From the beginning, breed associations agreed to cooperate with academic institutions.<sup>63</sup> In doing so, breed associations moved from purebred breeding's emphasis on ancestry breeding to Bakewell's progeny testing.

Quantitative animal genetics did not penetrate beef breeding either as easily or as early as it did dairy breeding. Industry structure was one problem. The beef industry did not lend itself to generating adequate data. The large herds and minimal management of the beef industry discouraged the extensive use of AI, and that fact alone hindered quantitative genetic work in beef cattle; the data needed for statistics did not exist. As of 2003 less than 5 percent of the world's beef cattle were artificially inseminated.<sup>64</sup> The attitude of the purebred beef associations was another issue. The purebred beef breed associations resisted change. The fact that the Thoroughbred horse culture embedded in purebred breeding was so strong within the purebred beef industry frustrated geneticists throughout this period. "[T]he propaganda about pedigrees and wins at fairs and shows, the dramatics of the auction ring, [and] the trivialities of breed characteristics . . . constitute a vocation, not a genetic exercise," wrote geneticists I. M. Lerner and H. Donald in 1966.<sup>65</sup> Attitudes of American organizations serve as an example of international patterns. The purebred beef cattle associations in the United States, which had controlled breeding since the 1880s, continued into the 1960s to evaluate breeding worth on the basis of ancestry, success in the show ring, and subjective visual appraisal. The influence of purebred animals, designed within that framework, could be felt throughout the industry. The terminal crossbreds that composed the end beef product were generated by combinations of purebred cattle produced under standards set by the breed associations.

The first association effort to provide a more objective view of purebred

quality (and therefore useable data for eventual quantitative progeny testing) was the Red Angus Association, which in 1959 required weaning weights to be provided before pedigree registration was possible. Over the 1960s other beef breed associations developed performance recording programs, although the Angus association remained the only one that required data reporting. It was largely the demands of American feeder operators in the 1940s and 1950s that led to improvements in performance recording of purebred beef cattle. A move to better orchestrate improvement programs began in 1965 and resulted in the Beef Improvement Federation, formed in 1967. The breed associations maintained a strong voice in that organization.<sup>66</sup> In the 1970s the purebred associations began to adopt performance evaluation systems based on a BLUP design. Evaluation systems revolved around what was known as EPDs, or estimated progeny differences, for a variety of traits—the numbers of which expanded over the years and in relation to the capacity of computers to handle complicated statistics. An EPD is a prediction of an animal's likelihood of passing on a trait in relation to breed average for that trait. The most common EPDs calculated were for birth weight, weaning weight, and yearling weight as gain per day after birth. The beef cattle revolution of the 1970s reflected an increased use of quantitative genetic principles and the importation of new beef breeds to replace herds ruined by excessive reverence to show-ring style.<sup>67</sup> These changes helped defuse antagonism between scientists and purebred breeders.

Effectively, quantitative genetics introduced principles reminiscent of Bakewell's to both purebred dairy and beef cattle breeding, and at the same time initiated a shift away from Thoroughbred horse breeding culture. The transition occurred earlier and more effectively in dairy than in beef breeding, but changes were clearly evident in the beef cattle industry by the 1970s. The revolution undermined the power and credibility of concepts that had become integral to purebred breeding. The emphasis on phenotypic beauty as quality, for example, declined. The entanglement of purity with beauty also came under scrutiny. Purebred breeding increasingly appeared to be nothing more than an art form. In fact, many of the quantitative genetic principles simply pushed purebred breeding back to its Bakewellian roots, but that was not obvious to breeders. They did not see the new emphasis on progeny testing and quantification, over ancestry breeding and individual worth, as a reintroduction of strategies that had originated in eighteenth-century Bakewellianism. Breeders viewed these changes as emanating out of the science of genetics. The vastly superior statistics used for quantification in the twentieth century,

when compared to the tools available in the eighteenth century, helped make the techniques look completely innovative. AI and its power to progeny test more effectively changed the landscape completely and thereby helped to hide Bakewellian foundations. Because the shifts meshed well with the breeding arm's traditional framework, a revolution was possible without reshaping the general industry. Basic historic industry structure remained the same: breeder and producer were linked together through common intent to produce true breeding lines, and breed associations continued to have relevance by virtue of the fact that they collected the data used in quantitative analysis. What is interesting, though, is the fact that this breeding revolution did not result from a shift away from the fundamental force-manipulation approach to heredity. It merely introduced principles that had been lost in animal breeding with the change from Bakewellianism to purebred breeding, and with the submergence of biometry within the naturalist/geneticist ranks.

Developments in Thoroughbred horse breeding strategies, the other eighteenth-century practical method and parent of purebred breeding, provide an interesting contrast to the effects quantitative genetics had on purebred cattle breeding. Thoroughbred horse breeding, unlike purebred breeding, had not evolved from Bakewell's principles, a fact that appeared to shape horse breeder reactions to quantitative genetics. Horse breeders clung to the culture of their past, evidenced by their adoption of statistics to work with pedigree/ancestry-driven breeding, rather than with statistical progeny testing, or the concept that heredity should be assessed in terms of groups or populations. Breeders elaborated and developed different theories that rested on eighteenth-century ancestry breeding, individual worth, and pedigrees, which supported the value of both. Two examples that are still part of Thoroughbred horse breeding culture today suffice to demonstrate this pattern: the use of dosage theory and the figure system.

Dosage theory originated from the work of a Frenchman, J. J. Vuillier, in 1902. He examined the pedigrees of successful race horses to the twelfth generation and noted that fifteen stallions and one mare appeared in all of them with roughly the same frequency. He devised a sort of formula or recipe for creating the ideal race horse. If one selected a horse that lacked the relative "dosage" needed to recreate a needed pedigree, the animal mated to that horse should compensate for that lack through his/her pedigree. Vuillier drew heavily on Francis Galton's interviews with Thoroughbred horse breeders. A foal represented a blend of hereditary material, usually thought of as being "blood," a conception that fit with force manipulation thinking. "Blood"

meant that some unknown laws existed driving the way inheritance worked, even if they were not understood. Dosage theory attracted attention throughout the period when animal genetics developed over the twentieth century. The third Aga Khan relied heavily on dosage during the 1930s when breeding Thoroughbreds. Vuillier's work also influenced Italian Franco Varola, who wrote about breeding in the 1970s and modified dosage theory. Further modifications would emerge in the 1980s and 1990s. Dosage remained concerned only with analysis of superior horses within the male line and still influences Thoroughbred breeding decisions today.<sup>68</sup>

The figure system is based on the work of nineteenth-century Australian Bruce Lowe, who spent years tracing every mare appearing in the General Stud Book back to her "taproot" in the original edition. He then gave numbers to each of these families, ranging from one to forty-three, and related mares to male winners over the time of the great races. His work was carried on in the twentieth century, even though DNA testing showed that the pedigrees on which the figure system was based were often flawed. That situation did not deter breeders from using statistics arising from the figure system in making breeding decisions. Pedigrees were at the heart of the figure system, as was reliance on ancestry breeding and an emphasis on individuals. It seemed evident to geneticists that the methods used to breed race horses had not improved their speed in the last half century before 2014.<sup>69</sup> The lack of AI use—AI is not allowed for registration in the Jockey Stud Book—did not help matters. With enforced natural service in place, stallion owners dictate stud fees and keep them high. But the restriction on AI use means insufficient data exists on breeding males for quantifying the relative quality of stallions against each other. Stallion owners control much of the way Thoroughbred horse breeding proceeds, because they play a critical role in directing how effective progeny testing will be with respect to males.

Changes in cattle breeding clearly showed that the biometric principles in quantitative genetics provided effective strategies to improve animals. As a result, the principles influenced hybrid chicken breeding by modifying methodology of the breeders. While the companies maintained their faith in inbreeding and crossing, by the 1960s they used strain crosses from parental lines with low levels of inbreeding (which had undergone selection using quantitative genetics), thereby abandoning the emphasis on extreme inbreeding for the lines used to make the hybrid cross.<sup>70</sup> Intense inbreeding had been an essential part of any form of hybrid breeding since the eighteenth century.

By the 1970s, however, quantitative genetics had lost some of its aura



among geneticists. The avoidance of a gene architecture approach, and the discipline's apparent over-reliance on statistics, had come to contrast sharply with the rapid advances made in a branch of genetics that was based on gene architecture: molecular genetics, initiated in the late 1940s but further stimulated by the discovery of DNA's structure in 1953. Recombinant DNA technology, which allowed for the transferring of sections of DNA from one organism into another, made it possible to study the functioning of actual genes at the molecular level.<sup>71</sup> The sense that gene interaction could be understood tended to bring the gene architecture approach back to the forefront and concurrently to push quantitative genetics, with its emphasis on statistics, into the background.

While studying biological issues in terms of statistics was anything but new, advances in biomathematics and statistics with a simultaneous avoidance of molecular biology intensified a dilemma: did assessing biological functions with no knowledge of the dynamics that caused them make sense? When did a biomathematical study cease to be biology and become simply mathematics?<sup>72</sup> For some geneticists, the ever-increasing emphasis on statistics in aspects of genetic research, particularly relevant when viewing quantitative genetics and evident by the 1970s, seemed to be taking the science too far from its main purpose—understanding gene dynamics. When scientists who used quantitative genetic tactics (animal biologists, evolutionary biologists, population geneticists, agricultural geneticists, and statisticians, to name a few) gathered together in 1976 at Ames, Iowa, for the first international conference devoted to quantitative genetics as a discipline, the nature of quantitative genetics itself and its approach to studies in genetics stimulated discussion. Oscar Kempthorne, a statistician and geneticist from Iowa State University, began the meetings by defining what quantitative genetics meant and in the process tried to put to rest “the not-uncommon tendency to regard a conference on quantitative genetics as a conference on population genetics.” He began with the following statements:

We wished to organize a conference, then, in quantitative genetics and not in population genetics as it is conventionally understood.... Many of the ideas of conventional population genetics are important to quantitative genetics. And, contrariwise, it seems clear that many of the ideas of conventional quantitative genetics are relevant to population genetics.... Part of the distinction between the two areas is simply that quantitative genetics should be called experimental population genetics, with the emphasis on the word “experimental,” connoting that we make genetic populations by controlled operations, while conventional population genetics is primarily observational population genetics, trying to

understand populations that have arisen by natural and not humanly directed processes.... The big thrust [of quantitative genetics] has been towards the species of direct relevance to the food needs of the human species, and this explains why quantitative genetics is dominated by [those interested in] animal and plant breed[ing].<sup>73</sup>

But, he admitted, quantitative genetics had not been able to understand the genetic architecture of traits in agricultural plants and animals that were economically valuable, a serious shortcoming within the contemporary environment of genetics.<sup>74</sup> R. E. Comstock, an agricultural plant geneticist in the United States, concurred, believing the discipline was inadequate in many ways, in spite of the fact that it had offered major contributions to breeding designs. "There are significant issues in the realm of quantitative genetics that have not been resolved," he stated. "Some of these appear tractable, others relatively intractable.... It appears from the perspective of the breeder that quantitative genetics still has a challenging future."<sup>75</sup> D. L. Harris, an American livestock geneticist, pointed out the significance of historical breeding. "It is well to remember," Harris noted, "that animal breeding was a serious activity of many stockmen prior to the discovery of [the] Mendelian basis of inheritance."<sup>76</sup> He implied value in practical thinking: early breeders had managed to breed without sophisticated statistics or Mendelism.

For Richard Lewontin, that was not the point. An American evolutionary biologist and population geneticist at Harvard University, Lewontin believed in the application of techniques from molecular biology to questions of genetic variation and evolution, and would pioneer strategies to do so throughout his life. He used the black box metaphor to explain why avoidance of molecular genetics did not serve quantitative genetics well. The black box theory basically states that, when causes can be attributed to bringing about certain results, but the laws governing the results remain unknown, it is a "black box" way of looking at a problem.<sup>77</sup> The dynamics between cause and result are hidden or encased in a black box. For Lewontin, black box thinking had no place in science and therefore should not be so dominant in quantitative genetics. Quantitative genetics may be used to predict results of certain selection methods, he stated, but we know nothing about the genetic architecture that would dictate the effectiveness of any such method. Genes and gene interaction "were treated as if occurring inside a black box," only knowable through observable output. In effect, quantitative genetics constituted "an attempt to produce knowledge by a systemization of ignorance." He elaborated: "We need to know the relations between gene and organism, how gene action ...

is translated into phenotype. The knowledge about these questions can come to us only by opening up the black box whose outer shape we have so far been describing, and seeing what the machinery inside really looks like.” Quantitative geneticists really should look to the methods used and work done by molecular geneticists, Lewontin noted, adding, “Our models of quantitative genetics must either take cognizance of these findings or else show how they are, in fact, irrelevant because of the robustness of our theory.”<sup>78</sup>

In a review of the 1976 conference, geneticist Peter E. Smouse addressed the statistical stance embedded in quantitative genetics in relation to the gene architecture approach of molecular genetics somewhat differently:

In recent years, the once thriving field of quantitative genetics (QG) has fallen on hard times. Both the discipline and its practitioners have been criticized for a total failure to deal with the genetic and biochemical details underpinning the phenotype. Such attacks are more than a little unfair, considering that QG was designed to deal with the sort of continuous phenotypic variation which largely defies Mendelian analysis or exact biochemical characterization, the sort of variation which is so complex as to admit of little more than statistical summarization. Quantitative genetics is nothing more (and nothing less) than a convenient statistical construct whose prime function is to permit estimation and testing of a set of summary measures. The grist for this statistical mill comes in the form of phenotypic resemblances between biological relatives. Since nary a gene is seen, the fact that these summary measures convey any genetic information at all must be viewed as a splendid accomplishment. It is precisely for the analysis of those phenotypes which are hopelessly complex that quantitative genetics was designed.<sup>79</sup>

The gene architecture approach supported the idea that an isolated gene/marker or DNA sequence model was the underlying conceptual way to look at the inheritance of traits considered to be economically valuable. The questions remained, though, as to how many genes/markers—described as quantitative trait locus/loci (QTL) located within DNA—went into a trait, and if those markers could be found.<sup>80</sup> If the answer was many, the ability to locate a few genes or markers was not necessarily helpful. Quantitative geneticists watched this QTL research with interest and even wondered if it should orchestrate a change in their approach to statistics. Over the years, Alan Robertson (who died in 1989), for example, became increasingly convinced that the number of loci responsible for valued traits was small, compared to the potentially large amount of DNA variation that might exist in an animal’s genetic profile.<sup>81</sup> Some began to question as well why the infinitesimal theory continued to have such influence when there was no real evidence wheth-

er inheritance of economic traits proceeded via a single or limited gene, or via multiple gene process.<sup>82</sup> This tendency away from both the infinitesimal model and black box thinking bore strong similarities to perceptions of the early Mendelists, who believed that single genes could explain such traits as egg and milk production levels. Discoveries might imply that at last simple answers to complicated questions would be available.

In spite of the questioning that surrounded the wisdom of relying on statistical breeding and the concurrent emphasis on gene architecture-based QTL research, most quantitative geneticists interested in livestock breeding did not fundamentally change their ways. At the second quantitative conference, held in 1987, it was apparent that statistical studies (effectively black box thinking) still dominated quantitative genetics and operated within the framework of the infinitesimal model. One participant noted: "One might ask why animal breeders have been so reluctant to recognize important major genes.... The main reason for this is that animal breeders are quantitative geneticists in their approach to problems. Therefore, they have, almost by definition, accepted the polygenic paradigm of inheritance of performance traits."<sup>83</sup> Not all geneticists at the conference had abandoned the hope that gene architecture theory would replace quantitative practical thinking, however. Two in particular emphasized the value of looking for specific DNA markers.<sup>84</sup> Yet no change with respect to better knowledge seemed to be on the horizon in the years after that conference. In 1998 it was noted that "knowledge of genetic architecture [was] ... very limited for economic traits of farm animals."<sup>85</sup>

The rise of genomics created new optimism in scientists supporting the gene architecture approach to animal breeding. Genomics, the study of DNA at the molecular level but across all chromosomes in any given species (as opposed to small sections or specific genes under recombinant DNA technology), brought hope that the repeated failures to advance any real way of using QTL, or even to locate such markers successfully, would be overcome.<sup>86</sup> It soon became evident that genomic technology, which located many thousands of random single-nucleotide polymorphisms (SNPs), parts of so-called junk DNA and not protein-coding genes, did not enhance useful knowledge concerning QTLs and therefore did not endorse a gene architecture outlook. SNP technology, instead, supported the statistical outlook of quantitative genetics. SNPs are evident deviations in an individual or group from population-norm sequencing patterns of the four bases in the DNA molecule.<sup>87</sup> That characteristic makes them valuable in developing a test to assess superiority for certain quantitative traits within a breeding population. If known supe-

rior animals (through quantitative genetic data) show this deviation, then it could be assumed that other animals with the same deviation (but with no data) were also superior. Genomic selection via SNPs clearly negated the idea behind single-trait marker theory and instead supported the black box/infinite model approach, which argued that a large number of unknown genes (or even parts of the DNA that were not genes), acting with each other also in an unknown way, were responsible for a trait.<sup>88</sup> In 2007 livestock geneticist J. van der Werf wrote, “this [SNP] approach seems to revert back to the black box, where the emphasis is on predicting genetic variability for observed traits, rather than on understanding the underlying biology.” He elaborated:

Animal breeders have always been working with the “black box” containing the biology of the animal. They have had enormous impacts on the black box, but are only really aware of the outputs. Some animal breeding scientists have argued that understanding the black box is important, especially for understanding the relationship between productivity and fitness.... With the advent of molecular genetics, there seemed a new chance to embrace biology. . . . Yet, the hunt for quantitative trait loci has been relentless, while the application in breeding programmes is still rather disappointing, and the biology possibly becoming more complicated rather than clarified.... For now, the latest revolution in genomic technologies is the dense SNP chip and our hopes rest on the application of genomic selection.<sup>89</sup>

If SNP technology was to work, however, it needed the input of data generated by quantitative genetics and purebred breeding.<sup>90</sup> Those adhering to the older hybridizing method (that is, the chicken breeders) could not capitalize on such testing because breeding for terminal hybrid crosses did not generate the necessary data. The fact that breeding companies kept their strains or lines secret, in order to protect intellectual property, did not help the situation. It was the international dairy industry—because of its massive statistical base that rested on the work of quantitative geneticists and, even earlier, of purebred breeders—that could provide the data needed to formulate a SNP test that could identify superior animals. In 2008 a high-density panel, containing over fifty thousand SNP markers across the genome (known as the Bovine SNP50 BeadChip), was developed by the company Illumina in California. Illumina created the panel by comparing statistics that had identified the superior ability of three thousand bulls to produce good milking daughters with characteristics of their DNA profile.<sup>91</sup> When the BeadChip became available the following year, it proved to be highly accurate in locating quality dairy bulls. (When the beef breeds collected genomic data on the basis of the

BeadChip a few years later, they had to pool their genomic and quantitative genetic/purebred information together in order to generate adequate accuracy rates.) It was soon clear, though, that the larger the number of animals used to develop a test and the greater the volume of SNPs profiled, the higher the accuracy rate. By assessing the genome in a more comprehensive fashion, in order to bring in a huge number of SNPs, it was possible to make better estimates of an individual's breeding worth. Complexity, Fisher's infinitesimal model theory, and black box thinking all took precedent over a genetic architecture approach in genomic methods of breeding.<sup>92</sup> In 2013, sixty years after the discovery of the molecular structure of DNA, *Nature* commented on the general illusiveness of understanding genetic architecture. "When the structure of DNA was first deduced, it seemed to supply the final part of a beautiful puzzle, the solution of which began with Charles Darwin and Gregor Mendel. The simplicity of that picture has proved too alluring."<sup>93</sup>

Over the twentieth century and early twenty-first century, a pervasive division or even oscillation between two approaches to the study of heredity continued to characterize geneticist attitudes, just as had been the case with naturalists in earlier times. No such oscillation with respect to hereditary theory took place in the animal breeding world: this outlook, generally speaking, continued to rest, as it always had, on a general force/black box view. These patterns reveal not only the fact that a mutual approach to heredity facilitated a genetic infiltration of practical breeding but also factors behind why that was the case. The interface between genetics and practical animal breeding within the cattle industries was successful because the two groups held similar opinions concerning breeding intent. Both worked with the idea of breeding for true lines to advance changes that were in effect quantitative over generations. Their views varied only in that, before the 1940s and in keeping with purebred breeding, breeders had focused on individuals within such a framework, while quantitative geneticists—reminiscent of Bakewell—assessed such shifts on a population basis. The move by breeders to supporting quantitative changes as a population issue did not interfere with the historic structure of the industries. Either outlook worked with an industry framework that developed over a two-hundred-year period to orchestrate the production of true breeding lines. Quantitative genetics, then, fit with general practical breeding intent and also industry structure. (The situation was similar in the sheep industry.<sup>94</sup>) That was not the case with hybridizing or specific DNA studies with their embedded gene architecture-based attitude. Only in the chicken industry did

the hybridizing method revolutionize breeding, but it did so because the declining emphasis on true breeding lines and the subsequent separation of breeder from producer both helped to create an environment conducive to such a change. Pig breeding has been affected by the technique as well, but not to the degree of totally removing breeding from farmers. Hybridizing in pigs is funded by AI companies interested in collecting data from farmers who use semen of company-owned boars.<sup>95</sup>

Today, a move away from the gene-dynamic dream of the nineteenth-century experimental breeders and twentieth-century scientists tends to characterize theoretical approaches in genetics. Described as epigenetics and/or as an aspect of postgenomics, this view holds that the study of inheritance should see some modifications of phenotypic expression as being beyond the interaction of genetic material in the DNA.<sup>96</sup> Such an outlook is likely to fit well with the vision of practical breeders because it supports a general force/black box attitude toward inheritance. Advancing technology could also play a role in how the future gene architecture versus black box problem works out and, in doing so, change the animal-breeding landscape. That is especially true if the dominant linkage of gene architecture theory with hybridizing for terminal crosses is broken. CRISPR Cas 9 has the capacity to work with either linkage. The technology can alter the structure of DNA and therefore might be able to redesign the basic DNA of farm animals; many think it will.<sup>97</sup> (SNP technology only identifies the structure of existing DNA, whereas CRISPR Cas 9 allows for its manipulation.) Whether CRISPR Cas 9 does so within a framework that supports the hybridizing linkage, or whether it breaks that linkage by aligning itself with true breeding lines, remains to be seen. If its gene architecture orientation leads to a classic union with hybridizing, dramatic change in most livestock industries is unlikely to take place. Corporate investment would probably be critical for funding a new technology designed for hybridizing. Companies will only invest if a reasonable guarantee of recovering the funds exists, which usually means the capacity to take at least some control over breeding. This is difficult to achieve with hybridizing when breeders and producers, first, are linked together and, second, aim for breeding true lines, both of which are the case in most livestock industries today. If the gene architecture-based CRISPR Cas 9 is used instead to design methods via reconstructing DNA in service of true breeding lines, the situation would look different. As in the case of SNP technology, corporate investment might fund the creation of a platform that breeders would buy and use in true line breeding. Who provides the input as to how to design a new DNA structure,



however, raises another interesting question. But corporate enterprise would not, under these conditions, necessarily take over breeding itself.

The future effects of CRISPR Cas 9 are especially tantalizing because the technology's impact on breeding cannot be seen separately from how changes will interact with the many support structures of the livestock industries. This analytic approach to theory and method has shown that animal breeding and the industries it serves are intimately linked. Whatever direction CRISPR Cas 9 takes, there will therefore be surprisingly wide implications. Simply appreciating that fact might even guide how the technology will ultimately be used.

## NOTES

1. The historiography is too vast to list here. Two important examples are: Jonathan Harwood, *Styles of Scientific Thought: The German Genetics Community, 1900–1933* (Chicago: University of Chicago Press, 1992); and Harwood, *Technology's Dilemma: Agricultural Colleges between Science and Practice in Germany, 1860–1934* (New York: Peter Lang Publishing Group, 2005).

2. See, for example, Phillip Thurtle, "Harnessing Heredity in Gilded Age America: Middle Class Mores and Industrial Breeding in a Cultural Context," *Journal of the History of Biology* 35 (Mar. 2002): 33–78; and Thurtle, *The Emergence of Genetic Rationality: Space, Time, and Information in American Biological Science, 1870–1920* (Seattle: University of Washington Press, 2008).

3. Nicholas Russell, *Like Engend'ring Like: Heredity and Animal Breeding in Early Modern England* (Cambridge: Cambridge University Press, 1986), 35; Jay L. Lush, *Animal Breeding Plans* (Ames, IA: Collegiate Press, 1937), 146. See also *Marcus Porcius Cato on Agriculture/Marcus Terentius Varro on Agriculture*, trans. W. D. Hooper and H. B. Ash (1934; Cambridge MA: Harvard University Press, 1960).

4. Russell, *Like Engend'ring Like*, 36.

5. Russell, *Like Engend'ring Like*, 58, 68; Vitezslav Orel and Roger J. Wood, "Scientific Animal Breeding in Moravia before and after the Discovery of Mendel's Theory," *Quarterly Review of Biology* 75 (2000): 151.

6. Russell, *Like Engend'ring Like*, 13. For a review of attitudes to heredity up to end of the eighteenth century, see Staffan Müller-Wille and Hans-Jörg Rheinberger, *A Cultural History of Heredity* (Chicago: University of Chicago Press, 2012).

7. See Hans Jörg Rheinberger and Staffan Müller-Wille, *The Gene: From Genetics to Postgenomics*, trans. Adam Bostanci (Chicago: University of Chicago Press, 2017), Chpt. 2; Müller-Wille and Rheinberger, *A Cultural History of Heredity*, 28–29, 72–75, 91–92.

8. Russell, *Like Engend'ring Like*, 40–41.

9. For more on the subject of environmental impacts on breeding, and especially in relation to colonial importations of animals, see Rebecca J. H. Woods, *The Herds Shot Round the World: Native Breeds and the British Empire, 1800–1900* (Chapel Hill: University of North Carolina, 2017); and Sandra Swart and Greg Bankoff, eds., *Breeds of Empire: The "Invention" of the Horse in Southeast Asia and Southern Africa* (Copenhagen: Nordic Institute of Asian Studies Press, 2007). For attitudes to breeding that existed before the Enlightenment period, see Keith Thomas, *Man and the Natural World: Changing Attitudes in England, 1500–1800* (London: Allen Lane, 1983).

10. For Bakewell, see Robert Trow-Smith, *A History of British Livestock Husbandry, 1700–*

1900 (London: Routledge & Kegan Paul, 1959); Henry Cecil Pawson, *Robert Bakewell: Pioneer Livestock Breeder* (London: Crosby Lockwood, 1957); Henry Cecil Pawson, "Some Agricultural History Salvaged," *Agricultural History Review* 7 (1959): 6–13; Roger J. Wood and Vitezslav Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel* (Oxford: Oxford University Press, 2001); Roger J. Wood, "Robert Bakewell (1725–1795): Pioneer Animal Breeder and His Influence on Charles Darwin," *Folia Mendelianna* 8 (1973): 231–42; David L. Wykes, "Robert Bakewell (1725–1795) of Dishley: Farmer and Livestock Improver," *Agricultural History Review* 52 (2004): 38–55.

11. J. V. Beckett, review of *Matthew and George Culley: Travel Journals and Letters, 1765–1798*, by Anne Orde, ed., *English Historical Review* 118, no. 477 (June 2003): 803–4; Bakewell to Culley, Feb. 8, 1787, "The Bakewell Letters," in Pawson, *Robert Bakewell*, 107; George Mingay, ed., *Arthur Young and His Times* (London: The Macmillan Press Ltd., 1975), 77–78; John Saunders Sebright, *The Art of Improving Breeds of Domestic Animals* (London: John Harding, 1809).

12. Wood and Orel, *Genetic Prehistory in Selective Breeding*, 89; Sebright, *The Art of Improving Breeds*.

13. See Sebright, *The Art of Improving the Breeds*.

14. Wood and Orel, *Genetic Prehistory in Selective Breeding*, 89.

15. Iwona Glazewska et al., "A New View on Dam Lines in Polish Arabian Horses Based on mtDNA Analysis," *Genetics Selection Evolution* 39, no. 5 (2007): 609–19; A. T. Bowling et al., "A Pedigree-Based Study of Mitochondrial d-Loop DNA Sequence Variation Among Arabian Horses," *Animal Genetics* 31, no. 1 (2000): 1–7.

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17. See Philip Kitcher, *In Mendel's Mirror* (Oxford: Oxford University Press, 2003), 63–64.

18. Carl Jay Bajema, ed., *Artificial Selection and the Development of Evolutionary Theory* (Stroudsburg, PA: Hutchinson Ross Publishing, 1982), 3, 4, 11–12.

19. Staffan Müller-Wille and Vitezslav Orel, "From Linnæan Species to Mendelian Factors: Elements of Hybridism, 1751–1870," *Annals of Science* 64, no. 2 (2007): 177.

20. Leslie Clarence Dunn, *A Short History of Genetics: The Development of Some of the Main Lines of Thought, 1864–1939* (New York: McGraw-Hill, 1965), 27–29; Kitcher, *In Mendel's Mirror*, 64. For more details on early hybridizing and concern with speciation, see Müller-Wille and Rheinberger, *A Cultural History of Heredity*.

21. Wood and Orel, *Genetic Prehistory in Selective Breeding*.

22. Wood and Orel, *Genetic Prehistory in Selective Breeding*.

23. Müller-Wille and Rheinberger, *A Cultural History of Heredity*, 80.

24. Müller-Wille and Rheinberger, *A Cultural History of Heredity*, 134.

25. See Alvin Howard Sanders, *Short-Horn Cattle: A Series of Historical Sketches, Memoirs and Records of the Breed and Its Development in the United States and Canada* (Chicago: Sanders, 1900), 14, 31, 34–35, 37–39, 44, 75, 81–85; Sewall Wright, "Mendelian Analysis of the

Pure Bred Breeds of Livestock, Part 2, The Duchess Family of Shorthorns as Bred by Thomas Bates," *Journal of Heredity* 14 (1923): 339–48; Cadwallader John Bates, *Thomas Bates and the Kirklevington Shorthorns: A Contribution to the History of Pure Durham Cattle* (Newcastle upon Tyne: Robert Redpath, 1897).

26. See, for example, *Farmer's Advocate*, Jan. 1876, p. 13; Feb. 1876, p. 27; Mar. 1876, p. 46; Dec. 8, 1910, pp. 1927–28; *Farming World and Canadian Farm and Home*, Jan. 1, 1906, p. 161. See also Sessional Papers (referred to as SP), Legislature of Ontario, SP 13, 1875, pp. 76, 31–32; SP 12, Ontario, 1877, 48.

27. See, for example, Barbara Kimmelman, "The American Breeders' Association: Genetics and Eugenics in an Agricultural Context, 1903–1913," *Social Studies of Science* 13, no. 2 (1983): 163–204.

28. See Nicholas Gillham, *A Life of Sir Francis Galton: From African Exploration to the Birth of Eugenics* (Oxford: Oxford University Press, 2001); Michael Bulmer, *Francis Galton: Pioneer of Heredity and Biometry* (Baltimore: Johns Hopkins University Press, 2003). For examples of Pearson's work, see "On the Systematic Fitting of Curves to Measurements and Observations: Part I," *Biometrika* 1 (1902): 265–303; and "On the Systematic Fitting of Curves to Measurements and Observations: Part II," *Biometrika* 2 (1902): 1–23.

29. In modern terminology, Mendel was able to establish two laws. First, when the gametes (or reproductive cells) form, the gene pairs separate (each unit of the pair is either recessive or dominant); and second, genes are both immutable and act independently (a view that subsequently has become somewhat modified).

30. See Rheinberger and Müller-Wille, *The Gene*, Chpt. 2.

31. See Sewall Wright, *Evolution and the Genetics of Populations*, vol. 3, *Experimental Results and Evolutionary Deductions* (Chicago: University of Chicago Press, 1977), 11, 29; Dunn, *A Short History of Genetics*, 125; George H. Shull, "What is 'Heterosis'?" *Genetics* 33 (Sept. 1948): 439–46.

32. Don C. Warren, "A Half Century of Advances in the Genetics and Breeding Improvement of Poultry," *Poultry Science* 37, no. 1 (1958): 3–5.

33. Geneticist Wilhelm Johanssen recognized the value of pure breeding lines—commonly followed by the practical breeders—for scientific experiments, but he still emphasized the hybridizing method. In the decade after the rediscovery of Mendel's laws, he believed Mendelist experiments followed one of two procedures: working with pure lines only or hybridizing by using those pure lines. Müller-Wille and Rheinberger, *A Cultural History of Heredity*, 128; see also W. Johanssen, "The Genotype Conception of Heredity," *American Naturalist* 45 (1911): 129–59.

34. *American Poultry Journal*, May 1913, 847, for Pearl's comments in the Maine Experiment Station Bulletin 305, 1913, p. 388. See also Kathy J. Cooke, "From Science to Practice or Practice to Science? Chickens and Eggs in Raymond Pearl's Agricultural Breeding Research, 1907–1916," *Isis* 88, no. 1 (Mar. 1997): 62–86; Margaret E. Dery, *Art and Science in Breeding: Creating Better Chickens* (Toronto: University of Toronto Press, 2012), 99–105.

35. H. H. Stoddard, "Stoddard on that Remarkable Bulletin," *American Poultry Journal* 44 (Apr. 1913): 672.

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37. W. E. Castle, "Some Biological Principles of Animal Breeding," *American Breeders' Magazine* 3 (1912): 271. See also Castle, *Heredity in Relation to Evolution and Animal Breeding* (New York: D. Appleton and Company, 1911); Castle, "Pure Lines and Selection," *Journal of Heredity* 5, no. 3 (1914): 93–97.

38. Donald F. Jones, "Dominance of Linked Factors as a Means of Accounting for Heterosis," *Genetics* 2, no. 5 (1917): 471.

39. Deborah Fitzgerald, *The Business of Breeding: Hybrid Corn in Illinois, 1890–1940* (Ithaca,

NY: Cornell University Press, 1990), 55; and Jack Ralph Kloppenburg Jr., *First the Seed: The Political Economy of Plant Biotechnology* (Cambridge: Cambridge University Press, 1988), 99.

40. Fitzgerald, *The Business of Breeding*.

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42. The chicken meat or broiler industry is a separate story involving not just hybridizing for biological locks but also structural changes that brought about vertical integration of the industry from breeder to producer to the end marketers of meat. Integration would play a role in the egg industry as well. See, in particular, Horowitz, “Making the Chicken of Tomorrow”; Sawyer, *The Agribusiness Poultry Industry*; and Derry, *Art and Science in Breeding*.

43. By the 1970s inbreeding/hybridizing began to affect the pig industry—especially in Britain and continental Europe—via companies who used the method to produce boars. While the situation did not match the chicken industry’s experience, the companies—who sold breeding rights on hybrid boars—relied on the same biological lock to protect their interests. See Paul Brassley, “Cutting across Nature? The History of Artificial Insemination in Pigs in the United Kingdom,” *Studies in History and Philosophy of Biological and Biomedical Sciences* 38, no. 2 (June 2007): 444–45, 452, 458–59. For more on pig breeding, see “Animal Breeding Practice,” in *Evolution and Animal Breeding: Reviews on Molecular and Quantitative Approaches in Honour of Alan Robertson*, ed. W. C. Hill and T. F. C. Mackay (Wallingford, UK: C.A.B. International, 1989), 195–97.

44. See R. W. Touchberry, “Crossbreeding Effects in Dairy Cattle: The Illinois Experiment, 1949–1969,” *Journal of Dairy Science* 75, no. 2 (1992): 640–67; J. L. Lush, “Dairy Cattle Genetics,” *Journal of Dairy Science* 39, no. 6 (1956): 693–94; J. M. White et al., “Dairy Cattle Improvement and Genetics,” *Journal of Dairy Science* 64, no. 6 (1981): 1310, 1311; R. C. Laben et al., “Some Effects of Inbreeding and Evidence of Heterosis through Outcrossing in a Holstein-Friesian Herd,” *Journal of Dairy Science* 38, no. 5 (1955): 525–35; F. R. Allaire and C. R. Henderson, “Specific Combining Abilities among Dairy Sires,” *Journal of Dairy Science* 48, no. 8 (1965): 1096, 1099; R. C. Beckett et al., “Specific and General Combining Abilities for Production and Reproduction among Lines of Holstein Cattle,” *Journal of Dairy Science* 62, no. 4 (1979): 613, 619.

45. White et al., “Dairy Cattle Improvement and Genetics,” 1310

46. File 4, Box 11, Series 11, Shaver Collection, Archival and Special Collections, University of Guelph; Derry, *Art and Science in Breeding*, 196–97.

47. Paul C. Henlein, “Cattle Driving from the Ohio Valley, 1800–1850,” *Agricultural History* 28, no. 2 (Apr. 1954): 83–95; Henlein, “Shifting Range-Feeding Patterns in the Ohio Valley before 1860,” *Agricultural History* 31, no. 1 (Jan. 1957): 1–12; Henlein, “Cattle Kingdom in the

Ohio Valley: The Beef Cattle Industry in the Ohio Valley, 1783–1860" (PhD diss., University of Wisconsin, 1957); M. E. Ensminger, *Beef Cattle Science* (Danville, IL: Interstate Printers and Publishers, 1987); Margaret E. Derry, *Ontario's Cattle Kingdom: Purebred Breeders and Their World, 1870–1920* (Toronto: University of Toronto Press, 2001); Terry G. Jordan-Byckov, *North American Cattle Ranching Frontiers: Origins, Diffusion, and Differentiation*, Histories of the American Frontier (Albuquerque: University of New Mexico Press, 1993); James A. Whitacker, *Feedlot Empire: Beef Cattle Feeding in Illinois and Iowa, 1840–1900* (Ames: Iowa State University Press, 1975), 55, 64, 82; Johann Heinrich von Thünen, *Von Thünen's Isolated State: An English Edition of Der Isolierte Staatt*, ed. Peter Hall, trans. C. Wartenburg (Oxford: Pergamon Press, 1966).

48. See Ernst Mayr and Will Provine, *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge, MA: Harvard University Press, 1980).

49. William G. Hill, "Applications of Population Genetics to Animal Breeding, from Wright and Lush to Genomic Prediction," *Genetics* 196 (2014): 1.

50. Animal genetics would in turn serve studies of evolution. See William G. Hill and Mark Kirkpatrick, "What Animal Breeding Has Taught Us about Evolution," *Annual Review of Ecology, Evolution, and Systematics* 41 (2010): 1–19.

51. Hill, "Applications of Populations Genetics to Animal Breeding," 2; Lush, *Animal Breeding Plans*; A. B. Chapman, "Jay Laurence Lush 1896–1982: A Brief Biography," *Journal of American Science* 69 (1991): 2674; A. E. Freeman, "Genetic Statistics in Animal Breeding," in *Proceedings of the Animal Breeding and Genetic Symposium in Honor of Dr. Jay L. Lush* (American Society of Animal Science and American Dairy Science Association, 1972), 6; Louis Ollivier, "Jay Lush: Reflections on the Past," *Lohmann Information* 43 (2008): 3–12; Gordon E. Dickerson, "Inbreeding and Heterosis in Animals," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, 54.

52. Hill, "Applications of Populations Genetics to Animal Breeding," 2; Hill, ed., *Quantitative Genetics: Part I, Explanation and Analysis of Continuous Variation* (New York: Van Nostrand Reinhold Company, 1984), 16; Hill, ed., *Quantitative Genetics: Part II, Selection* (New York: Van Nostrand Reinhold Company, 1984), 1, 2, 10, 11, 12; Michael Lynch and Bruce Walsh, *Genetics and Analysis of Quantitative Traits* (Sunderland, MA: Sinauer Associates, Inc., 1998); E. P. Cunningham, *Quantitative Genetic Theory and Livestock Improvement* (Armidale, NSW: University of New England Press, 1979).

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69. Hill, “Applications of Populations Genetics to Animal Breeding,” 12.

70. Oscar Kempthorne, “An Overview of the Field of Quantitative Genetics,” in *Proceedings of the International Conference on Quantitative Genetics*, ed. E. Pollak et al. (Ames: Iowa State University Press, 1977), 48.

71. Recombinant DNA technology means the transferring of sections of DNA from one organism into another, in order to study that DNA. Recombinant DNA technology opened up the possibility of assessing genes at the DNA level and laid the basis for genomics.

72. See Giorgio Israel and Ann Millán Gasca, eds., *The Biology of Numbers: The Correspondence of Vito Volterra on Mathematical Biology*, Science Networks: Historical Studies, vol. 26 (Berlin: Birkhäuser Verlag, 2002), 1–54; and Sharon E. Kingsland, “Mathematical Figments, Biological Facts: Population Ecology in the Thirties,” *Journal of the History of Biology* 19, no. 2 (1986): 235–56.

73. Oscar Kempthorne, “Introduction,” in *Proceedings*, ed. Pollak et al., 5–9, 10; see also Cunningham, *Quantitative Genetic Theory and Livestock Improvement*, 9; Michael Lynch and Bruce Walsh, *Genetics and Analysis of Quantitative Traits* (Sunderland, MA: Sinauer Associates, Inc., 1998), 390.

74. Kempthorne, “Introduction,” 10–11.

75. R. E. Comstock, “Quantitative Genetics and the Design of Breeding Programs,” in *Proceedings*, ed. Pollak et al., 705–18.

76. D. L. Harris, “Past, Present and Potential Contributions of Quantitative Genetics to Applied Animal Breeding,” in *Proceedings*, ed. Pollack et al., 588.

77. For the classic discussion concerning black box thinking and black box theory in various disciplines, see Bruno Latour, *Science in Action* (Cambridge, MA: Harvard University Press, 1987).

78. R. Lewontin, “The Relevance of Molecular Biology to Plant and Animal Breeding,” in *Proceedings*, ed. Pollack et al., 56.

79. Peter E. Smouse, review of *Proceedings*, ed. Pollak et al., *American Journal of Human Genetics* 31, no. 6 (Oct. 1979): 754–55.

80. QTL (quantitative trait loci) are the loci of genetic material proven to relate to productive traits in livestock. The loci can be genes or simply stretches of DNA that do not code for protein, meaning they do not specify how the protein used to build cells in the body will develop and function, if these stretches are known to be close to the genes that regulate sought-after traits.



Ben Hayes, "QTL Mapping, MAS, and Genomic Selection" (Animal Breeding and Genetics Group, Department of Animal Science, Iowa State University, 2007), 55. For plants and QTL, see Kendall R. Lamkey and Michael Lee, "Quantitative Genetics, Molecular Markers, and Plant Improvement," in *Focused Plant Improvement: Towards Responsible and Sustainable Agriculture. Proceedings of the 10th Australian Plant Breeding Conference* (1993): 104–15.

81. T. F. C. Mackay, "Alan Robertson (1920–1989)," *Genetics* 125, no. 1 (1990): 1–7.

82. See James N. Thompson, "Quantitative Variation and Gene Number," *Nature* 258 (1975): 665–68.

83. F. Pirchner, "Finding Genes Affecting Quantitative Traits in Domestic Animals," in *Proceedings of the Second International Conference on Quantitative Genetics*, ed. B. S. Weir (Sunderland, MA: Sinauer Associates, Inc., 1988), 243, 244, 249.

84. M. Soller et al., "Genomic Genetics and the Utilization for Breeding Purposes of Genetic Variation between Populations," in Weir, *Proceedings of the Second International Conference*, 161.

85. A. John Clarke, ed., *Animal Breeding: Technology for the 21st Century* (Amsterdam: Harwood, 1998), 7.

86. G. E. Pollott, "Bioinformatical Genetics—Opening the Black Box of Quantitative Genetics," *Proceedings of the 8th World Congress on Genetics Applied to Livestock Production* (2006), 23.21; D. Habier, R. Fernando, and D. Garrick, "Genomic BLUP Decoded: A Look into the Black Box of Genomic Prediction," *Genetics* 194, no. 3 (2013): 597–607; Hill, "Applications of Populations Genetics to Animal Breeding," 9.

87. The DNA molecule forms a double helix, in which two long chains of nucleotide subunits twist around each other, forming a right-handed helix. There are four bases in the chains—A (adenine), T (thymine), G (guanine), or C (cytosine). Where one strand has an A, the other has a T, and where there is a G on a strand, its partner has a C. Species differ only by the sequence of the A, G, T, and C nucleotides.

88. A seminal paper behind genomic breeding is T.H.E. Meuwissen et al., "Prediction of Total Genetic Value Using Genome-wide Marker Maps," *Genetics* 157, no. 4 (2001): 1819–29; see also Hill, "Applications of Populations Genetics to Animal Breeding."

89. J. van der Werf, "Animal Breeding and the Black Box of Biology," *Journal of Animal Breeding and Genetics* 124, no. 43 (2007): 101.

90. J. W. Keele et al., "Databases and Information Systems Needed for Maps and Marker-Assisted Selection," in *Biotechnology's Role in the Genetic Improvement of Farm Animals*, ed. R. H. Miller et al. (Beltsville Symposia in Agricultural Research, American Society of Animal Science, 1996), 300.

91. S. S. Moore, "The Bovine Genome Sequence—Will it Live up to the Promise?" *Journal of Animal Science and Genetics* 126, no. 4 (2009): 257; G. R. Wiggans, "Selection of Single-Nucleotide Polymorphisms and Quality of Genotypes Used in Genomic Evaluation of Dairy Cattle in the United States and Canada," *Journal of Dairy Science* 92, no. 7 (2009): 3431.

92. See Hill, "Applications of Populations Genetics to Animal Breeding," 1–16; Margaret E. Derry, *Masterminding Nature: The Breeding of Animals, 1750–2010* (Toronto: University of Toronto Press, 2015).

93. Philip Ball, "DNA: Celebrate the Unknowns," *Nature* 496 (2013): 420.

94. It is interesting to note the sheep industry's interconnection with genetics, with reference to either inbreeding/hybridizing or quantitative strategies. In both cases sheep breeding responses matched those of the beef cattle industry. For the history of sheep breeding, see M. L. Ryder, *Sheep and Man* (London: Duckworth, 1983); Ryder, "The History of Sheep Breeds in Britain," *Agricultural History Review* 12, no. 1 (1964): 1–12; Ryder, "The History of Sheep Breeds in Britain (Continued)," *Agricultural History Review* 12, no. 2 (1964): 65–82. For similarities to beef breeding, see R. M. Bourdon, "Shortcomings of Current Genetic Evaluation Systems,"

*Journal of Animal Science* 76, no. 9 (1998): 2308–23.

95. Brassley, “Cutting across Nature?” 444–45, 452, 458–59; Bert Theunissen, *Beauty or Statistics: Practice and Science in Dutch Livestock Breeding, 1900–2000* (Toronto: University of Toronto Press, 2020).

96. For an assessment of epigenetics, see Rheinberger and Müller-Wille, *The Gene*, Chpt. 10.

97. For example, see Rheinberger and Müller-Wille, *The Gene*, Chpt. 10; Clemens Driessen, “Deliberating with Crispr Creatures—When Bioethics Becomes a Matter of More-Than-Human/Cultural Geography” (unpublished paper, Uppsala University, Sweden, May 2018). See S. S. Richardson and H. Stevens, eds., *Postgenomics* (Durham, NC: Duke University Press, 2015). For CRISPR Cas 9, see A. C. Komor et al., “CRISPR-Based Technologies for the Manipulation of Eukaryotic Genomes,” *Cell* 168, no. 1–2 (Jan. 2017): 20–36; Yue Mei, “Recent Progress in CRISPR/Cas9 Technology,” *Journal of Genetics and Genomics* 43, no. 2 (2016): 63–75; “Gene Editing Research Review,” [https://www.illumina.com/content/dam/illumina-marketing/documents/products/research\\_reviews/publication-review-gene-editing-research.pdf](https://www.illumina.com/content/dam/illumina-marketing/documents/products/research_reviews/publication-review-gene-editing-research.pdf) (accessed June 14, 2018).