

NATIONAL ACADEMY OF SCIENCES

JAY LAURENCE LUSH

1896—5/22/82

A Biographical Memoir by
ARTHUR B. CHAPMAN

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Biographical Memoir

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WASHINGTON D.C.



Jay L. Lush

JAY LAURENCE LUSH

January 3, 1896–May 1, 1982

BY ARTHUR B. CHAPMAN

JAY LAURENCE LUSH made the following autobiographical statement in 1967¹:

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 ungraded 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

¹ Autobiographical statement, National Academy of Sciences, 1967.

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 an award 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 Hausrath, a son, David Alan, and seven surviving grandchildren.

Lush's history, as recounted by him in 1967, continues below:

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 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, Portugese, 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 1972 a symposium² was held in his honor. All the papers presented except one by Lush himself, "Teaching Animal Breeding and Training Graduate Students" (1973), were by Lush's former students or one-time colleagues at Iowa State University. These papers reflect the high esteem in which Lush was held—as research worker, teacher, and human being—by those who knew him best. The deep insight and extensive coverage given by these papers to Lush's life and contributions to his chosen field have led me to quote extensively from them in this biographical memoir.

A former student, R. R. Shrode, introduced the symposium and captured the essence of Lush's contributions:

In effect, the field of Animal Breeding is a program of intellectual "linebreeding" 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.³

² The Animal Breeding and Genetics Symposium in honor of Dr. Jay L. Lush, sponsored jointly by the American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, July 29, 1972 (1973). Copies of the symposium proceedings may be obtained from Business Office, American Society of Animal Science, 309 West Clark St., Champaign, Illinois 61820.

³ R. R. Shrode, "Introduction—Why We Are Here," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of

An Iowa State University colleague, A. E. Freeman, 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 [see Lush's obituary for Wentworth (1962) and his response during the dedication of the Jay L. Lush Auditorium at Iowa State (1974)] who was later his major professor for the M.S. degree [at Kansas State Agricultural College]. . . .

[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.⁴

G. E. Dickerson, 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:

Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), p. iii.

⁴ A. Freeman, "Genetic Statistics in Animal Breeding," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), pp. 1, 2, 3.

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).⁵ 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 1939, 1946), using the technique of Wright and McPhee (1925)⁶ 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 (1921,⁷ 1922⁸) 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 linebreeding in pigs, with concurrent individual and progeny test selection. During this same period (1933), Lush's famous bulletin on linebreeding was published. It eloquently stated 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)⁹ ideas on optimum population structure for evolution.¹⁰

⁵ S. Wright, "The Effects of Inbreeding and Crossbreeding on Guinea Pigs," *U.S. Department of Agriculture Bulletin*, 1090(parts 1 and 2, 1922); 1121 (part 3, 1922).

⁶ S. Wright and H. C. McPhee, "Approximate Method of Calculating Coefficients of Inbreeding and Relationship from Livestock Pedigrees," *J. Agric. Res. (Washington, D.C.)*, 31(1925):377-83.

⁷ S. Wright, "Systems of Mating," *Genetics*, 6(1921):111-78.

⁸ S. Wright, "Effects of Inbreeding and Crossbreeding," 1090.

⁹ S. Wright, "Evolution in Mendelian Populations," *Genetics*, 16(1931):97-159.

¹⁰ G. E. Dickerson, "Inbreeding and Heterosis in Animals," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), pp. 54-77.

Freeman also pointed to Sewall Wright's influence on Lush's thinking: "Lush commuted [in 1931] to the University of Chicago to audit Sewall Wright's course in Statistical Genetics and other Zoological courses there. The influence of this training and these visits with Dr. Wright on Dr. Lush's teaching and research is evident."¹¹ Lush said, at the Poultry Breeders Roundtable in 1969: "Those were by far the most fruitful ten weeks I ever had."

R. A. Fisher's work was also called on frequently by Lush, as Freeman 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."¹²

In what specific areas of animal breeding were Lush's contributions made? Freeman notes the following:

Many of his early papers explored husbandry problems; others considered the mode of inheritance of qualitative traits; some were concerned with measurement and description of economically important traits; and others are clearly a start of current-day animal breeding theory. In the early years, the first three types of papers were more numerous than the last type. Of course, this changed. As Dr. Lush was confronted with questions that stemmed from practical problems, he tried to answer them from the existing knowledge in classical genetics, plant breeding or allied theory. If existing knowledge did not yield an acceptable answer, he used statistical methods to better describe problems or relations existing between traits, then put this statistical description into a form usable by the breeder. . . . Many of Dr. Lush's publications from 1926 to 1930 could be described as developing and using more accurate ways to measure quantitative traits.¹³

Lush undertook studies using records collected on swine, dairy cattle, beef cattle, sheep, goats, poultry, and honeybees.

¹¹ Freeman, "Genetic Statistics," p. 4, 5.

¹² *Ibid.*, p. 5.

¹³ *Ibid.*, p. 3, 4.

In 1930 he also initiated an experiment on “closed-herd” selection in dairy cattle as well as the 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.

R. W. Touchberry, another former student, gives a detailed discussion in his symposium paper¹⁴ of “some of the pertinent points in a few of what I [Touchberry] consider to be his [Lush’s] most important papers.” For those who are familiar with the terminology of genetics, statistics, and animal breeding, Touchberry’s paper provides a summary of many of Lush’s contributions to the field. I will attempt to give the essence of these contributions.

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 litter mates when choosing boars and gilts to use for breeding.” The problem developed into the more general one of asking how much a population mean would be changed by selecting 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 (con-

¹⁴ R. W. Touchberry, “The Life and Contributions of Dr. Jay Laurence Lush,” in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), p. 89.

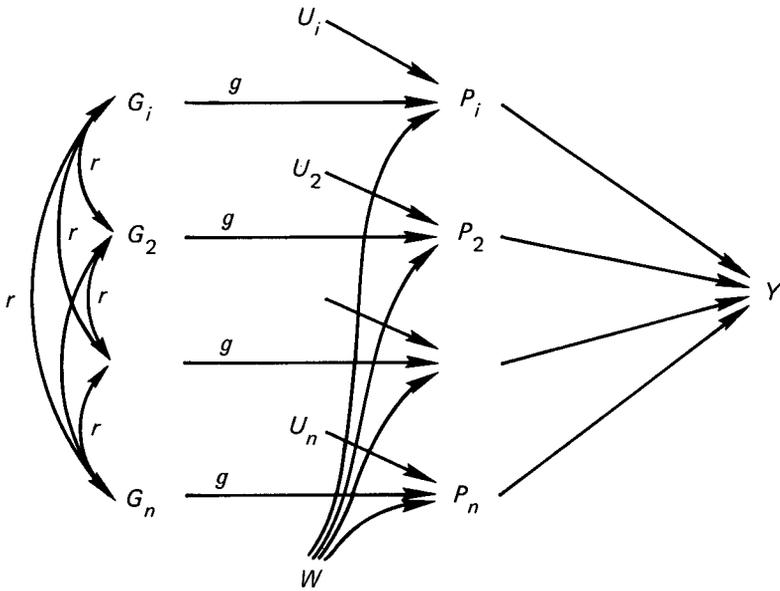
tinuous distributions, quantitative or measurement differences). In this *American Naturalist* paper, Lush points out: "The process of selection consists only of predicting the breeding value [genetic make-up or transmitting ability for the trait under consideration] of each individual which is being considered and then keeping it or culling it on the basis of that prediction. If the same fraction of the population must be saved but there is a choice of bases on which selection may be made, then the difference in results depends only on how accurately each individual's breeding value can be predicted from each of these bases."¹⁵

In comparing the three bases of selection in this paper, Figure 1 is used as a graphic way of looking at the interrelationships between the variables. The arrows in this diagram lead from "cause" to "effect," and the value attached to each one is defined as a path coefficient (standard partial regression coefficient) by Sewall Wright, who developed this procedure.¹⁶ The bidirectional arrows refer to simple correlations between the variables. In this diagram P_i stands for the phenotype (observed measured value) of an individual, i ; Y , the average phenotype of a family; G_i , the breeding value of an individual (average effects of the genes it contains—Fisher's "expected value"¹⁷); W , the factors other than G_i that affect each P_i in a family the same way but may differ from family to family; U_i , the factors other than G_i that affect P_i but that are no more alike for members of the same family than they are for individuals that belong to different families;

¹⁵ J. L. Lush, "Family Merit and Individual Merit as Bases for Selection," *American Naturalist*, 81(1947):243–44.

¹⁶ S. Wright, "On the Nature of Size Factors," *Genetics*, 3(1918):367–74; "Correlation and Causation," *Journal of Agricultural Research (Washington, D.C.)*, 20(1921):557–85; "The Method of Path Coefficients," *Annals of Mathematical Statistics*, 5(1934):161–215.

¹⁷ R. A. Fisher, *The Genetical Theory of Natural Selection* (New York: Oxford University Press, 1930).



$$r_{GP} = g$$

$$r_{GY} = g \frac{1 + (n - 1)r}{\sqrt{n[1 + (n - 1)t]}}$$

$$r_{PY} = \sqrt{\frac{1 + (n - 1)t}{n}}$$

$$t = r_{PP} = g^2 r + r^2_{WP}$$

FIGURE 1 Path coefficient diagram of biometrical relations involved in mass, family, and combination selection.

Source: J. L. Lush, "Family Merit and Individual Merit as Bases for Selection," part I, *American Naturalist*, 81(1947):246.

and r , the correlation between the breeding values of members of a family (Wright's relationship coefficient¹⁸).

The algebra to which this approach leads has been spelled out by Wright (see note 16) in a form that relates correlation coefficients to their path coefficient components. Some of the pertinent correlations—in terms of path coefficients—are given below the diagram in Figure 1. The correlations (r_{GP} , r_{GY} , and r_{GI}) reflect the relative progress expected under the three methods of selection, "where I is the index or most probable breeding value of an individual, as estimated from the optimum linear combination of attention to its own phenotype and attention to the average phenotype of the family to which it belongs." The phenotypic correlation between members of a family is denoted by t .

As an example of the use that can be made of these correlations in terms of their path coefficient components, let's look at the make-up of r_{GP} and r_{GY} . If selection is practiced on family average (Y) alone, the progress made would be expected to be $1 + (n - 1)r/\sqrt{n[1 + (n - 1)t]}$ times as rapid as mass selection (selection on individual performance); that is, $r_{GY} = g[1 + (n - 1)r]/\sqrt{n[1 + (n - 1)t]}$ versus $r_{GP} = g$, where g = the path of influence from G to P or the square root of heritability (the portion of the phenotypic variance due to genetic differences between individuals), and n = the number of individuals in the family. By inserting the values for g , n , r , and t that apply in a particular case, the difference in predictive value for transmitting ability from Y and P becomes evident.

As a graphic representation of the relative effectiveness of the three methods of selection, Lush (1947) gives the following diagram (Figure 2) for a case where $n = 21$. The progress from mass selection is represented by a level plane

¹⁸ S. Wright, "Coefficients of Inbreeding and Relationship," *American Naturalist*, 56(1922):330-38.

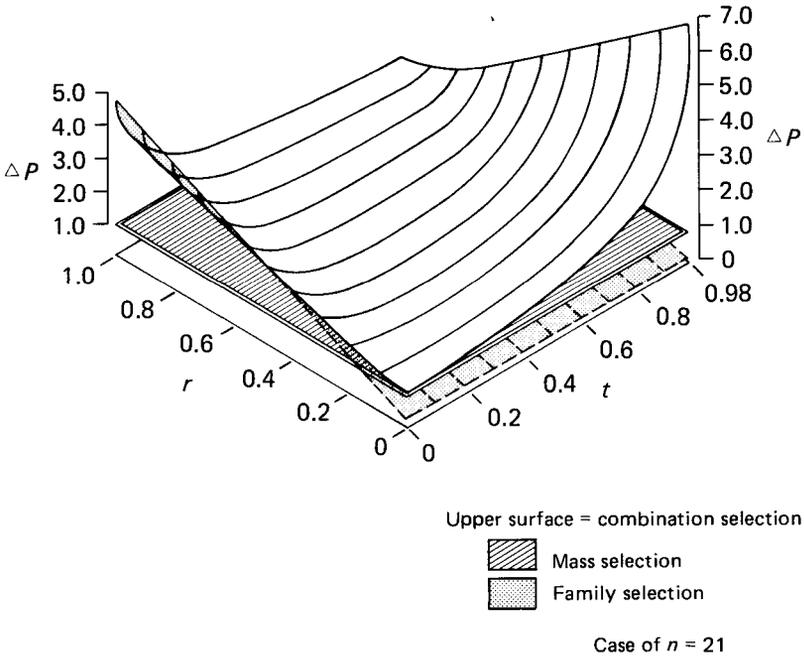


FIGURE 2 Relative effectiveness of the three methods of selection at all combinations of r and t when families contain 21 individuals.
 Source: J. L. Lush, "Family Merit and Individual Merit as Bases for Selection," part I, *American Naturalist*, 81(1947):256.

at height 1.0 above the base and where all combinations of r and t are given.

The above gives the basic approach used in this paper and many others by Lush, but the full substance of this study goes much further. Readers of Lush's papers were usually made aware (as they are in this one) of the danger of accepting conclusions without taking into account the role played by chance, the frequent need for making 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.

As an illustration of one of the caveats stemming from the above in the paper under discussion, he points to this possibility:

If the actual effects of a gene substitution upon P are sometimes larger and sometimes smaller than the average effect of that gene substitution in that population, depending upon what other genes are present, the differences between the actual and average effects are termed epistatic or dominance deviations. These give rise to "special" breeding values. That is, they cause some matings to produce better offspring and some to produce poorer ones than would be expected if one knew the kind of offspring those same parents would produce if mated to a representative sample of the whole population. Most of the dominance and epistatic deviations from the additive scheme are included in U , but a small part are in W .

He also points 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; the need for experiments to check on the theory involved in this work; and "the naive view, repeatedly disproven but still often inferred to be axiomatic, that family, breed, and race are unimportant, or even unreal, unless the families, breeds, or races are so distinct that they do not overlap at all." Lush showed statistically that "family selection is most superior to mass selection when family members resemble each other least; i.e., when the families overlap widely in their phenotypes and t is therefore low!"

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

Furthermore, he provides, in regression form, the equa-

tions for predicting breeding value of the individual based on its own phenotype and its family average. He discusses under what conditions negative attention is 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, is clearly discussed. A number of other qualifications and special conditions are also mentioned. And finally, the implications of these conclusions for man are given consideration. This is a paper 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 his other papers also have a significant bearing on problems in several fields.

The other papers summarized by Touchberry,¹⁹ which follow the same pattern as the one just discussed, made major contributions to animal breeding by clarifying problems involving progeny tests, individual performance, pedigree information, heritability, selection, and the role played by chance.

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 provided an insight 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 view on teaching is given in the paper "Teaching Animal Breeding and Training Graduate Students," which he presented at the symposium in his honor in 1973. His introductory remarks in this paper reflect an attitude of his that was clearly evident to his students in his teaching.

¹⁹ Touchberry, "Life and Contributions," pp. 89-104.

Immediately on completing my Ph.D. degree, I did research for more than 8 years, with almost no interruption for teaching. I'm glad it happened that way. If I had taught the same course as much as three times in succession, using the available texts and my graduate notes and all the rest of what I thought I knew, I would surely have come to believe those things myself so 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.²⁰

Lush had a penchant for those apposite sayings that are so helpful to students trying to think through what is meant by some of the more esoteric concepts of genetics, statistics, and animal breeding. In my symposium paper,²¹ I have quoted a number of these. One that I found myself using quite frequently in my teaching because of the effect it had had on me is one that he used because "Some of us think we have seen signs that many populations [being selected] do not actually change [as] rapidly [as we think they should]: Heritability may not be as high as we think. Selection may not have been as intense as we think. Perhaps the rate of

²⁰ J. L. Lush, "Teaching Animal Breeding and Training Graduate Students," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), p. 78.

²¹ A. B. Chapman, "Selection Theory and Experimental Results," in *Proceedings of the Animal Breeding and Genetics Symposium in Honor of Dr. Jay L. Lush*, American Society of Animal Science, American Dairy Science Association, and Poultry Science Association, Blacksburg, Virginia, July 29, 1972 (1973), pp. 42–53.

progress actually is substantially as much as it should be.” Dr. Lush then points out that “we ought to think of the old adage that when one is asked to explain how it is that witches can turn milk blue, the first thing is to find out is whether witches really can turn milk blue!”²²

His success as a teacher and director of graduate students (26 who earned the M.S. and 124 a Ph.D. under his direction) is admirably presented in Touchberry’s symposium paper, which he concludes by saying:

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.²³

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

He played a major role in establishing and was an active participant in the regional laboratories for animal breeding research—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, an organization of commercial poultrymen and academic staff that meets annually to discuss research in genetics and in animal and plant breeding. The meeting in 1969 (Eighteenth Annual Session, May 7–8) was held in his honor.

²² J. L. Lush, “Summary (Symposium on Selection, Chicago, November 1949),” *Journal of Animal Science*, 10(1951):18–21.

²³ Touchberry, “Life and Contributions,” p. 104.

Lush acted in an advisory capacity to these and many other organizations, both foreign and domestic. (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 countries.

Lush received a number of honors and awards, one of which was to dedicate to him the Iowa State University Auditorium in 1973. His remarks on this occasion (1974) illustrated his humility and include a typical "Lush" analogy: "I'm proud of this occasion, of course, although I am uncomfortably aware that others deserved the honor more. Also, I know that sheer luck had much to do with the things I did accomplish. In some ways they resemble the occurrence of an avalanche in the mountains. For an avalanche to occur at all requires some snow, of course, but the small event which actually triggers the avalanche might just as well have happened a hundred yards to the right or to the left, or it might as well have happened yesterday or not until day after tomorrow! An avalanche is contagious in that once it starts, it jars things loose for hundreds of yards around."

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."²⁴

²⁴ Ibid.

HONORS AND DISTINCTIONS

HONORARY DOCTORAL DEGREES

- 1957 Royal Agricultural College of Sweden
- 1957 Justus Liebig University, Giessen, Germany
- 1958 Royal Veterinary and Agricultural College of Denmark
- 1964 Michigan State University
- 1969 University of Illinois
- 1970 Kansas State University
- 1970 University of Wisconsin
- 1971 Swiss Federal Institute of Technology, Zurich
- 1975 Agricultural University of Norway

AWARDS

- 1946 Morrison Award of the American Society of Animal Science
- 1956 Honored Guest, American Society of Animal Science
- 1957 Charles F. Curtiss Distinguished Professor in Agriculture, Iowa State University
- 1958 Borden Award for research in dairy production, American Dairy Science Association
- 1960 Herman von Nathusius Medal of the German Society for Animal Breeding
- 1965 Armour Award for animal breeding and genetics, American Society of Animal Science
- 1965 Medal of the Mendel Centennial Association, Czechoslovakia
- 1966 Order of Merit in Science, Italy
- 1968 National Medal of Science

MEMBERSHIPS

- 1967 Member, National Academy of Sciences
- 1972 Member, Royal Society of Edinburgh
Foreign member of the Academies of Science or Agriculture of Sweden, Norway, and Italy

BIBLIOGRAPHY

1921

Inheritance in swine. *J. Hered.*, 12:57-71.

1922

An hereditary notch in the ears of Jersey cattle. *J. Hered.*, 13:8-13.

The influence of age and individuality upon the yield of wool. *Proc. Am. Soc. Anim. Prod.*, 1922:105-9.

1923

With E. N. Wentworth. Inheritance in swine. *J. Agric. Res.*, 23:557-82.

With J. M. Jones and J. H. Jones. I. Fattening steers on cottonseed meal and hulls with and without corn. II. The influence of age on fattening steers. *Tex. Stn. Bull.* 309.

With J. M. Jones. The influence of individuality, age and season upon the weight of fleeces produced by range sheep. *Tex. Stn. Bull.* 311.

1924

Twinning in Brahma cattle. *J. Hered.*, 15:25-27.

"Double ears" in Brahma cattle. *J. Hered.*, 15:93-96.

With J. M. Jones. The influence of individuality, age and season upon the weights of fleeces produced by Angora goats under range conditions. *Tex. Stn. Bull.* 320.

1925

The possibility of sex control by artificial insemination with centrifuged spermatozoa. *J. Agric. Res.*, 30:893-913.

With J. M. Jones. Methods of selecting wool samples in shrinkage studies. *Proc. Am. Soc. Anim. Prod.*, 1925:115-17.

1926

Practical methods of estimating the proportions of fat and bone in cattle slaughtered in commercial packing plants. *J. Agric. Res.*, 32:727-55.

Inheritance of horns, wattles, and color in grade Toggenburg goats. *J. Hered.*, 17:72–91.

With W. H. Black. How much accuracy is gained by weighing cattle three days instead of one at the beginning and end of feeding experiments. *Proc. Am. Soc. Anim. Prod.*, 1926:206–10.

1927

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