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**INTRA-SIRE CORRELATIONS OR REGRESSIONS OF
OFFSPRING ON DAM AS A METHOD OF
ESTIMATING HERITABILITY OF
CHARACTERISTICS***

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The idea of heritability concerns whether the differences actually observed between individuals arose because they started life with different genotypes or were exposed to different environmental forces. Every characteristic is both hereditary and environmental since its expression can be changed by appropriate changes either in its heredity or in the environment under which that genotype develops.

The degree of heritability may be defined as the fraction of the observed variance which was caused by differences in heredity. This fraction is a statistic describing a particular population. It can be made larger or smaller if either the numerator or the other ingredients in the denominator can be altered. Thus it may vary from population to popula-

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tion for the same characteristic and may vary from one characteristic to another even in the same population.

All ways of estimating heritability rest on the degree to which animals with similar genotypes resemble each other more than less closely related animals do. But resemblance between relatives and the degree of heritability, in the broad sense defined above, may not parallel each other perfectly. The major reasons for discrepancy are:

1. Sampling errors. These may be made harmlessly small by increasing the amount of data if that is physically and economically possible.

2. Environmental deviations for certain kinds of relatives may be correlated. Thus among mammals maternal sibs develop in the same uterus and usually suckle the same dam and hence tend to be affected in the same direction by peculiarities in the pre-natal or pre-weaning environment. In data collected from two or more herds or from one herd extending over so many years that time trends in management are likely to have occurred, daughter and dam are likely both to have been exposed to better-than-average or both to worse-than-average environment. Environmental contributions to the resemblance between relatives are often difficult to measure.

3. The mating system may deviate from random more (or less) than the investigator thinks. Thus his allowance for this may be inaccurate.

4. The genotype as a whole may actually function in a way different from the sum of the average separate effects of its constituent genes. This leads to a broad and to a narrow definition of "hereditary" and to some discrepancies between outward resemblance and resemblance gene by gene.

As far as the animal itself is concerned its genotype functions as a unit. This actual functioning of the genotype as a whole is what is meant in the broad definition of "hereditary." But the gene, not the whole genotype, is the unit in transmission from parent to offspring. If we assume that each gene substitution has in every genotype exactly the same effect as the *average* effect which it actually does have in that population, then by adding all these average effects of the constituent genes we can get an "expected" functioning or value for each genotype.* Variance among these "expected" values constitutes the additively genetic variance in that population. The fraction which this additively genetic variance is of the actually observed variance is the narrowest definition of heritability. Discrepancies between the "expected" function-

* We do this in applied genetics whenever we classify some genes as "good" or "bad" or, for example, speak of a gene for high test or for low fat production.

ing and the actual functioning of a genotype we call dominance deviations if they are due to non-additive combination effects of allelic genes, or epistatic † deviations if the interacting genes are not allelic to each other.

The difference between the narrow and the broad definitions of "hereditary" consists in whether the epistatic and the dominance deviations are considered as hereditary (since they are the effect of genes) or as physiological incidents of the chemistry by which genes produce their effects, since the gene combinations are not transmitted as units and the epistatic and dominance deviations (which are properties of the combination themselves) are not as transmissible from parent to offspring as the additive individual effects of the constituent genes are. In case the dominance deviations and epistatic deviations are zero (which is probably never entirely true although they may perhaps be unimportantly small in some cases), the two definitions coincide and we have the simple case often used to introduce students to the subject of quantitative inheritance and multiple factors. Figure 1 illustrates the difference between the two definitions together with an item, probably usually small but necessary for logical completeness, for non-linear combination effects of genotypic and environmental differences.

Dominance deviations generally lower the correlation between relatives in much the same way as random environmental variations do. However when two individuals are related through both parents of each they get a partial rebate because there is some correlation between their dominance deviations. Full sibs are the only common relationship in which the dominance contribution to phenotypic likeness is at all important.

An epistatic effect requiring the simultaneous presence of two genes would be transmitted from parent to offspring only half as often as would an additive effect dependent on the presence of one gene, an epistatic effect requiring the simultaneous cooperation of three genes would be transmitted only one-fourth as often, a four-gene effect only one-eighth as often, etc., thus giving rise to the general situation that only a small portion of the epistatic effects present in the population would contribute to the correlation between relatives, at least when

† This definition of "epistatic" (apparently first used by Fisher in 1918) is a bit more inclusive than what Bateson originally meant. Advancing knowledge of the multiplicity of possible kinds of non-additive interactions of genes has destroyed the distinctness of the original definition. If this broadening of the original definition proves too confusing, perhaps these epistatic deviations will ultimately be called merely "interactions."

mating is nearly random. In populations consisting of partially inbred lines unrelated to each other, a larger share of the epistatic effects are possessed in common by relatives.

FRACTIONS OF THE OBSERVED VARIANCE

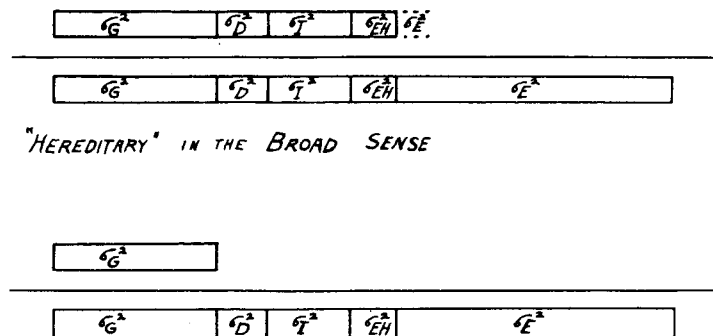


FIGURE 1. Meanings of "hereditary." Above: The broadest definition which includes as hereditary the differences caused by epistatic and dominance deviations and even by the joint non-linear interactions of heredity and environment. An estimate derived from comparing the variance within a freely interbreeding population and that within isogenic lines would approach this. Below: The narrowest definition which includes as hereditary only the additively genetic variance.

σ_G^2 = additively genetic variance.

σ_D^2 = variance due to dominance deviations.

σ_I^2 = variance due to epistatic interactions.

σ_{EH}^2 = variance due to non-linear interactions of heredity and environment.

σ_E^2 = variance due to environmental variations.

The relative proportions chosen here to illustrate the partitioning of the observed variance (the denominator) into these five portions are arbitrary.

Thus it comes about that when heritability is estimated from the likeness of relatives the estimate includes all of the variance which can be construed as additively genetic but only a portion (almost always less than half) of the epistatic variance and usually none but sometimes as much as a quarter of the variance caused by dominance deviations.

Ways of Estimating Heritability

Isogenic lines. Comparison of the variance within isogenic lines and the variance in the population being analyzed could show how much of

the variance in the population is hereditary in the broad sense. But isogenic lines are not now available in farm animals nor likely to become so, except for identical twins. Those are rare and difficultly recognizable in farm animals, although perhaps they deserve more study than they have yet received.

Experiments with selection. If we know the amount by which the average of the parents exceeded the average of the generation in which they were born, we can divide that into the amount by which the average of the offspring exceeds the average of the generation in which their selected parents were born and thus get an estimate of heritability. For adequate control of environment it is usually necessary that selection in the opposite direction shall be practiced in a contemporary control line. If selection continues for more than one generation, replacements must come from within each line itself. The classical example of this method in plants is "Student's" (1934) interpretation of the Illinois selections for high and low oil content in corn.

Correlations between relatives. This method was used by Galton and has never fallen entirely into disuse, although a clearer understanding of the necessity of appraising correctly the mating system used and of discounting the environmental correlations has made geneticists more wary about its use on incompletely known material than they were formerly. In a well designed experiment the environmental correlations between relatives will be made zero, but this is not always wholly possible. For example, maternal sibs in mammals will have been exposed alike to any permanent peculiarities of the intra-uterine environment provided by their dam. In practice it is sometimes difficult to randomize even post-natal environment as, for example, by distributing pigs at birth in such a way as to induce each sow to rear some of her own pigs and some foster pigs. In data collected from the herds of breeders it is rarely possible to make even a beginning at such randomization of environmental effects.

Relatives most useful. The resemblance between parents and offspring is generally most useful because (1) it is expected to be fairly high if the characteristic is highly hereditary, (2) it does not include dominance deviations, and (3) it is less likely to have been seriously affected by environmental contributions than is the resemblance between maternal sibs. Paternal half-sib resemblance is often useful although the correlation is expected to be smaller and, because it is therefore multiplied by four instead of by two, the sampling errors are more serious than in full sib or parent-offspring resemblance. Half-sib populations are more likely to be unselected than parents are. Resemblance of the indi-

vidual to its grandparents may sometimes be useful, particularly where environmental contributions exist in the parent-offspring resemblance but not directly between grandparent and grandson or granddaughter. Resemblances between more distant relatives are rarely of much use in estimating heritability. The expected genetic resemblances are low and therefore the sampling errors are relatively high.

Intra-sire correlations or regression of offspring on dam. In many kinds of data often encountered in animal husbandry there are some distinct advantages in estimating heritability by computing the correlation or regression of offspring on dam within groups of offspring by the same sire.* This is essentially a parent-offspring resemblance but computing it on an intra-sire basis goes far toward automatically discounting environmental contributions and any peculiarities of the mating system. These two difficulties are not solved outright; they are merely dodged by restricting the analysis to such variance as is found *within* groups of females which get mated to one sire. Differences *between* such groups of females remain unanalyzed as to the extent to which they are hereditary or environmental in origin.

For example, in the butterfat records used for proving dairy bulls in Iowa before 1940 the average intra-sire regression of daughter on dam was about $+.14$ (data as yet unpublished). To obtain heritability this regression coefficient is doubled, in accordance with Schmidt's principle of diallel crossing. This yields the estimate that about 28 percent of the variance among the butterfat records of mates of a sire was due to additively genetic differences between those cows, including also a small part of the epistatic differences. However the record used for each cow was an average of all the records she had. If allowance is made for what this averaging has done to extinguish variance from temporary environmental circumstances, it appears that something like 20 to 25 percent of the variance in single butterfat lactation records among cows which are mated to the same sire can be construed as additively genetic, with a small portion of the epistatic variance being included in this.

* Correlation and regression are interchangeable for this purpose if the dams were an unselected group. Selection of the dams will tend to lower the correlation coefficient but will not bias systematically the regression of offspring on dam, although the dependability (fiducial limits) of that regression will be decreased. Selection of the offspring of course would impair the validity of any estimate of heritability based on them. Presumably some selection will have been practiced among the parents in most animal husbandry data, although the question may well be raised whether that selection has often been as intense as is popularly supposed. Therefore regression is generally to be preferred to correlation for the purpose discussed here.

The intra-sire regression dodges most of the environmental correlations because (1) the daughters and mates of a sire are nearly always kept in the same herd (This needs scrutiny in each set of data) and therefore the effects of heterogeneity of management from herd to herd would be left in the differences between sires instead of contributing to daughter-dam resemblance, and (2) the offspring of one sire are usually nearly contemporary and this keeps time trends in management from contributing much to the outward resemblance between daughter and dam, as is otherwise likely to be the case in data collected from a single herd over a period of many years.

The intra-sire regression dodges questions about departures from random mating because it expresses heritability as a fraction of the variance which existed among the females mated to the same sire. If, for example, it were applied to a population being split into partially inbred lines, the females being mated to each sire would belong to the same line. The estimate of heritability thus obtained would concern the variance then existing within lines and would throw little or no light on differences between lines.

No good way has yet been devised for estimating the extent to which, in data collected from several herds, the differences between the

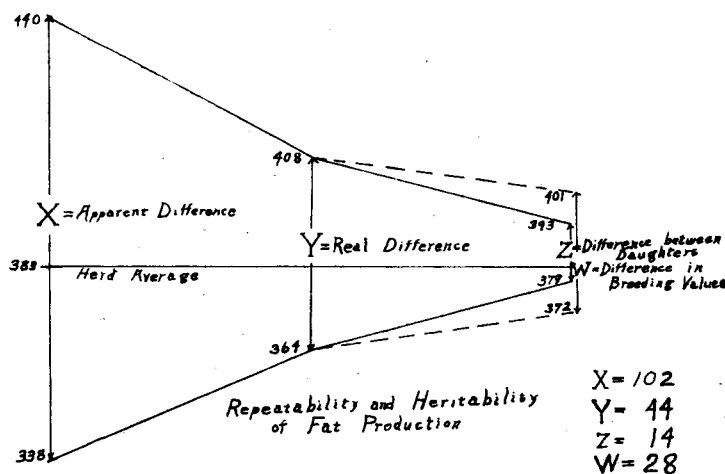


FIGURE 2. Intra-sire regression from first record (X) of mates to the later records of the same cows (Y) and to the records of their daughters (Z). Y/X = repeatability of differences in single records. W/X = heritability (additive plus a little of the epistatic) of differences in single records. Y minus W includes σ_D^2 and nearly all of σ_I^2 and whatever of σ_E^2 is due to intra-herd environmental peculiarities which persisted over the first and later lactations of the same cow.

averages of the dams mated to each sire are genetic or environmental. Studies of inbreeding within pure breeds have generally shown that there is not enough subdivision into separate families for such departures from random mating to have contributed much to differences between herds. Yet there is at least a little herd differentiation in average genetic value. The daughters of various sires are of course not at all evenly distributed between herds. Within a few breeds considerable genetic heterogeneity between herds may have been produced by conflicting ideals whereby some breeders have selected in one direction while others have selected toward a different ideal. Even where all breeders have had the same ideals in mind there will have been some herd differentiation in most breeds because some men have selected more effectively than others. In general it does not seem that these causes of genetic heterogeneity between herds will have been highly important although there may be special cases where they were. Such considerations as these point toward the probability that most of the differences between-herd averages are largely due to differences in environment and management but it would be a remarkable coincidence if they ever were wholly so. More definite and general information on this point would be highly desirable.

A convenient approximation to the least squares regression line can be had by dividing the mates of each sire into a high half and a low half. The difference between the means of their offspring, when doubled and divided by the difference between the means of the dams, yields an estimate of the additively genetic portion of the variance within that group of dams. A part of the epistatic variance is included also. Where the characteristic being studied is a repeatable one, as butterfat production by cows, the mates can be sorted on their first records and then their later records can be treated as dependent variables, just as their daughters' records are. Figure 2 shows the results of doing this with 676 daughter-dam pairs which were used to prove 103 sires in Iowa Cow Testing Associations, before 1937. Each dam had at least two records. Obviously the non-hereditary variance in single records was mostly due to circumstances which changed from one lactation to the next; i.e. to temporary environmental variables. Dominance and epistasis together can hardly have been half as important as the additively genetic portion of the variance and were much less important than that of permanent environmental influences which operate on one cow (but not on her contemporaries) all through her life (such as an udder spoiled by injury or by bad feeding during calfhood) were at all important. This method of dividing the mates into a high half and a low half avoids computing squares and cross-products. For some audiences it could be ex-

plained more simply and plausibly than a regression computed by the least squares method. However it is only an approximation to that method and is not statistically as efficient in getting out of the data as much as possible of the information they contain.

Why Determine Heritability?

A dependable estimate of the heritability of a characteristic is perhaps the most important consideration in deciding which of several possible breeding plans is likely to be most effective. If the breeding plan is merely that of mass selection of the most desirable individuals to be parents, the progress per generation which one should expect is only the heritability fraction (in the narrowest sense) of the amount which is actually reached for when selecting the parents. If the desired characteristics are highly hereditary the best method will be mass selection with little real use for pedigree, relatives, progeny test or inbreeding. If heritability is low, but there is not much epistatic variance either, considerable use of pedigree and much use of progeny tests and selection on a family basis would be a better plan but there would be little use for any more inbreeding than is needed to make families distinct or to make full use of the progeny test. On the other hand, if there is little additive variance but much epistatic variance, this calls for a considerable use of inbreeding to create lines distinct from each other, with subsequent interline selection and crossing and the creation of future lines from the results of the more favorable of these crosses.

When choosing an efficient breeding system, a usable accurate rough estimate of heritability of the important characteristics is the first thing a breeder needs to know after he has decided upon his goal.

