JAY LAURENCE LUSH, 1896–1982:
A BRIEF BIOGRAPHY

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Jay Laurence Lush made the following autobiographical statement for the National Academy of Sciences in 1967:

I was born in a log house on a farm in southwestern Iowa [Shambaugh], the second of six children. My father was born in Canada. His parents were brought as children from southern England. My mother's father came from northern Ireland, but her mother was of old American stock, Scotch and Scotch-Irish in origin.

In our home we read many books of the kinds which were still considered classics around 1900 to 1910. Although money was scarce, we always had enough to eat, plenty to read, and clothing enough to keep warm. I went to an upgraded country school and entered a high school in Kansas at the age of 11. At Kansas State Agricultural College (now Kansas State University) I majored in animal husbandry. Mathematics was easy but not intriguing. History, physical geography, geology and parts of chemistry and biology were most interesting. I was active in debating. About 1914 I got my first intriguing glimpses of genetics. Also I encountered several interesting, friendly and challenging professors, mostly in biology or some of its applications.

After receiving the B.S. degree in 1916, I taught agriculture and chemistry in a Kansas High School for a year; then returned to KSU for my Master's degree and an apprenticeship in agricultural research. My first contribution to science was an article printed in the Journal of Heredity 12:57–71 in 1921. This was what I then thought was worth publishing from my Master's degree.

I spent nine months in the Air Force immediately after receiving the M.S. degree and I was commissioned as a Second Lieutenant in the reserve in February of 1919. I installed the Smith-Hughes program of agricultural instruction in another Kansas High School in the early part of 1919. I went to the University of Wisconsin in June of 1919 to do more graduate study in genetics.

Immediately after finishing my Ph.D. work there [1922], I went to the Texas Agricultural Experiment Station at College Station, Texas.
An important bit of Lush's personal history for the following year, 1923, was his marriage to Adaline Lincoln. Mrs. Lush, a second cousin once removed of Abraham Lincoln, is a truly remarkable person. She graduated from high school at the age of thirteen and from the University of Arkansas at sixteen; she then earned a Master's degree at the University of Chicago at age seventeen. In a speech given when Lush was being honored at the Poultry Breeders Roundtable meeting in 1969, the speaker, Arthur Heisdorf, made this remark about Mrs. Lush: "I think she is the person who has been the secret catalyst [who] has sparked Dr. Lush onto the accomplishments he has made." To this tribute should be added how important a role she has taken as a gracious hostess and "foster mother" to countless students. She also found time, and had the ability, to teach French, German, Italian, Latin, and Spanish to private pupils; to conduct a number of trips to Europe; and to be active in a number of organizations. She was named Iowa Mother of the Year in 1963, Dr. and Mrs. Lush have a daughter, Mary Elizabeth Haus- rath, a son, David Alan, and seven surviving grandchildren.

Lush's history, as recounted by him in 1968, continues:

For more than eight years I did research in animal husbandry [in Texas]. Most of that pertained to animal breeding, but some of it was in the other areas of animal production. The necessities of the research drew me further into biometry. In January of 1930 I came to Iowa State University (then Iowa State College) as Professor in the Department of Animal Husbandry to do research and teaching in Animal Breeding. . . . All of my work has hinged around finding ways to apply genetics more efficiently in improving animals and plants. For these purposes I used many biometrical tools developed by others and for myself made a few minor innovations in those. Most of my discoveries were small ones, usually growing out of some actual problem in application. These are put together in some 200 research papers and in my textbook, Animal Breeding Plans [1937] which has sold more than 22,000 copies. It is currently being printed in its fourth language [Spanish; earlier in Polish, Portuguese, and Rumanian]. Perhaps the most important single paper was one in the American Naturalist in 1947 entitled 'Family merit and individual merit as bases for selection.'

In a symposium held in 1972 (Literature Cited part A) in honor of Professor Lush the papers presented, except for one by Lush himself, were by Lush's former students or one-time colleagues at Iowa State University. These papers reflect the high esteem in which he was held — as a research worker, teacher and human being — by those who knew him best. The deep insight and extensive coverage given by those papers to Lush's life and contributions to his chosen field have led me to quote from several of them in this biographical sketch.

A former student, R. R. Shrode (1973), introduced the symposium and captured the essence of Lush's contributions in the following statement:

In effect, the field of Animal Breeding is a program of intellectual ‘line breeding’ to Lush. . . . It is with tremendous professional respect and personal affection for our honoree that we dedicate this symposium to our friend and teacher, Jay L. Lush, who has contributed more than any other individual, directly and indirectly through his many students, toward the continuing evolution of Animal Breeding from an art into a science.

One of his Iowa State University colleagues, A. E. Freeman (1973), phrased it this way:

As problems arose and could be defined in a mathematical or statistical sense, he and his students found answers to them in a way useful to improving domestic animals. The emphasis on breeding plans did not preclude interest and work on problems of a more theoretical nature. He clearly contributed to problems of almost purely theoretical interest, at least at the time; but it is safe to say that most of this work was started by seeing an actual problem arise that generated the germ of an idea for the theoretical work . . . . Dr. Lush's special interest in animal breeding was definitely aroused in 1914 by the teaching and enthusiasm of E. N. Wentworth, his major professor for the
M.S. degree [see Lush’s (1962) obituary for Wentworth].

[Lush] continued his graduate training at the University of Wisconsin under the direction of Dr. L. J. Cole. Though it may now seem a bit strange, Dr. Lush was a physiologist. His Ph.D. thesis was “The possibility of sex control by artificial insemination with centrifuged spermatozoa” (Lush, 1925). He didn’t succeed in this venture, but neither has anyone since. His interest in measurement and use of statistical tools was clear in this work. The data were arrayed by expected sources of variability, correlation coefficients were computed and probable errors were used to help determine if associations were real. Also, he fit normal curves to distributions of sperm head length measurements and tested these for goodness of fit. So, even as a physiologist, Dr. Lush’s interest in measurement and statistics was evident.

G. E. Dickerson (1973), a former colleague at Iowa State University, referred in his symposium paper to the influence Sewall Wright’s work had on Lush’s biological and statistical thinking:

How packed with meaning this subject [inbreeding and heterosis in animals] is for animal breeders! And how greatly our understanding of the potential usefulness of inbreeding and heterosis in animal improvement has expanded during the last four decades as a result of the research, writing and teaching of Dr. Jay Laurence Lush! While Dr. Lush was busy at Texas A&M from 1922 to 1930 publishing studies of inheritance and performance evaluation, he must also have been studying Sewall Wright’s interpretations of the U.S.D.A. inbreeding and crossbreeding work with guinea pigs (1922). This seems clear from his 1927 paper clarifying the limitations of “percentage of blood” in describing genetic likeness, particularly among collateral relatives and from the subsequent series with his students and collaborators on the amount and kind of inbreeding, occurring during breed development in cattle, sheep and swine (1932 to 1936, 1946), using the technique of Wright and McPhee (1925) for sampling random lines of ancestry.

When Dr. Lush arrived at Iowa State in 1930, earlier experiments with full-sib inbreeding in swine at Iowa and elsewhere had been discontinued due to loss of fertility. However, Wright’s theoretical analyses and some results with guinea pigs (1921, 1922) had indicated that selection might be able to offset unfavorable effects of milder inbreeding and that inbreeding was a powerful tool for creating genetic diversity among lines.

This led Dr. Lush to initiate an experiment in 1930 comparing intense and mild inbreeding in pigs, with concurrent individual and progeny test selection. During this same period, Lush’s famous bulletin on linebreeding was published (1933). It eloquently states the case for subdivision of breeds into many lines, each mildly linebred to carefully selected ancestors, with continuous elimination of the poorer ones and recombining of better ones, closely paralleling Wright’s (1931) ideas on optimum population structure for evolution.

When this author was a graduate student with Lush at Iowa State in 1931, Lush made frequent trips to the University of Chicago to audit Sewall Wright’s course on Statistical Genetics and to consult with Wright. He returned to Ames inspired by these sessions. In fact, Lush said at a Poultry Breeders’ Roundtable in 1969: “Those were by far the most fruitful ten weeks I ever had” (National Poultry Breeders’ Round Table, 18th Annu. Session, p 104, 1969).

R. A. Fisher’s work was also called on frequently by Lush, as Freeman (1973) states:

Before about 1930, the primary statistical tools used in animal breeding were correlation and regression methods. R. A. Fisher lectured at Iowa State through the summers of 1931 and 1936. Fisher’s work greatly advanced the knowledge and use of statistics. Dr. Lush was unique in combining the work of both Fisher and Wright to solve animal breeding problems. Many of Dr. Lush’s papers from 1926 to 1930 could be described as developing and using more accurate ways to measure quantitative traits.
Lush undertook studies using records collected on swine, dairy cattle, beef cattle, sheep, goats, poultry and honeybees. In 1930 he also initiated an experiment on "closed-herd" selection in dairy cattle as well as one on selection and inbreeding in swine. Both of these long-term experiments provided data for many M.S. and Ph.D. theses and resulted in major contributions to the field of animal breeding.

There is one paper (Lush, 1947) that serves well as a prototype for many of his papers. It is also the one that Lush considered his "most important single paper." It can be used to illustrate his way of thinking about a problem and how that approach leads to a solution.

The study began, as did so many of Lush's projects, with a practical problem: "... how much attention ought to be paid to the merits and defects of littermates when choosing boars and gilts to use for breeding" (Lush, 1947). The problem developed into the more general one of asking how much a population mean would be changed by selection on individual performance alone versus selecting on family merit alone, versus selecting on a combination of the two.

How did Lush approach this and similar problems? He started with the fundamental principles of genetics; then, by invoking a deductive argument, he gave them effect through the use of the tools of population genetics (discontinuous classes, qualitative differences) and biometrical genetics (continuous distributions, quantitative or measurement differences).

Readers of Lush's papers were usually made aware (as they were in the 1947 paper) of the danger of accepting conclusions without taking into account the role played by chance, the frequent need to make simplifying (possibly oversimplifying) assumptions in order to grapple with a problem, and the errors likely to be made by semantic arguments that are not supported by experimental evidence or by quantitatively evaluated, deductive arguments.

He also pointed, in the 1947 paper, to the need to keep in mind other factors: the fiducial limits of the estimates, the role that mutations might play, the effect of selection in the same or in a different direction within the population, and the need for experiments to check on the theory involved in this work. He showed statistically that "family selection is most superior to mass selection when family members resemble each other least" (i.e., when families overlap widely in their phenotypes).

As is usual in Lush's papers, he not only answered the specific questions asked but expanded the answer to encompass much more. In this case he stated the solution in terms of interclass correlations, and he then translated the solution into analysis of variance and intracllass correlations in the hope that the "biometrical relations may be clearer." These translations undoubtedly helped students understand the equivalent meanings of two important ways of stating the solution statistically.

Furthermore, he provided, in regression form, the equations for predicting breeding value of an individual based on its own phenotype and its family average. He discussed under what conditions negative attention should be paid to family average and the effect inbreeding would have on the results. Family selection for "all-or-none" characteristics, as well as characteristics distributed continuously, was clearly discussed. A number of other qualifications and special conditions were also mentioned. His 1947 paper is one in which the conclusions and interpretations make a contribution to genetics, to animal and plant breeding, to statistics, and to sociology and anthropology. Many of this other papers also had a significant bearing on problems in several fields.

Some of the sources of information used by Lush in his research were the records from private farms enrolled in the Iowa Cow Testing Association, on animals registered in the breed associations, and on poultry of the Kimber Poultry Farm. These records provided insights into the genetic and environmental sources of variation in economically important traits under commercial conditions. Lush was also associated with an Atomic Energy Commission research project on the genetic effects of ionizing radiation in swine.

Lush's (1973) view of teaching was given in his symposium paper "Teaching Animal Breeding and Training Graduate Students":
firmly that the errors among them could scarcely have been corrected by any amount of subsequent experience.

... As it was, the cattle and sheep and goats talked back to me. Having no papers to grade or class rolls to call, I listened. Usually the animals were saying something like: “Most of the things you think you know may be true in principle but you have many of them out of all proportion to their actual importance. When you draw a conclusion, you often overlook circumstances which, if you considered them properly, would upset your recommendations badly.” Trying to solve these apparent inconsistencies drove me, whether I wished it or not, in the direction of measuring more accurately the factors in the problems. I was always needing to be surer of how the various factors interacted in any whole operation we might be considering.

His success as a teacher and director of graduate students (26 who earned the M.S. and 124 the Ph.D. under his direction) was admirably presented in Touchberry’s symposium paper, which he concluded by saying that “as an advisor of graduate students, Dr. Lush was highly respected and admired. He was firm without being threatening and he got his points and message across without raising his voice or using profanity. He was a warm and friendly person with a tremendous respect and tolerance for students.”

Lush’s influence on animal breeding around the world has been enhanced greatly by the wide distribution of his classic book Animal Breeding Plans (1937). His authoritative mimeographed notes, “The genetics of populations” (1948), have also played a major role in the thinking of animal breeders who were fortunate enough to have read them.

He played a major role in establishing, and was an active participant in, the regional laboratories for animal breeding research, which were joint ventures of cooperating states and the U.S. Department of Agriculture. He was also instrumental in the formation and guidance of the National Poultry Breeders’ Roundtable (now, National Breeders’ Roundtable), an organization that meets annually to discuss research in genetics and in animal and plant breeding. The meeting in 1969 (18th Annu. Session, May 7–8) was held in his honor. Lush acted in an advisory capacity to these and many other organizations.

He traveled extensively abroad and served as an advisor on animal breeding in a number of countries. As a result, he was responsible for a profound change in the approaches to animal breeding research and practice in many parts of the world.

Dr. Lush received honorary doctoral degrees from Michigan State University, University of Illinois, Kansas State University, University of Wisconsin, Royal Agricultural College of Sweden, Justus Liebig University, Royal Veterinary and Agricultural College of Denmark, Swiss Federal Institute of Technology, and Agricultural University of Norway.

His awards included the Morrison Award of the American Society of Animal Science; Honored Guest, American Society of Animal Science; Charles F. Curtiss Distinguished Professor in Agriculture, Iowa State University; Borden Award for research in dairy production, American Dairy Science Association; Herman von Nathusius Medal of the German Society for Animal Breeding; Armour Award for animal breeding and genetics, American Society of Animal Science; Medal of the Mendel Centennial Association, Czechoslovakia; Order of Merit in Science, Italy; and United States National Medal of Science. Dr. Lush was elected to the National Academy of Sciences in 1967, to membership in the Royal Society of Edinburgh, and to membership in the Academies of Science or Agriculture of Sweden, Norway, and Italy.

A fitting ending to this biographical memoir is the symposium statement of Touchberry:

He [Lush] has defined the problems of genetically changing farm animals in a logical, biological, quantitative and economic way. Further, he has shown how genetics and mathematics can help in solving problems of animal breeding. In doing this he has beneficially affected the lives of many. Thus, to me, it seems fitting to say that, rather than having followed a profession, he has, for the past 40 years, led a profession.

Literature Cited

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