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Review Article

Heritability and its Use in Animal Breeding -

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Abstract

Heritability (h^2) refers to the degree of resemblance between relatives i.e. how much the progeny resemble its parents. Heritability (h^2) is the most important genetic parameter on which different breeding strategies depend. The knowledge of h^2 is a frontline for the formulation of breeding plans on scientific lines, which are used for selection of parents for future breeding program. In order to make breeding plans, there is need to know the h^2 of different characters (traits). The extent of genetic control is different for different traits. The higher the h^2 , the greater is the genetic control on the trait, and the more rapidly selection will result in genetic progress. For highly heritable traits, differences in breeding values of animals have large effect on performance, and differences in environments have less important effect on performance. The opposite is true for lowly heritable traits. In other words, heritability could increase if genetic variation increases and it might also increase if the environmental variation decreases. As a rule, significant genetic change can be made by selecting for highly heritable traits. For lowly heritable traits, selection is less effective; so performance may be improved through management. Therefore, the aim of this review is to define heritability (h^2) and assess its role in animal breeding.

Keywords: Breeding program; Environment; Genetic control; Management; Selection

INTRODUCTION

Breeding works for next generation in order to improve the mean of the next generation from the present one, to do this task different tool is essential; from those tools h^2 is the front line. It is one of the most important considerations in determining appropriate animal evaluation methods, selection methods and mating systems [1]. It measures the relative importance of hereditary and environmental influences on the development of a specific quantitative trait, more specifically; it measures that part of the total variability of the trait caused by genetic differences among the animals on which the measurements were taken [2]. Heritable traits are measured by estimating the relative contributions of genetic and non-genetic differences to the total phenotypic variation in a population. Heritability is an important concept in quantitative genetics, particularly in selective breeding and behavior genetics but is less widely used in population genetics [3]. Heritability could increase if genetic variation increases, causing individuals to show more phenotypic variation, like showing different levels of intelligence. On the other hand, h^2 might also increase if the environmental variation decreases, causing individuals to show less phenotypic variation, like showing more similar levels of intelligence [4].

Heritability tells the breeder how much confidence to put in the phenotypic performance of an animal when choosing parents of the next generation [2]. For highly heritable traits where h^2 exceeds 0.40, the animal's phenotype is a good indicator of genetic merit or breeding value, for lowly heritable traits, where h^2 is below 0.15, an animal's performance is much less useful in identifying the individuals with the best genes for the trait. So h^2 is one important component of the equation used to predict genetic progress from selection to improve a trait [5]. In other words, heritability measures the relative importance of genetic variance in determining phenotypic variance. It describes the percentage of phenotypic variance that is heritable [1]. In general, the aim of this review is to define the term heritability and assess its use in animal breeding.

BROAD (H^2) AND NARROW (h^2) SENSE DEFINITION OF HERITABILITY

Heritability in broad sense definition, indicates that all the genetic contributions to a population's phenotypic variance including additive, dominant (intragenic) and epistatic (intergenic) [3]. Because of gene combination, values (dominance and epistasis) cannot be transformed in to next generation, so it does not reflect the relationship between the performance of animals and their potential as parents. Therefore, when we see from a selection perspective it is not a useful measure [6].

$$H^2 = GV/PV \text{ or } H^2 = \sigma^2 A + \sigma^2 D + \sigma^2 I / \sigma^2 p$$

In reverse, narrow sense definition indicates the only response of additive genetic effect on the total phenotypic performance of an individual. If a selective pressure such as up grading of livestock is exerted, the response of the trait is directly related to narrow-sense definition [7]. The observed response to selection leads to an estimate of the narrow-sense heritability or realized heritability. This is the guideline underlying artificial selection or breeding program. This indicates the proportion to which phenotypes are determined by the genes inherited from their parents. This type of heritability is interesting one by the animal breeder [1].

$$h^2 = \sigma^2 A / \sigma^2 p \text{ or } h^2 = \sigma^2 A / PV$$

HERITABILITY IN ANIMAL BREEDING

Heritability plays an important role in the formulation of breeding plans for animal performance improvement. An important aspect of these plans is 'selection', this is, the processes of choosing parents to produce the next generation, on which the improvement depends. For the selection to be effective it is necessary that the members of the population on which the selection is practiced vary in their genetic make-up with regard to the character in question [8]. In other words, it is only the genetically determined variation which can be utilized for a permanent improvement of the production characteristics in a population. If all (or most) of the variation existing in the population

Table 1: Form of analysis of covariance.

Source	d.f.	S.S.(x)	S.S.(z)	S.P.(xz)
Between sires	s-1	Bxx	Bzz	Bxz
Within sires	N-s	Wxx	Wzz	Wxz

Table 2: Form of analysis of half-sib families.

Source	d.f.	M.S	E(M.S.)
Between sires	s-1	M1	$\sigma^2 w + \lambda \sigma^2 s$
Within sires	N-s	M2	$\sigma^2 w$

Table 3: Form of analysis of Full-Sib Correlation Estimate.

Source	d.f	M.S	E(M.S.)
Between sires	s-1	M1	$\sigma^2 w + \lambda 2 \sigma^2 d + \lambda 3^2 s$
Between dams/sires	$\sum (di-1)$	M2	$\sigma^2 w + \lambda 1 \sigma^2 d$
Between progeny/dams/sires	$\sum i \sum j (nij-1)$	M3	$\sigma^2 w$



is attributable to environment, selection of phenotypically superior individuals will not result in any (or material) alteration in the genetic composition of the next generation [9]. Hence, a basic pre-requisite to the planning of a breeding program is that of the total variability existing in the population, how much of this is caused by differences in the genetic make-up of the individuals. A quantitative measure of this is provided by the heritability coefficient [2].

HOW IS HERITABILITY USED IN BREEDING PROGRAMS

Heritability tells the breeder how much confidential to the phenotypic performance of an animal when choosing parents of the next generation. Heritability is one of the important components of the equation used to predict genetic progress from selection to improve a trait. For the most simple form of selection called “mass selection” or selection on phenotypes measured on individuals in a population, so it shows how important efforts to improve a trait through improved management or environmental conditions may be compared to genetic selection [5]. Using the definition above where h^2 is the percentage of differences between animals due to genetic effects, then “ $1 - h^2$ ” is the percentage of differences between animals not due to genetic causes that can be transmitted. The higher that percentage is, the more likely it would be that improved through management (or some other genetic techniques such as crossbreeding) might be used to improve these lowly heritable traits [5].

IMPORTANCE OF HERITABILITY FOR SELECTION

Heritability has an important role for selection of polygenic traits. The final object of selection is to choose those animals with the best breeding values to become parents of the next generation. To do this, we need good information about the heritable traits of animals for selection. Because the only information available for selection is phenotypic information of the animals, so heritability is very meaning full. When the trait is highly heritable, selection is more important than crossbreeding and management, but when the trait is lowly heritable selection is no appropriate rather than crossbreeding and management of the animals [10]. 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 [8].

PREDICT THE GENETIC GAIN FROM SELECTION

When the more desirable animals are chosen as parents of the next generation, the predicted change is the result of heritable fraction of the superiority of the parents over the average of the population from which they were chosen [1]. Therefore, the expected change in the mean of the next generation will be predicted by this equation:

$$\Delta M = h^2 \times SD$$

Table 4: Analysis of variance for isogenic lines.

Source	d.f.	M.S.	E(M.S.)
Between lines	L-1	MG	$\sigma^2 E + \lambda \sigma^2 G$
Within lines	N-1	ME	$\sigma^2 E$

Table 5: Estimates of heritability for some traits in dairy cattle: Source: Bennet [5].

Trait	Holstein	Jersey	Trait	Holstein	Jersey
Production Traits					
ME (mature equivalent) Milk Yield	0.30	0.35	Lifetime Actual Milk Yield	0.15	
ME Fat Yield	0.30	0.35	Lifetime Actual Fat Yield	0.15	
ME Protein Yield	0.30	0.35	Lifetime Actual Protein Yield	0.14	
Fat Percent	0.58		Days of Productive Life	0.13	
Protein Percent	0.51		Somatic Cell Score, Lactation Average	0.10	
Lactose Percent	0.43		Lifetime Net Income	0.20	
Age at First Calving	0.14		Productive Life, USDA	0.085	
First Calving Interval	0.05				
Linear Type Traits					
Stature	0.42	0.39	Feet and Leg Score	0.17	
Strength	0.31	0.25	Fore Udder attachment	0.29	0.22
Body Depth	0.37	0.25	Rear Udder Height	0.28	0.26
Dairy Form	0.29	0.23	Rear Udder Width	0.23	0.23
Rump Angle	0.33	0.31	Udder Cleft	0.24	0.20
Thurl Width	0.26	0.20	Udder Depth	0.28	0.38
Rear Legs Side View	0.21		Front Teat Placement	0.26	0.24
Rear Legs Rear View	0.11	0.10	Teat Length	0.26	0.26
Foot Angle	0.15	0.10	Final Score	0.29	0.23
Health, Fitness, and Reproductive Traits					
Dry Matter Intake	0.30		Incidence of Mastitis	0.06	
Body Condition Score	0.25		Incidence of Ketosis	0.01	
Energy Balance	0.20		Incidence of Retained Placenta	0.02	
Persistency of Milk Yield	0.11		Incidence of Metritis	0.01	
Days to First Breeding	0.04		Days to Last Breeding	0.06	
Number of Inseminations	0.02		Interval to First Luteal Activity	0.16	

Where,

- h^2 Heritability
- ΔM is the expected change in the mean of the next generation
- SD is the selection differential of the selected parents

Heritability 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. In general the percentage of h^2 dictates the choice of selection method and breeding system. High h^2 estimates indicate that additive gene action is more important for that trait, and selective breeding i.e. mating of the best to the best animal should produce more desirable progeny. Low estimates, on



Table 6: Estimates of heritability for some traits in beef cattle and Merino de palas sheep breed.

Beef Cattle		Merino de palas Sheep Breed	
Trait	h ²	Trait	h ²
Conception Rate	0.05-0.17	Wight at Birth	0.24
Calving Ease	0.1-0.13	Wight at Weaning	0.29
Scrotal Circumference	0.48	Wight at Sheering	0.36
Birth Weight	0.31	Average Daily Increase	0.39
Weaning Weight	0.24	Wool Yield	0.52
Yearling Weight	0.33	Finesse	0.22
Frame Score	0.61	Waves	0.33
Mature Weight	0.53-0.79	Gloss Wool Oil	0.34
Carcass Weight	0.39	Total Milk Yield	0.3
Fat Thickens	0.0-0.34		
Marbling score	0.46		
Source: Bertand [14]		Source: Creanga <i>et al.</i> [15]	

the other hand, indicate that probably non-additive gene actions such as over dominance, dominance, and epitaxy are important and are not heritable [8].

ESTIMATION OF HERITABILITY

A heritability estimate is a partial description of one trait in one group of animals at some particular time. It may vary (for each trait) during one time period from herd to herd, or it may vary in the same herd from time to time. This is natural because herds differ in genetic makeup and because there are many different environmental circumstances from herd to herd or within a herd from year to year. These genetic and environmental differences influence the size of the numerical value of the terms (i.e., genetic variance, V_g and total variance, V_p) used in the estimation of heritability [2].

The numerical value of a heritability estimate can be increased or decreased by changes in either of its component parts. An increase results from a reduction in the environmental variance or from an increase in genetic variance. Conversely, a decrease results from an increase in environmental variance or from a reduction in genetic variance [2].

Being one of the most important characteristics of metric traits, heritability is a very important indicator on the decisions that must be taken in the process of genetic breeding of animal populations. Genetic differences between populations, specific effects of environment conditions resulted in the determination of stable heritability for each population [11-13]. Heritability is the most important estimator as concerns the estimate of the weight of additive genetic variance, as well as of the environment. In case of populations with a high degree of homozygosity, higher values were registered in comparison with heterozygote populations, under conditions of the same traits [11]. As we know, heritability is the ratio of the additive genetic variance to the total variance, and the additive genetic variance is the chief determinant of the resemblance between relatives, this suggests that the heritability can be derived from estimates of either a regression coefficient or an intra-class correlation among related individuals. This is the basic principle on which all the different methods of estimation of heritability rest [8].

There are different methods, in order to estimate heritability

the most common are discussed below, based on regressions and correlations among related individuals. Regression Estimates, Half-Sib Correlation Estimate, Full-Sib Correlation Estimate, and Isogenic Lines Correlation Estimate are among the methods [8]. Combinations of half-sib and full-sib families, Regression of off-springs on mid-parents and Regression of F2 on F1 data are also used.

Regression estimates

$$\text{Model: } z_{ij} = \mu + s_i + x_j + e_{ij}$$

Where: s_i is effect of i^{th} sire; x_j is the measurement on dam and e_{ij} is the environmental deviation.

The intra-sire regression of offspring on dam is W_{zx}/W_{xx} and hence, $h^2 = 2 W_{zx}/W_{xx}$

Half-Sib correlation estimate

$$\text{Model: } Z_{ij} = \mu + s_i + e_{ij}$$

Where: z_{ij} is the observation on the progeny of j^{th} ($j = 1, 2, \dots, n_i$) dam mated to the i^{th} sire ($i = 1, 2, \dots, s$), in μ is the general mean, s_i is the effect of the i^{th} sire and e_{ij} is the uncontrolled environmental and genetic deviations attributable to individuals within sire groups.

Where: σ^2_s is the between-sire component and σ^2_w is the within-sire component. Here, $N = \sum n_i$ (the total number of daughters). Hence the heritability of the concerned character can be estimated as: $h^2 = 4 (M_1 - M_2) / M_1 (\lambda - 1) M_2$

Full-Sib correlation estimate

$$\text{Model: } Z_{ijk} = \mu + s_i + d_{ij} + e_{ijk}$$

Where: z_{ijk} is the observation on the k^{th} progeny of the j^{th} dam mated to i^{th} sire; μ is the general mean; d_{ij} is the deviation common to the progeny of the j^{th} dam and i^{th} sire; and e_{ijk} is the random deviation.

Isogenic lines correlation

When data are available on Isogenic lines such as identical twins, clones or highly inbred lines, these can be analyzed to obtain the estimate of intra-class correlation within lines. If it is the intra-class correlation within lines, then t itself is an estimate of heritability in broad sense [8].

$$\text{Model: } X_{ij} = G_i + E_{ij}$$

Where: G_i is the genotypic value, and E_{ij} is the environmental deviation. We also have: $\sigma^2_x = \sigma^2_p = \sigma^2_G + \sigma^2_E$

Where: total phenotypic variance is partitioned into two components: 'between lines' and 'within lines' as shown in the table 4 given below. Where $N = \sum n_i$ (total number of individuals).

So the broad sense heritability coefficient is given by: $\sigma^2_G / \sigma^2_E + \sigma^2_G$

Estimates of heritability serve as a useful guide to the breeder, to appreciate the proportion of variation, which is due to genotypic or additive effects [1]. But each estimate of heritability listed above have its own limitations.

CONCLUSION

Heritability is one of the most important concepts in animal breeding. The magnitude of heritability dictates the choice of selection method and breeding system. High heritability estimates indicate that



additive gene action is more important for that trait, and selective breeding i.e. mating of the best to the best should produce more desirable progeny. Low estimates, on the other hand, indicate that probably non-additive gene action such as, dominance, and epistacy is important so we go for management. There are several working definitions, as heritability is used to help plan breeding programs, determine management strategies, estimate breeding values of individual animals and predict response to selection.

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