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Heritability in retrospect

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WHO COINED the term "heritability"? This question recently evoked considerable debate in an interdepartmental genetics seminar, organized around the general theme "Genetics in the Bicentennial." As chairman of the seminar I had suggested the concept of heritability for one of six sessions devoted to population and quantitative genetics. The graduate student selecting this topic, Stephen Rich, had little difficulty in documenting the tremendous contributions made by J.L. Lush to the understanding and application of both *broad* and *narrow sense heritability*, especially as these concepts relate to the genetic improvement of farm animals. In due course, the student traced the basic concepts to the classical papers of Fisher[5] and Wright[21]. In fact, no problem arose until he sought to establish the origin of the term "heritability."

Since my own graduate student days I had assumed that Dr. Lush originated the term. Who else? But when challenged for documentation, I became apprehensive after checking unsuccessfully Lush's *Animal Breeding Plans*[15], his mimeographed *The Genetics of Populations*, and my personal notes from his animal breeding classes. Then I turned to more general information sources. For example, a couple of genetics dictionaries[11,12] define heritability without giving its origin. A third[18] cites Lush's 1939 paper[16] which simply lists the various methods of estimating heritability. Cook's[2] chronology of genetics gives the origins of many genetic terms and concepts, including the major milestones of biometry and animal breeding, but has no mention of heritability. Many textbooks (e.g., Kempthorne's *An Introduction to Genetic Statistics*[10], p. 464) cite the 1937 edition of Lush's *Animal Breeding Plans* as their source reference. Much to my surprise, I could not find the word heritability in the 1937 edition (the concept is accurately presented in terms of the relative importance of hereditary and environmental sources of variance). Yet Lush's second edition (1943) uses heritability extensively without any historical reference.

My previously stated conviction as to the originator of the term was reinforced by Sewall Wright's 1961 comments[22]: "There has been considerable drifting in the meaning of the term heritability and the symbol h^2. I think I introduced the latter in a paper in 1920 as the degree of determination by heredity. . . . I think Lush introduced the term heritability and the narrow sense of the additive component. . . ."

Following Wright's suggestion, I traced Lush's usage of the term to a 1936 publication[14] where he titled a major section "Summary of Evidence on Heritability." Yet the word heritability was not defined or used again in this section or elsewhere in the bulletin. In this and later papers from that period, Dr. Lush frequently used heritability without a hint that he might be coining a new term, but with the implication that its usage was understood. Nevertheless, in these early papers he obviously preferred such terms as "hereditary in the narrowest sense" and "portion of the individual variance due to additive gene effects."

At this dead end and with the initial question unresolved. I gave up the search and posed the question to Dr. Lush. His carefully considered reply went far beyond the immediate question and detailed historical background in a manner that merits a wider audience than my seminar group. Any attempt to paraphrase his remarks would distract, so I quote directly.

> My answer won't be as clear-cut and definite as you might wish, but that is the way things happen. The ideas themselves overlap. Especially when they change a little with time. And the operations, which really define them, may vary at least a little from one user to another.
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> The following comments I take from a little 3" by 5" card, such as I keep in a file headed "definitions." On such cards I put details about various definitions whenever I have occasion to consider the history and discordances of some of those. These comments come from the card entitled "heritability."
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> Darwin, in the chapter on "Natural Selection" in the ninth edition of his book *The Origin of Species*, says ". . . as well as the strength of the hereditary tendency." This seems to come close to heritability as we use it today although, of course, it implies nothing about the discrete nature of the units, or their segregation or how the variation is conserved.
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> Galton must have said many things about this general subject after about 1885. He wrote voluminously about heredity and always tried to quantify his ideas as much as possible. I have not, however, noted that he used "heritability" specifically.
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> E.D. Davenport, in 1907 on pages 486–490 et seq. of his book *Principles of Breeding*, uses as "the coefficient of heredity" the correlation between relatives, although I think he was not discriminating clearly between different kinds of relatives nor was he using any factors to multiply those correlations. Also, he seems somewhat confused about the difference between regression and correlation for interpreting "the strength of heredity." He draws freely on Galton. Perhaps he generalizes even more broadly than Galton did?
>
> Wilhelm Johannsen deserves credit for distinguishing

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clearly between variance caused by differences among the individuals in their genotypes and variance due to differences in the environments under which they grew. This is close to what I call "heritability in the broad sense." I take it that "Erblichkeit" can be translated fairly as *heritability*. He did not subdivide clearly the genetic variance into that which is additive, that which is due to dominance, and that which is due to epistasis. He had little need of the latter two in his own material because he worked mostly with populations of pure lines. His most pertinent warning against generalizing too freely is in the second edition (1913) of his text book where, on page 210, he warns against, "Die falsche Vorstellung, das Ähnlichkeit ohne weiteres ein Austruck von Verwandtschaft sein muss—oder dass gar "Erblichkeit" durch "den Grad der Ähnlichkeit zwischen Verwandten' ausgedrückt werden könne." On page 358 (the 1913 edition of his text "Elemente der exakten Erblichkeitslehre") he does use "Erblichkeitsziffer" for regression on mid-parent. On page 122 he uses regression of offspring on mid-parent to estimate "Grad von Erblichkeit."

Much in Johannsen's text is still worth reading, even today. When he put his ideas and evidence on "pure lines," "genotype" and "phenotype" in German (1903) for circulation in other countries, he left out some interesting material about why he undertook these experiments in the first place (this is in the slightly earlier report which was printed in Danish). Briefly, he ws trying to see how far he could generalize "Galton's Law" and whether it could be reconciled with the Mendelian ideas of DeVries. He dedicated the 1903 paper to Galton as the creator of genetics (Schöpfer der exakten Erblichkeitslehre).

Lauprecht (in a letter to me dated February 3, 1962) thinks that Jacob Peters in 1913 was the first to use the idea of heritability in agriculture practice. Peters worked at Königsberg in East Prussia. He was, I think, the first man to use sire indexes, although he didn't carry them far. He used them mainly to correct the sire's progeny test for the phenotypes of his mates.

Apparently my own usage of the word "heritability" began with the second edition of my book, rather than with the first. At least I do not find it in the first edition on a casual scanning with that in mind. Nevertheless, pages 63 to 70 in that first edition are *entirely* about what we would now call heritability. I was, at that time, using variance components or various expressions such as "the genetic portion of the variance in . . ." (page 477 in the *Journal of Heredity*, Vol. 23, 1932); ". . . the relative importance of the different causes of variance in production records"; "to what extent are the observed differences an accurate guide to the hereditary differences . . ."; "how much of the observed variation is hereditary . . ."; and as long ago as 1923 on page 32 of Texas Bulletin 311, "therefore the hereditary benefits to be derived from culling are going to depend entirely and the present benefits will depend somewhat on the amount of hereditary variation in wool production in the flock which is to be culled."

The first place I notice where heritability was used systematically was in Research Bulletin 204 on the Danish progeny testing stations published by the Iowa station in 1936, but actually written in 1935. There on pages 182 to 184 is a systematic section entitled "Summary of Evidence on Heritability." There is also a fairly good statement on the limitations and qualifications of the ideas which were derived from these operations.

From looking at these bits and from memory I think I must have been systematically avoiding the use of a single word, lest the readers oversimplify it and apply it too widely to conditions for which it was not suited. That is, I was trying to guard against a single term being overworked and used illegitimately, as happened often with statements like those by Davenport. At least I used longer sentences or clauses than I would now use. This amounted to using the definition of the word repeatedly instead of the word itself.

I think I was moved out of that position by the practical necessities in summarizing the Danish work. That is, the point of view, that one should use only the variance components or their ratios, works well enough when comparing two rather similar populations, as when one asks whether the heritability of milk production in DHIA records differs from that in semiofficial records, or the heritability of rate of gain in pigs is larger when the pigs are about five months old or is larger when they are about two months old. It gets almost hopelessly confused, however, if one tries to compare the heritability of traits which are different in kind, or are expressed on a different scale, such as I was doing with the Danish records, or one might do concerning percentage of butterfat in milk and quantity of milk and so forth. There may, of course, always be a question of whether it "makes real sense" to compare the heritabilities of different traits or in widely different populations. Doing that does often give us some information we would miss otherwise, however.

I used *diagrams* showing the partitioning of variance in fractional form at least as long ago as 1933 (*Journal of Dairy Science* 16:516). Also I used a tabular form to express this at least as long ago as 1934 (*Genetics* 19:341). Leaving it in variance components, rather than as fractions of those, seems to have certain technical statistical advantages when one is concerned *only* with *statistical significance*. Fisher and Snedecor were stressing unduly the testing for significance in the early 1930's. Many of us were going along with that. (I'm not sure we have yet recovered completely but that is another story!) I merely mention that as part of the explanation for the widespread preference for expressing our findings in variance components, rather than to express them as fractions of variance. Perhaps this was only a minor skirmish in the sometimes-heated expression of our opinions about the relative merits of correlation coefficients and regression coefficients.

I tried to summarize my thoughts on heritability for the Genetics Congress at Stockholm in 1948. I still regard that as one of my best summaries on the topic although, of course, there are still other ways for saying many of these things.

In none of my work did I go much into variance due to interaction between heredity and environment. I merely mentioned that. Perhaps Falconer has so far made the best stab at that? [Perhaps Wrights's circular causation should point the way?]

I think none of us has yet taken a detailed, hard look at variance due to cooperation or to competition. It is imaginable that these could be highly important in some populations and for some traits. Obviously, the whole field of the genetics of such traits as altruism, patriotism, aggressive self-interest and so forth could be very important in species living under semi-social conditions and in experimental plants and animals which are grouped in physically separate plots or in pens and must use resources which are always somewhat limited. I have never pursued this much further than to get the feeling that these things would act like negative intraclass correlations between members of the same social or competing subgroup. Since it is mathematically impossible for an intraclass correlation to be *both* negative *and* large when there

are many members in each group, the very existence of such a situation would be hard to measure experimentally with statistically significant results. Yet, if they do compete for several different limited elements in the environment, the total effect could be large. I don't see how to break through this log jam experimentally.

In summary of what is in this rather rambling and long letter, I would say:

1) The idea of heritability is so old and so general that establishing the history of its use is almost impossible.

2) So many people have had the general idea, since even long before Darwin's time, that it almost certainly emerged many times in the literature and submerged again.

3) I got my impetus for whatever I did in this area primarily from the demands of the practical problems on which I was working. Starting out with *repeatability* of fleece weights in sheep and Angora goats, I extended these to problems of breeding dairy cattle and pigs. The most useful steps naturally varied a little according to the material.

4) I got my biggest boost in the area and general nature of the problem from following Wright's analysis of the inheritance of amount of white spotting in piebald guinea pigs in 1920. Then I extended it by trying to understand thoroughly his classical work on mating systems in 1921 and by auditing his class in statistical genetics at Chicago in the spring of 1931. Had I known in detail Johannsen's articles from 1902 until 1914 I might have been five or ten years further along the road. I think we give him less credit in this area, than any other man, compared to what his work really deserved. Probably Fisher should be given credit for first separating the variance due to dominance from the rest of the genetic variance in 1918, although others, such as Jennings, had made small steps in this direction. However, Fisher's paper, like the 1902–1903 Danish papers of Johannsen, was not very widely read; its main influence came much later.

5) Wright, more than anyone else, clarified the effects of *systems of mating* on estimates of, and indeed on the very idea of, heritability.

6) If I and my colleagues deserve any special credit it would be more for having assembled and tried to bring under a common interpretation the estimates and ideas of heritability of many traits in various farm animals. The relation of heritability to what is ideal in breeding plans in a given instance was never far from our thoughts. This area was much explored by the corn breeders, notably Richey and Sprague.

7) I was helped very much by ideas I got from Fisher when he lectured here for five weeks in the summer of 1931. He then generally dismissed mating systems as of little importance on the ground that, if a species in nature was small enough in numbers for the effects of inbreeding to become important, that species was likely to be on the verge of extinction already and would soon slip over the edge. Therefore, inbreeding and its consequences had little bearing on evolution, however spectacular their results might be for a few generations with domestic plants and animals.

8) Apparently it does little good to warn against oversimplifying the idea of heritability. Some feel it necessary to repeat those warnings each time they write. Others ignore the warnings. Much of *the bulk* of which has been written in recent years about heritability in man comes from this. Of course, much of that bulk is because people simply do not *like* the conclusion! No amount of expounding about heritability would alter that by more than a little, I think. Only time and continued efforts of the researchers to remain unbiased seem likely to clarify this at all.

9) Perhaps this is a basic argument for coining a new word (preferably from Greek roots) when an idea is to be presented *precisely* and in a way in which it *cannot be misunderstood*. Concerning the latter aim, however, perhaps the following "law of frustration" is pertinent: "If you work hard to state something so precisely and clearly that nobody can misunderstand it, somebody will!"

On receipt of the above, I suggested to Dr. Lush that he should submit it as a historical note to an appropriate journal. His negative response is characteristic of the thoroughness with which he treats a question. To him, the finding and verifying of all borderline cases would take more time than he felt it was worth. To illustrate, he noted in reply that by accident he had recently come on a 1926 usage of heritability[9].

Dr. Lush's response stimulated me to spend another afternoon in our library where I found that Kearney[8] had used heritability as early as 1921 in reference to small continuous fluctuations in cotton and the expected response to selection. And in 1920, Whipple[19] used "heritability of fluctuations" and "nonheritability of fluctuations due to environment" in describing selection studies with potatoes.

These early papers by plant breeders used heritability in a descriptive sense, rather than statistical, and reflected Johannsen's concepts of phenotypic variation arising from environmental as well as genotypic fluctuations, yet no reference was made to Johannsen's well known findings[6,7]. Animal breeders at the turn of this century were actively studying quantitative traits with most following the Galton–Pearson biometrical approach.

Among the books from this period, Dr. Lush has commented on Darwin's use of "strength of hereditary tendency" and Davenport's use of "coefficient of heredity." Another, somewhat typical of that era, was Lock's[13] *Recent Progress in the Study of Variation, Heredity and Evolution* which emphasizes the Galton–Pearson approach. Included is a separate chapter describing Johannsen's pure-line concepts from which he quotes, "Individuals which differ (in size) from the mean of the population give rise to offspring which differ from that mean value in the same direction but to a smaller extent, . . . but selection within a pure line produces no effect." However, Lock makes no effort to interrelate the opposing points of view, nor does he translate Erblichkeit or use heritability. Yet by 1920 some plant breeders were using heritability as noted above. It is possible that even earlier plant breeders had actually translated Johannsen's Erblichkeit to heritability (as suggested by Dr. Lush), but I have been unable to document this hypothesis. Maybe some reader can provide the missing evidence.

While modern German–English science dictionaries[4,20] translate Erblichkeit as heritability, such was not the case for early geneticists. Many English publications have referred to Johannsen's pure-line concepts without translating Erblichkeit. A 1938 Swedish publication[1] makes the English translation as variation and Crew[3] chose heredity. This apparent reluctance of early geneticists to translate Johannsen's Erblichkeit to heritability, combined with the early usage of the latter term by plant breeders without reference to Johannsen, suggested to me that the term heritability must have had a broader

general usage prior to Johannsen's classical findings. Thus the older and more general term would be avoided in describing Johannsen's more precise concepts of genotype and phenotype. For the same probable reason, the term was avoided in the Galton–Pearson biometrical studies of heredity. Support for this hypothesis comes from a 1901[17] definition of heritability as "The quality of being heritable or capable of being inherited", and gives 1832 as the earliest recorded use of the word in Fraser's Magazine as "This tax, thus securing the heritability of offices, was not perpetual." Also listed was a 1882 quotation by the naturalist A. Gray: "The importance of heritability, which is an essential part of Darwinism, would seem to have had a significant illustration in the person of its great expounder."

Summary

The origin of the word heritability remains unknown. Its usage has evolved through three stages, becoming more restrictive in its meaning along the way. In the initial stage, 1832 and possibly earlier, heritability was used to denote the hereditary transmission of characteristics or material things, simply having the capability (legally or biologically) of being inherited. The second stage, beginning around the turn of this century, followed Johannsen's classical definition of nongenetic or environmental fluctuations distinct from genotypic differences, and usage closely approximated "broad sense heritability" and Johannsen's Erblichkeit. Finally, in 1936, we come to the modern day usage of *narrow sense* heritability, the ratio of additive genetic variance to the total phenotypic variance within a population, and credit Dr. J.L. Lush with its origin.

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