HERITABILITY IN RELATION TO SELECTION DIFFERENTIAL IN CATTLE

G. E. BRADFORD¹ AND L. D. VAN VLECK

Cornell University, Ithaca, New York

Received December 27, 1963

THE concept of heritability as generally used involves the assumption that additive genetic variance is a constant proportion of total variance over the entire range of phenotypes. If this assumption holds, selection response will be linearly related to selection differential. If not, prediction of selection response will not be possible from a knowledge of the phenotypic selection differential and the average proportion of additive genetic variance. Thus the validity of this assumption has a bearing on the design of efficient selection schemes for many situations. In the field of applied animal breeding, for example, this will affect such important questions as the increase in rate of genetic improvement to be expected from the use of artificial insemination.

Situations in which genotype-phenotype interrelationships lead to buffering, or canalization, of phenotypic development obviously do not conform to this assumption. The phenotypic distributions in such cases are of course markedly nonnormal (see, for example, WADDINGTON 1957; RENDEL 1959; FRASER and KINDRED 1960). However, it seems possible that traits with a more nearly normal distribution might have an underlying canalization component which would result in some distortion of the phenotype-genotype curve from linearity. CLAYTON, MORRIS and ROBERTSON (1957) compared different intensities of selection for abdominal bristle number in *Drosophila*, and found that realized heritability was higher at higher selection intensities, for both up and down selection. BEARDSLEY, BRATTON and SALISBURY (1950), on the other hand, studying butterfat yield in dairy cattle, found evidence for lower heritability as deviation from the mean increased.

Critical evidence on this point would be provided by selection experiments involving widely different selection intensities. However, such experiments spanning several generations can only be carried out with species with high reproductive rates, which will for the most part restrict studies of this kind with animals to laboratory species. The patterns of genetic variability and of genotype-phenotype relationship may differ in such species from those in economic species, because of differences in selection history, recombination frequency, traits which can be measured, range of environments and other factors.

Estimation of offspring-parent regression in a population large enough to determine heritability of extreme deviations with a reasonable degree of precision is feasible for some traits in livestock. This would constitute, in effect, a one

¹ Department of Animal Husbandry, University of California, Davis.

generation selection experiment using different intensities, a technique which could probably be used for a variety of traits in many species to obtain estimates of at least the short term response to different intensities of selection. This paper reports the results of such a study based on milk records of dairy cows.

MATERIALS AND METHODS

Data on 5740 pairs of Holstein cows in which both dam and daughter made a first lactation record between 1958 and 1962 were taken from the files of the New York State Dairy Records Processing Laboratory. The observations used were deviations of mature equivalent 305-day milk yields from season-herdmate average, thus minimizing herd, season and age effects. The restriction of the time period from which the pairs were taken was such that all of the daughters were either first or second calves of their dams, most being first. This was expected to provide an essentially unselected group of dams, i.e. a group providing a maximum range in selection differential. As will be seen from the results, some culling of dams had been practiced, but this should not affect the conclusions.

The data were sorted on dam deviations, which ranged from approximately +10,000 pounds to -8,000 pounds of milk. The distribution of dam deviations is shown in Figure 1. Relationship of response to selection differential was evaluated by plotting daughter deviations against dam deviations, and by calculation of the daughter-dam regressions for different segments of the dam distribution. Quadratic and cubic polynomials were also computed to test for curvilinearity of the regression line.

RESULTS AND DISCUSSIONS

Milk yield of dams and daughters, classified on dam's milk yield deviation and listed in groups each containing 10 percent of the sample, are presented in Table 1. A noticeable feature of these data is that, although mean production of all daughters exceeded that of all dams, mean daughter deviation was negative whereas mean dam deviation was positive. Higher mean daughter than dam production was expected, since milk production per cow for all herds in the state increased sharply during the period involved. This is believed to be due primarily

FIGURE 1.—Frequency distribution of milk yield deviations from season herdmate average of 5740 dams. Deviations are expressed as $\text{lb} \times 10$.

TABLE 1

Performance of daughters from dams classified according to milk yield deviation from season-herdmate average

Group*	Dams		Daughters	
	Average deviation†	Actual milk†	Average deviation	Actual milk
1	422	1702	50	1445
2	252	1554	10	1404
3	163	1462	3	1377
4	97	1398	-10	1369
5	47	1357	-13	1366
6	4	1295	-31	1342
7	-59	1247	-56	1317
8	-120	1192	-67	1297
9	-201	1120	-88	1285
10	-364	976	-114	1264
Average	+23	1330	-32	1347
Variance	48903		62251	

* Arranged in descending order of dam deviations. Each group contains 574 pairs.

† Units are lb $\times$ 10 (Imperial gallons).

to changes in feeding and management. Evidence for positive genetic trend due to sire selection is also available (VAN VLECK and HENDERSON 1961).

Mean deviation of first lactation records is commonly found to be negative, owing presumably to the fact that first lactation cows are unselected on the basis of their own production, whereas in the group with which they are compared, herdmates of all ages, considerable culling has occurred. Incorrect estimation of age-correction factors could also bias the mean deviation of first lactation values. Thus, the negative mean deviation of daughter records can be explained. However, the dams' records in this study were also all first lactations, hence are also expected to have a negative mean deviation. The most probable explanation of the positive value is selection of dams, i.e. some of the poorer dams were not represented by daughters with a first lactation. If the mean daughter deviation (-320 lbs.) is taken as an estimate of the bias in first lactation deviations, the dams represented by daughters had in fact a mean plus deviation of 550 lb of milk. (The true deviation is probably somewhat larger than this, since with selection of dams, the true mean daughter deviations should not be zero, but $+h^2/2$ times the selection differential for dams.) A difference of 550 lb is approximately one fourth of a phenotypic standard deviation, thus equivalent to truncation culling of the poorest 15 percent of dams. That the culling was not truncation culling on milk yield may be seen from Figure 1. The decrease in variance of dams' compared to daughters' deviations (Table 1) is equivalent to that resulting from truncation culling of approximately the poorest 6 percent.

Daughter deviations are plotted against dam deviations, by 5 percent increments, in Figure 2. The upper graph is based on the noncumulative distribution, thus each point represents 5 percent of the data, or 287 pairs. The lower graph is

FIGURE 2.—Regression of daughter milk yield deviation (response) on dam milk yield deviation (selection differential). Units are $\text{lb} \times 10$. Each point on the noncumulative graph represents 5 percent of the sample, or 287 pairs. The points from right to left on the cumulative graph represent 287, 574 5740 pairs.

based on the cumulative data, with the points from right to left being based on 5 percent, 10 percent, 15 percent etc. of the data.

No departure from linearity is evidenced by either of these graphs. The negative mean daughter deviation results in some negative heritability estimates if these are computed as twice daughter superiority divided by dam superiority. However, the slope of the line provides the information of interest. Adjustment for the factors discussed above would shift the position of the line with respect to the origin, but would not change the slope. The unadjusted data were, therefore, used in plotting this graph.

The regression of daughter deviation on dam deviation as estimated from this graph is approximately .21, yielding an estimate of heritability of .42.

The regression was also measured by the usual product-moment method, within 10 percent groups based on dam's deviations and for the entire sample of data. The results are shown in Table 2.

The noncumulative regression coefficients suggest that heritability of differences near the mean is lower than that of more extreme deviations. However, the standard errors, which are related inversely to variance of the independent variable, are very large. If there is in fact a curvilinearity of the regression line in this area, this should have been reflected in a significant increase in the multiple correlation coefficient by fitting of a second or third degree polynomial. The actual correlation coefficients, based on linear, linear + quadratic, and linear + quadratic + cubic terms, were, respectively, .192, .192 and .193. Thus there is no evidence for curvilinearity of heritability, either from a direct plot of daughter and dam records or from a regression analysis. This is in contrast to the results of

TABLE 2

Daughter-dam regression in relation to dam's deviation from season-herdmate average

Noncumulative		Cumulative	
Proportion*	$b \pm s_b$	Proportion	$b \pm s_b$
.10	.22 $\pm$.10	.10	.22 $\pm$.10
.10	.70 $\pm$.35	.20	.25 $\pm$.06
.10	.37 $\pm$.48	.30	.21 $\pm$.05
.10	.25 $\pm$.65	.40	.20 $\pm$.04
.10	— .35 $\pm$.67	.50	.18 $\pm$.03
.10	.07 $\pm$.64	.60	.18 $\pm$.03
.10	.04 $\pm$.61	.70	.20 $\pm$.02
.10	.49 $\pm$.49	.80	.21 $\pm$.02
.10	.72 $\pm$.37	.90	.22 $\pm$.02
.10	.12 $\pm$.11	1.00	.217 $\pm$.015
Heritability = $2b = .43 \pm .03$			

* Dam deviations sorted in descending order.

BEARDSLEY *et al.*, (1950), referred to earlier, who found some evidence for decreasing heritability with increasing deviation of dam's production from the mean. The present study involves larger numbers, and differs also in being based on first lactations only, which in general have a higher heritability than later lactations (see for example RENDEL *et al.*, 1957).

The question under investigation in this study, that of the relationship between deviation from mean and heritability of deviations, should not be confused with the question of association between heritability and level of performance due to environmental factors. A number of studies on this topic for this species have been reported, for example ROBERTSON, O'CONNOR and EDWARDS (1960), LEGATES (1962) and VANVLECK (1963). The level of production of herdmates of dams in the different deviation categories of this study, which can be obtained by a simple subtraction of the appropriate values in Table 1, were quite similar for all groups of dams. The results obtained should therefore be relatively unaffected by any association which may exist between heritability and level of production due to environment. These results then indicate that heritability of milk production is independent of selection intensity (and also of direction of selection), and that selection response is predicted to be linearly related to selection differential.

A relevant question is whether or not evidence for some departure from linearity was expected for this trait, or more generally, for what kinds of traits is canalization likely to exist? As WADDINGTON (1957) has pointed out, it might be assumed that traits closely related to fitness are most likely to have evolved a buffering of developmental pathways. However, this reasoning is not supported, in any obvious fashion, by the array of traits which have been shown to exhibit this phenomenon, which includes such characteristics as wing veins and scutellar bristles in *Drosophila* (WADDINGTON 1957; RENDEL 1959) and vibrissa number in the mouse (FRASER and KINDRED 1960). The pattern of variation in rib and vertebra numbers in swine described by FREDEEN and NEWMAN (1962) also

appears to represent a partially canalized system. It is probable that studies on many traits and species will be needed before a pattern, if such exists, can be discerned.

The trait under consideration here, milk production in cattle, is one which was no doubt directly subject to natural selection, quite possibly for an intermediate level, in the undomesticated ancestors of present day breeds. However, artificial selection has long since modified the expression of the trait to a point where the mean exceeds the estimated level in the "natural" ancestor populations by a factor of five to ten, or more. It may be that continuous directional selection precludes the development of canalization systems, and that these will be found only for traits not subjected to this kind of selection. It seems probable that the traits referred to above which have been shown to exhibit canalization have in common an absence of such a selection history, and may have been subject to natural selection for an intermediate level of expression. On the other hand, one might argue that a plateau resulting from continuous directional selection is an aspect of canalization. In any case, the results presented here show no evidence for a canalized pattern of expression, and in fact a substantial additive genetic component of variance, for a trait with an undoubtedly long history of directional selection.

The estimate of heritability of milk production obtained here, .43, is substantially higher than the estimate of .25 obtained by the paternal half-sib method in a recent study of similar data (VANVLECK 1963). To determine if method of estimation might be the basis for the difference, heritability was estimated by the paternal half-sib method from the deviations of the 2568 artificially sired daughters in these data. There were 147 sires represented. This yielded an estimate of .25, with approximate standard error of .053. The estimate from the daughter-dam regression based on these 2568 pairs only was $.44 \pm .044$. Thus it appears that the method of estimation, rather than a peculiarity of the data, is the reason for the difference. At least two other comparisons of estimates of heritability of first lactation milk yield, using these two methods on the same data, have been made (RENDEL *et al.* 1957; GRAVERT 1959). Both report better agreement between the two estimates than found here.

Selection of sires could result in a downward bias in the paternal half-sib correlation. However, the mean daughter deviations for these 147 sires (based on all daughters of all ages) included nearly as many negative as positive values, and averaged over all sires was only +140 lb of milk. Thus there appears to have been only a limited amount of selection among the sires.

A large additive $\times$ additive component of variance would be expected to contribute to a higher estimate of heritability from daughter-dam regression than from paternal half-sib correlation. The difference between the two should estimate one-fourth of this component, hence the difference in this case, .19, can not be explained on this basis alone. However, the results do suggest that this type of epistasis may be an important source of variation in milk yield.

Another possible source of upward bias in the daughter-dam regression is an environmental correlation between daughter and dam deviations, due to the fact

that some of the same cows are included in the herdmate averages with which both dam and daughter records are compared. It is estimated that this could account for no more than a fourth of the observed difference.

A maternal effect on milk production could also contribute to the observed difference. BRUMBY (1960) concluded from a study of twin data that about 10 percent of the variation in milk production is attributable to maternal effects. Further, it seems not unreasonable to assume that if strictly maternal inheritance exists for any traits, it is most likely to be found for traits, such as milk production, expressed by females only. Since most of the selection pressure which can be applied in species with a low reproductive rate is a result of selection of males, it would appear important to determine whether maternal effects are of major importance and if so, whether these are transmitted by both sexes or are cytoplasmic in nature.

Positive assortative mating would increase the estimated heritability by both methods. There was no evidence of such a departure from random mating in these data. The top 50 percent of dams were mated to sires with an average daughter level superiority of 141 lb milk; mates of the poorer 50 percent of dams had an average proof of +140 lb milk. Further, almost exactly the same fraction of daughters from each group of dams were by A.I. (artificial insemination) sires.

It is probable that the difference between the two estimates of heritability found in this study is due to a combination of some of the factors discussed and possibly others. The important question is, of course, which if either of these two estimates predicts selection response. DICKERSON (1962) presented data from poultry indicating that selection for egg production traits was effective only in maintaining the existing level of performance, even though resemblance between relatives indicated moderate heritability. Other examples of plateaux in selection response in the presence of considerable genetic variation have been reported, although few demonstrate this situation as conclusively. Such a situation is a definite possibility for milk production, since as mentioned previously, the trait has a long history of directional selection. Further, it is known that selection in dairy cattle has not been for milk yield only, and realized response less than that predicted due to the phenomenon termed genetic slippage by DICKERSON (1955) is also a possibility. Actual response to selection for this trait is difficult to estimate accurately from available data. The values obtained, however (for a recent estimate and a review on this subject see ARAVE, LABEN and MEAD 1964) suggest response reasonably consistent with at least the lower estimate of heritability from the present study, and hence a more optimistic picture than that which apparently exists for egg production traits in poultry.

The primary purpose of this study was to estimate whether or not heritability is linear over the range of phenotypes. The conclusion reached, from a daughter-dam regression analysis, is that it is, in fact strikingly so. Coincidentally it was discovered that, in these data at least, daughter-dam resemblance is higher than would be predicted from paternal half sib resemblance and possibly also from response to past selection. This poses a question as to whether the same conclusion would have been reached from an analysis involving sires. This question cannot

be answered directly, since the trait involved is sex-limited. It is possible that a different slope of the regression line would be associated with a different finding with respect to linearity. However, there seems no reason to assume this, on the basis of present knowledge. It is therefore concluded that, to the extent that heritability estimated from parent-offspring regression predicts selection response for milk yield, the prediction should hold over a wide range of selection intensities.

SUMMARY

Milk production records from 5740 first lactation dam-daughter pairs were studied to determine if the heritable fraction of total variation is related to selection differential. Heritability was essentially constant over the entire range of phenotypic variability, there being no evidence for curvilinearity of the offspring-parent regression line. Thus at least short-term selection response is predicted to be linearly related to selection differential, and also to be independent of direction of selection. The estimate of heritability from the total data was $.43 \pm .03$, substantially higher than many published estimates for this trait. The estimate by the paternal half-sib method from the proportion of the data provided by artificially sired daughters (2568) was .25, while the daughter-dam estimate from the same subsample was .44. Possible reasons for the difference between the two estimates are discussed.

LITERATURE CITED

- ARAVE, C. W., R. C. LABEN, and S. W. MEAD, 1964 Measurement of genetic change in twelve California dairy herds. *J. Dairy Sci.* (In press).
- BEARDSLEY, J. P., R. W. BRATTON, and G. W. SALISBURY, 1950 The curvilinearity of heritability of butterfat production. *J. Dairy Sci.* **33**: 93-97.
- BRUMBY, P. J., 1960 Cattle twins: the maternal environment and animal production. *Proc. New Zealand Soc. Animal Prod.* **20**: 95-107.
- CLAYTON, G. A., J. A. MORRIS, and A. ROBERTSON, 1957 An experimental check on quantitative genetical theory. I. Short-term responses to selection. *J. Genet.* **55**: 131-151.
- DICKERSON, G. E., 1955 Genetic slippage in response to selection for multiple objectives. *Cold Spring Harbor Symp. Quant. Biol.* **20**: 213-224. — 1962 Experimental evaluation of selection theory in poultry. 12th World's Poultry Congr. *Proc. Symp.*, 17-25.
- FRASER, A. S., and B. M. KINDRED, 1960 Selection for an invariant character, vibrissa number, in the house mouse. II. Limits to variability. *Australian J. Biol. Sci.* **13**: 48-58.
- FREDEEN, H. T., and J. A. NEWMAN, 1962 Rib and vertebral numbers in swine. I. Variation observed in a large population. *Can. J. Animal Sci.* **42**: 232-239. — II. Genetic aspects. *Can. J. Animal Sci.* **42**: 240-251.
- GRAVERT, H. O., 1959 Zur Bewertung der Milchfettleistung in absoluten oder prozentischen Zahlen. *Züchtungskunde* **31**: 345-355.
- LEGATES, J. E., 1962 Heritability of fat yields in herds with different production levels. *J. Dairy Sci.* **45**: 990-993.
- RENDEL, J. M., 1959 Canalization of the scute phenotype of *Drosophila*. *Evolution* **13**: 425-439.

- RENDEL, J. M., A. ROBERTSON, A. A. ASKER, S. A. KISHIM, and M. T. RAGAB, 1957 The inheritance of milk production characteristics. *J. Agr. Sci.* **48**: 426-432.
- ROBERTSON, A., L. K. O'CONNOR, and J. EDWARDS, 1960 Progeny testing bulls at different management levels. *Animal Prod.* **2**: 141-152.
- VANVLECK, L. D., 1963 Genotype and environment in sire selection. *J. Dairy Sci.* **46**: 983-987.
- VANVLECK, L. D., and C. R. HENDERSON, 1961 Measurement of genetic trend. *J. Dairy Sci.* **44**: 1705-1710.
- WADDINGTON, C. H., 1957 *The Strategy of the Genes*. Allen and Unwin, London.