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Overview on heritability concept, application and its importance in quantitative genetics

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Abstract
The proportion of phenotypic variability that may be attributable to genetic variation is measured by heritability. Without any genetic changes, heritability can alter. The concept of the scope for implementing genetic improvement through selection is thrown into doubt when the size of the problem is understood. It is a measure of the precision with which a genotype may be selected from an individual's or a group of people' phenotype. The core principles of heredity were created by the concepts of quantitative variation. In the formation of quantitative genetics, the perspective acquired from scientific explanations on the reality of inconsistency and its random derivation was crucial. Heritability is a simple, dimensionless measure of the importance of genetic factors in elucidating individual variations, and it allows for a quick comparison of individuals. It also allows for direct comparisons of the same characteristic between populations as well as between different qualities within a group. It is crucial for forecasting how people will react to selection. To enhance the agronomic characteristics of crop varieties based on heredity of desirable features, most breeding curricula routinely use grain yield as the primary selection criterion. As a result, in gene-mapping investigations that use pedigree information, heritability is an essential metric that determines statistical power. Heritability, on the other hand, does not reveal anything about the genetic architecture of the traits. To summarize, heritability is used to determine genetic advance, which shows the degree of increase in features achieved through intentional selection compression, as well as its utility advancements. As a result, genetic progress is a risky selection characteristic that aids the breeder in a selection technique.

Keywords: Environment, heritability, genotypic variation, phenotypic variation, broad, heritability, narrow heritability

Introduction
Heritability is formally defined as a ratio of variances, specifically as the proportion of total variance in a population for a particular measurement, taken at a particular time or age, that is attributable to variation in additive genetic or total genetic values termed the narrow-sense heritability (or just heritability, h^2) and the broad sense heritability (H^2), respectively. It has become standard to use the symbol h2 for heritability because (Sewall Wright 1920) used h (for heredity) to denote the correlation between genotype and phenotype in his path coefficient model (Sewall Wright 1920). The square of that correlation (that is h^2) is per definition, the proportion of variation in the phenotype that is attributable to the path from genotype to phenotype. The heritability of a metric character is one of its most important properties. It shows the degree of resemblance between relatives. The knowledge of heritability is a prerequisite for the formulation of breeding plans on scientific lines. Information on heritability is obtained through empirical studies of the data obtained either from specially designed experiment or from farms where these are generated in the normal course of breeding of sizeable herds/flocks under regulated management. There are quite a few methods available for their estimation.
Heritability measures the fraction of phenotype variability that can be attributed to genetic variation. This is different from saying that this fraction of an individual phenotype is caused by genetics. In addition, heritability can change without any genetic change occurring. For example, if both genes and environment have the potential to influence intelligence, but if a given sample of individuals shows very little genetic variation and a great deal of environmental variation, then the contribution of genetic variability to phenotype variability in that sample will be lower than if the sample showed greater genetic variability. Because of this heritability is specific to a particular population in a particular environment (Falconers D, 1981) [12].

Individuals with the same genotype can exhibit different phenotypes through a mechanism called phenotypic plasticity, which makes heritability difficult to measure in some cases. Recent insights in molecular biology have identified changes in transcriptional activity of individual genes associated with environmental changes. However, there are a large number of genes whose transcription is not affected by the environment (Falconers D, 1981) [12].

The parameter of heritability is so enduring and useful because it allows the meaningful comparison of traits within and across populations, it enables predictions about the response to both artificial and natural selection, it determines the efficiency of gene-mapping studies and it is a key parameter in determining the efficiency of prediction of the genetic risk of disease. Heritability provides a measure of genetic variation, that is, the variation upon which all the possibilities of changing the genetic composition of the population through selection depend. In other words, knowledge of its magnitude gives the idea about the scope for effecting genetic improvement through selection. It also gives a measure of the accuracy with which the selection for a genotype can be made from a phenotype of the individual or a group of individuals.

Objectives

To review the Historical development and concepts of estimating Heritability.

To review the Application and Importance of Heritability in Quantitative Genetics.

Literature review

History of the heritability concept

It has become standard to use the symbol h2 for heritability because (Sewall Wright 1920) used h (for heredity) to denote the correlation between genotype and phenotype in his path coefficient model (Sewall Wright 1920). The square of that correlation (that is, h^2) is, per definition, the proportion of variation in the phenotype that is attributable to the path from genotype to phenotype. Ronald Fisher, in his classical 1918 paper, parameterized the resemblance between relatives in terms of correlation and regression coefficients, but also gives an example of the percentage of the total variance in stature in humans that can be ascribed to genotypes and to essential genotypes (Fisher R, 1918) [13]. These percentages correspond to what we now call broad-sense and narrow-sense heritability. It is thought that J. L. Lush was the first to formally use the term "heritability" to describe the proportion of variation that is due to hereditary factors (Lush J L, 1940) [26].

An appreciation of the concept of heritability can be gained from its historical development. Concepts of quantitative variation formed the underlying principles of heritability. Knowledge derived from empirical observations on the existence of variability and its random origin was paramount in the emergence of quantitative genetics (Wearden 1979) [47]. Mendelian principles rediscovered in the late nineteenth century, about thirty years after Mendel's publications on peas, introduced complexities in the understanding of quantitative genetics, where discrete classifications of characteristics were not apparent. The merger of the concept of inheritance with that of continuous variation, expressed by Galton (1897) [16] as the regression of offspring on parents, was not without controversy in the scientific community. The hypothesis that several genes contributed to quantitative traits (Yule 1907) [53] was supported by observations on color genes in wheat and oats, recorded by Nillson-Ehle early in the twentieth century. The development of a statistical theory involving correlation between relatives by Fisher (1918) [13] represented a breakthrough in the analyses of quantitative traits, and was enhanced by the publication on systems of mating by Wright (1921) [51]. The exact origin of the term-heritability is obscure, but Wright (1921) [51] used the symbol h^2 to define the proportion of the variance that can be ascribed to heredity in the piebald color pattern in guinea pigs. The term heritability appears frequently in the animal breeding literature (e.g., Lerner, 1950) [25] where it is defined in a broad sense as the proportion of the total variance that is directly due to genetic differences. $h^2 = \sigma^2G/\sigma2P$, where σ^2G = the genetic variance, and σ^2P = the phenotypic variance of the stock.

Heritability is defined in a narrow sense as the fraction of the genetic variation that is due to genes with a simple additive effect, $h^2 = \sigma^2A/\sigma^2P$ (σ^2A = the additive genetic variance). The realized heritability is defined as R/S, where R (the response to selection) is the difference in average phenotype between the unselected stock and the progeny of the selected parents reared under the same conditions, and S (the selection differential), is the difference in average phenotype between parents and the stock from which they were selected (Ricker 1981) [32]. However, environmental conditions are not necessarily the same between generations and estimates of R/S often involve control populations (Example, Friars *et al.* 1997) [15]. Growth rate and size, age at maturation, and survival or survival indicator traits were included in the search. Most heritability studies on farmed fish were carried out in the twenty-five years prior to 2001 and in the subsequent nine years through 2009, but the results provide a background for understanding changes in comparable traits in wild fisheries. Developments in molecular biology provide the opportunity for new applications, including heritability estimates and the prediction of genetic gains. The establishment of genetic markers may be feasible in populations mixed during rearing (Ritland 1996) [33].

Heritability and genetic advance

Information on the nature and magnitude of variability and heritability in a population is one of the prerequisites for successful breeding program in selecting genotypes with desirable characters (Dudly and Moll, 1969) [9]. It is therefore, of great importance for breeders to know the heritability of the agronomical characters to improve the yield of the crop effectively. According to Falconer and Mackay (1996) [10], heritability is defined as the measure of the correspondence between breeding values and phenotypic values. Thus, heritability plays a predictive role in breeding, expressing the reliability of phenotype as a guide to its breeding value. It is the breeding value which determines how much of the phenotype would be inherited in to the next generation (Tazeen *et al.*, 2009) [44].

The broad sense heritability is the relative magnitude of genotypic and phenotypic variance for the traits and it gives an idea of the total variation accounted to genotypic effect (Allard, 1960) [4], whereas, heritability in narrow sense expresses the extent to which phenotypes are determined by the genes transmitted from the parents. There is a direct relationship between heritability and response to selection, which is referred to as genetic advance. High genetic advance with high heritability estimates offer the most effective condition for selection (Larik *et al.*, 2000) [24]. The utility of heritability therefore increases when it is used to calculate genetic advance, which indicates the degree of gain in character obtained under a particular selection pressure. Most effective yield component breeding to increase yield could be achieved, if the component

traits are highly heritable and positively correlated with yield**.** However, it is very difficult to assess whether observed variability is highly heritable or not, by reason of polygenic nature of quantitative traits. Likewise, knowledge of heritability is essential for selection-based improvement as it indicates the extent of transmissibility of a character into future generations (Sabesan *et al*., 2009 [36], Ullah *et al*., 2011) [46].

Most of the important agronomic traits are quantitative in nature and manifested in terms of degree rather than kind. Plant breeders require knowledge that will help them to identify superior genotypes efficiently to select them and concentrate their genes in a line or variety that is commercially acceptable. To execute this, it is essential to learn first whether the trait is heritable and then understand the kind and extent of the genetic components of the variation. Genetic advance expected from selection refers to the improvement of characters in genotypic value for the new population compared with the base population under one cycle of selection at a given selection intensity (Singh, 2001) [39]. Since high heritability does not always indicate high genetic gain, heritability with genetic advance considered together should be used in predicting the ultimate effect for selecting superior varieties (Ali *et al*., 2002) [3]. Genetic advance gives clear picture and precise view of segregating generations for possible selection. Higher estimates of heritability coupled with better genetic advance confirms the scope of selection in developing new genotypes with desirable characteristics (Ajmal *et al*., 2009) [2].

Heritability and the partitioning of total variance Population parameters

Observed phenotypes (P) of a trait of interest can be partitioned, according to biologically plausible nature–nurture models, into a statistical model representing the contribution of the unobserved genotype (G) and unobserved environmental factors (E):

Phenotype (P) = Genotype (G) + Environment (E) (1)

The variance of the observable phenotypes (α^2P) can be expressed as a sum of unobserved underlying variances

($\alpha^2G + \alpha^2E$): $\alpha^2P = \alpha^2G + \alpha^2E$)

Heritability is defined as a ratio of variances, by expressing the proportion of the phenotypic variance that can be attributed to variance of genotypic values: Heritability (broad sense) = $H^2 = \alpha^2G / \alpha^2P$. The genetic variance can be partitioned into the variance of additive genetic effects (breeding values; α^2A), of dominance (interactions between alleles at the same locus) genetic effects (α^2D), and of epistasis (interactions between alleles at different loci) genetic effects (α^2I): $\alpha^2G = \alpha^2A + \alpha^2D + \alpha^2I$ and heritability (narrow or strict sense): $h^2 = \alpha^2A / \alpha^2P$.

In general, α^2E can be broken down into any number of identifiable, but random, contributing factors that can be specific to the phenotype. Examples include the environmental variance that is common to specified groups, for example, siblings and litters (α^2CE), and the non-genetic variance that is common to repeated measures of individuals (α^2PE). We define the remainder of the environmental variance, which cannot be attributed to other factors, as the environmental residual variance, which includes individual stochastic error variance and measurement error

(α^2RE): $\alpha^2E = \alpha^2CE + \alpha^2PE + \alpha^2RE$

In the simplest partitioning, no specific factors that contribute to α^2E are identified and $\alpha^2RE = \alpha^2E$ Both the genetic and environmental variances can be partitioned further for a trait such as birth weight of the offspring to include genetic and environmental maternal effects that are attributable to the mother (Willham RL, 1963) [49]. The partitioning of the phenotypic variance (equation-2) assumes the absence of genotype by environment covariance (GXE). Examples leading to a positive covariance are parents with a high intelligence quotient (IQ) providing an IQ stimulating environment for their children, and dairy cattle being fed according to production. A further term that is ignored in equations 1 and 2 is the interaction between genotype and environment (GXE), when the effect of the genotype depends on the environment. The most studied, yet still controversial, example of GXE in humans is the interaction between stressful life events (the environment) and the length polymorphism of the serotonin transporter gene (the genotype) and their effects on major depression (the phenotype), (Caspi, A. *et al.* 2003) [7].

If GXE exists, P = G + E + GXE, so a more complete partitioning of phenotypic variance is: $2P = \alpha^2G + \alpha^2E + \alpha^2G$, $E + \alpha^2G*E$ Both G and E co-variation and G*E interaction are often ignored, usually because they cannot be estimated. If either is present, ignoring the former will inflate estimates of α^2G and ignoring the latter will inflate estimates of α^2E.

Estimation of heritability

Heritability and the variances that contribute to them are parameters of a population. In reality, the only understanding that we have about these parameters are estimates, although often the distinction between parameter and estimate is not made, which has led to some confusion (Jacquard A, 1983) [20]. Heritability can be estimated from empirical data of the observed and expected resemblance between relatives. The expected resemblance between relatives depends on assumptions regarding its underlying environmental and genetic causes. When selection is applied, the ratio of the observed selection response (R), the change in the mean phenotype between generations) to the observed selection differential (S, the difference in mean phenotype between the parents selected for breeding and the overall mean in their generation) can be used to estimate heritability. This relationship is summarized in the breeder‘s equation (Lynch M & Walsh, B 1998) [27], $R = h^2S$. For an experiment that runs over several generations, the realized heritability has been defined as the ratio, or regression, of cumulative selection response (the sum of all responses) to cumulative selection differential (the sum of all selection differentials), (Falconer, D. & Mackay T, 1996) [10].

Traditionally, heritability was estimated from simple and often balanced designs, such as simple functions of the regression of offspring on parental phenotypes, the correlation of full or half sibs, and the difference in the correlation of monozygotic (MZ) and dizygotic (DZ) twin pairs (Falconer D & Mackay T, 1996) [10]. When phenotypic measures are available for individuals with a mixture of relationships both within and across multiple generations or in general when the design is unbalanced, estimates of additive genetic variance and environmental components are most efficiently estimated from a linear mixed model. The accuracy of a heritability estimate depends on its sampling error, which is a function of the sample size and pedigree structure, and on bias, which can come from confounding. Bias can occur, for example, through Assortative mating and selection. The sampling variance of the estimate of heritability is inversely proportional to the relationship of

individuals squared, the number of families and, to a lesser extent, the number of individuals in a family (Falconer D & Mackay T, 1996) [10]. Therefore, hundreds of observations are needed to obtain a standard error less than 0.1, and thousands are needed to attain very precise estimates.

Approximability (estimation) refers to the number of parameters that can be estimated from data and depends on the extent to which the experiment to estimate heritability enables partitioning of the total observed variance into putative causal sources. Sometimes, a number of these sources are unavoidably confounded in the experimental design, so that their contribution to the overall variance cannot be separated. For example, estimates of dominance variance and common environmental variance are confounded when partitioning of the variance is carried out using observations on full sibs. In the classical twin design of MZ and DZ twin pairs, there are only three essential statistics that can be estimated from their phenotypes, namely the MZ resemblance (for example, covariance or correlation), the DZ resemblance and the overall phenotypic variation in the sample. Therefore, only three variance components can be estimated, although many more genetic and non-genetic causal components of variance can be postulated to influence MZ and DZ resemblance (Lynch M & Walsh B, 1998 [27] and Falconer, D & Mackay T. 1996) [10].

Confounding might lead to severe bias in the estimate of heritability. For example, if the resemblance of parents and offspring is partly due to common environmental effects, then an estimate of heritability that is based on their resemblance will be biased upwards. Although correlations of distant relatives are less likely to be biased by non-genetic factors, their relationship is so small that heritability estimates that are based on distant relatives have a high sampling error. The denominator of heritability is the total phenotypic variance, which is estimated as the variance of the trait after correcting for known fixed effects such as sex, age or cohort. If identifiers for these factors are unknown then estimates of phenotypic variance will be greater (and the estimate of heritability less). For example, in humans, if the average difference in height of 15 cm between males and females was ignored, the estimate of heritability would be reduced to 0.6 compared with 0.8 when this difference is taken into account. Should the total phenotypic variance be adjusted for known fixed effects when estimating the fraction of variance that is due to genetic factors? Plant and animal breeders would say yes, because they obtain the best prediction of future performance by working with the amount of variation that is not accounted for by known effects. Similarly, human geneticists would say yes, because heritability is used to understand the genetic component of risk to disease, independently of known environmental risk factors. Evolutionary geneticists might say no, because the raw material of natural selection is the total variation between individuals. Prediction of the response to natural selection depends on whether selection takes place within or across the factors that cause variation. For example, if year-to-year fluctuations in climate have a large effect on the mean viability of an annual plant but natural selection operates within years, then the best prediction of response would be based on a heritability that is estimated by adjusting for between year variations.

Applications of heritability

The parameter of heritability is so enduring and useful because it allows the meaningful comparison of traits within and across populations, it enables predictions about the response to both artificial and natural selection, it determines the efficiency of gene-mapping studies and it is a key parameter in determining the efficiency of prediction of the genetic risk of disease. Heritability is a simple dimensionless measure of the importance of genetic factors in explaining the differences between individuals, and it allows an immediate comparison of the same trait across populations and of different traits within a population. Such comparisons can lead to insights into the biology of the phenotype, or can have practical consequences for plant and animal breeding programs. For example, the heritability of body size (or stature) is generally high across a wide range of species, signifying developmental processes that seem to be robust to environmental insults.

In medicine and human genetics, estimates of heritability can be compared across diseases to gauge the relative influence of genetic and environmental factors. Because disease is usually measured on an all-or-none scale, allowance has to be made for the incidence of disease when making comparisons. Heritability for such categorical traits can be defined on the observed discontinuous scale or on an unobserved continuous liability ‘scale (Falconer, D. 1965) [11]. The continuous scale is more general because it is independent of the incidence of each category. For example, consider the psychiatric disorders schizophrenia and major depression, which differ considerably in the relative risks to first-degree relatives of affected individuals: 9 for schizophrenia (Sullivan ,. 2005) [41] but only 3 for major depression (Sullivan P, *et al.* 2000). However, the lower incidence of schizophrenia of 1% (Sullivan P, 2005) [41] compared with 3% (Sullivan P, *et al.* 2000) for major depression results in similar estimates of heritability on the observed scale of 0.16 and 0.12, respectively. Conversely, heritability that are estimated on the underlying liability scale19 are quite different at 0.81 and 0.37, respectively. For risk prediction that is based on family history or measured genotypes, it is the heritability on the observed 0-1 risk scale, however, that is most important (Wray N, *et al.* 2007) [50].

In artificial-selection programs, heritability has a crucial role because it determines the precision with which the genetic value can be predicted from phenotypic information, and therefore determines the design of breeding schemes. The correlation between the observed phenotype and unobserved breeding value is h, the square root of the heritability (Falconer D & Mackay T, 1996) [10]. Therefore, for a trait with a high heritability, the phenotype of an individual is highly informative for its breeding value. So, for traits that are easy to measure and have a high heritability (for example, growth or weight traits) an easy and effective breeding scheme is to choose the best individuals for further breeding on the basis of their phenotypes. For traits with a low heritability (for example, litter size) information from many relatives is needed to predict breeding values accurately, but the accuracy of prediction of breeding values remains a function of the heritability. Hence, heritability is central in predicting the response to selection. Heritability is an important parameter that determines statistical power in gene-mapping studies that use pedigree information.

A large heritability implies a strong correlation between phenotype and genotype, so that loci with an effect on the trait can be more easily detected. However, heritability by itself does not provide information about the genetic architecture of the traits, for example, how many loci contribute to genetic variation. In principle, a trait with a low heritability can have a single locus that causes variation and a trait with a high heritability can have hundreds of contributing loci.

Importance of heritability

Heritability provides a measure of genetic variation, that is, the variation upon which all the possibilities of changing the genetic composition of the population through selection depend. In other

words, knowledge of its magnitude gives the idea about the scope for effecting genetic improvement through selection. The genetic variety contained in the breeding material employed in the program is critical for a successful plant breeding program (Khan *et al*., 2017) [21]. When heritability is utilized to determine genetic advance (GA), which reflects the degree of gain in characteristics achieved under specific selection pressure, its usefulness improves. As a result, genetic progress is a critical selection attribute that supports the breeder in a selection procedure (Shukla *et al*., 2004) [38].

It also gives a measure of the accuracy with which the selection for a genotype can be made from a phenotype of the individual or a group of individuals.

Smulders (2015) [40] reiterates a valid point that it is critical to know which specific traits are heritable, as a trait of interest may be the outcome of multiple and necessarily coincident factors. In such cases, any additive genetic variance detected in that trait may be due to these confounding factors. This problem, however, can often be resolved via conventional experimental approaches aimed at isolating the trait of interest from any potential confounds. For example, Smulders (2015) [40] suggested that heritability estimates of the number of hippocampal neurons might be affected by potentially heritable motivation to hoard food, which is necessarily tied to hoarding behavior. If that were the case, we would expect that animals hoarding less should have fewer neurons. However, for chickadees that spent their entire life in captivity and had little motivation to cache, the total number of hippocampal neurons is similar to that of their wild, highly motivated counterparts (Pravosudov and Roth 2013) [30]. Therefore, in this example, the motive for storing food is unlikely to directly promote hippocampal development. Similar experimental approaches can be used with careful consideration of which exact traits are being measured so that heritability estimates are not confused with other behavioral or cognitive traits. Thornton and Wilson (2015) [45] found that heritability of traits is due to the fact that traits act collectively and selection does not affect individual traits, and that heritability estimates do not predict the current selective response. Warn against what is called "excessive emphasis" in the study. Any of several phenomena known to affect gene expression. Instead, they propose to focus on the genetic structure of the trait. We do not propose to abandon efforts to identify specific genes associated with the trait of interest. However, the genetic structure that underlies cognitive traits is usually complex, involving multiple less-affected genes, and it can be difficult to identify the individual genes involved (Rockman 2012) [35]. However, studies on fruit flies have shown that such work is challenging but feasible (Shorter *et al.* 2015) [37]. I suggest that attempts to understand the evolution of a trait, including revealing its genetic basis, must begin with a logical statement that the trait is hereditary. It is clear that the method and extent to which heritability estimates can provide insights into the evolution of traits depends entirely on the question asked (Mulders 2015) [40]. Rausher and Delph (2015) [31] found that evolutionary biologists are often primarily interested in the selective pressures that drive phenotypic evolution, and by answering questions about phenotypic heritability, evolutionary phenotypic changes. He points out that it can be completely explained. Clear answers to these questions are often obtained without identifying the underlying gene (Rausher and Delph 2015) [31].

Summary and Conclusion

In genetics, heritability is and will be an essential characteristic. It is a critical measure for forecasting the response to artificial and natural selection, since it permits a comparison of the relative relevance of genetic and non-genetic factors across species, traits, and recognized environments. However, it is limited, as are all other parameters, because heredity is a ratio of variances and does not tell us about the size of each component; it only considers a single population and environment, not their differences. Furthermore, because it is a composite measure, it provides little information regarding specific gene activities or interactions. Because it allows for meaningful comparisons of traits within and across populations, it enables predictions about the response to both artificial and natural selection, it determines the efficiency of gene-mapping studies, and it is a key parameter in determining the efficiency of disease genetic risk prediction, heritability is an enduring and useful parameter. Heritability is a measure of genetic variety, or the variance on which all options for changing the genetic composition of a population through selection are based. Heritability estimates have spawned a slew of new scientific problems that scholars have only begun to explore. It is a depressing thought that, despite over a century of genetics research using the concept of heredity, we still do not fully understand why heritability, in both wide and narrow senses, has the values it does. I have tried to bring together studies from a wide range of situations within the constraints of this short Review, touching on many active areas of research in quantitative, population, and evolutionary genetics, such as the maintenance of genetic variance in natural populations, the magnitude of additive and non-additive variation, the nature and amount of mutational variance, and the genetic control of phenotypic variance. I have been reviewed articles related to heritability and conclude that there is misconception regarding to Heritability and Heritability have many application importance and different methods for estimation of heritability ones should know.

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