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Potential of Cytoplasmic Effects for Selection in Dairy Cattle

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ABSTRACT

Maternal cytoplasmic inheritance may cause an upward bias in heritability estimates from daughter on dam regression. Inaccurate evaluations of bulls or dams of future sires would result if such estimates were used in genetic evaluation. Expected genetic selection differential for bulls would be overestimated, but genetic gain would be little affected by incorrect heritability estimates. Genetic evaluations of dams of sires would be less accurate when incorrect heritability estimates are used, but actual selection differentials would be only slightly less than optimum. If cytoplasmic effects were ignored during selection, less genetic improvement would seem to be the result. However, expected genetic gain would be only slightly increased if selection considered both nuclear and cytoplasmic components of inheritance rather than nuclear inheritance only. Reasons for both results are that selection for cytoplasmic effects can be done directly only through dams of cows for which selection is not very intense and that overestimates of heritability have little effect on genetic selection differentials as compared to using correct estimates of heritability. Expected genetic gain, if based on overestimates of heritability, however, will be considerably greater than can be realized.

INTRODUCTION

Recent studies have suggested that cytoplasmic inheritance may affect production traits in dairy cattle (2, 4). The presence of extranuclear genes, and their maternal transmission, have been known for many years. Because of its

cytoplasmic location, inheritance of mitochondrial DNA (mtDNA) is not governed by the same laws that apply to chromosomal genes. Extranuclear genes are replicated in the cytoplasm without a chromosomal template. Although a great deal is known about the structure and expression of mtDNA, including the entire sequence in the bovine (1), the cause of its maternal inheritance is poorly understood. Cytoplasmic organelles are genetically autonomous and have genetic transmission systems of their own, but nuclear genes may affect their development. Hereditary defects may be either chromosomal and transmitted in a Mendelian fashion, or they may show non-Mendelian, maternal inheritance (3).

Cytoplasmic genes (such as those on mtDNA) may affect production traits in dairy cattle, especially since mitochondria are essential for any reaction in an organism which requires or produces energy, such as fatty acid synthesis, oxidative phosphorylation, and glycolysis. Mitochondria also may have a role in disease resistance.

Research results supporting the existence of maternal cytoplasmic effects are 1) higher heritability estimates for production traits in dairy cattle from daughter on dam regression than from paternal half-sister correlations (9, 10, 11), 2) the ability of dam's records to predict daughters' performance better than their son's progeny tests (6), and 3) differences between reciprocal crosses in dairy breeds (8). Other factors, however, can explain such results. In a more direct analysis, pedigrees of 4461 cows in North Carolina herds were traced to the original female in a maternal line (the cytoplasmic origin). After records were adjusted for sire, herd, and calving month and year, cytoplasmic effects were estimated to account for 2.0, 1.8, 1.8, and 3.5% of total variation of milk yield, milk fat yield, 3.7% FCM yield, and milk fat percent in first lactation (2). In a similar study, Huizinga et al. (4) concluded that cytoplasmic origin was a significant source of variation for

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first lactation production of milk yield as well as for fat and protein yield but an insignificant source of variation for reproductive traits. However, apparently significant effects of cytoplasmic inheritance were observed from a similar analysis of 4500 lactation records simulated on a computer under an additive genetic model with no cytoplasmic effects. Eight of 10 replicates for milk yield and all replicates for milk fat percent showed significant variance due to apparent cytoplasmic effects, an average of 1.4% of phenotypic variance for milk yield and 3.2% for fat percent. These results were attributed to random genetic drift (5). Comparison of heritability estimates from daughter-dam and granddaughter-granddam regressions for milk yield, milk fat yield, and milk fat percent suggested that cytoplasmic effects accounted for no variation in these traits (7). The difference between daughter-dam and granddaughter-granddam heritability estimates should estimate twice the fraction of variance due to cytoplasmic effects; however, the differences were negative and not statistically significant for milk and milk fat yield and negative but highly significant for milk fat percent (7).

Heritability estimates from daughter on dam regression would be biased upward because of cytoplasmic variance and would alter evaluations of bulls and of dams of future sires. An entirely different problem is that even if heritability estimates might be accurate, when cytoplasmic variance is ignored during selection, all of the potential total genetic gain from nuclear and cytoplasmic inheritance will not be realized. The objective of this study was to determine the effects on selection and genetic gain resulting from inaccurate selection due to cytoplasmic effects.

Effect of Inaccurate Heritability Estimate Due to Cytoplasmic Variance

Heritability in the narrow sense might be overestimated from daughter on dam regression because of an unknown bias from variance due to cytoplasmic effects:

$$h_*^2 = h^2 + 2(\sigma_t^2/\sigma_x^2)$$

where h^2 is true heritability (assumed for calculations to be .25 for milk yield, .50 for milk fat percent); h_*^2 is the overestimate of heritability

(the symbol * will be used throughout to signify altered values resulting from overestimates of heritability); σ_t^2 is variance of cytoplasmic effects; σ_x^2 is total phenotypic variance (assumed for examples to be $(1134 \text{ kg})^2$ for milk yield and $(.3\%)^2$ for milk fat percent); σ_t^2/σ_x^2 is proportion of phenotypic variance caused by cytoplasmic effects (values of 1, 2, 3, 4, and 5% were used for examples in this study with 5% used for the examples in the text). For example, if 5% of the variance of milk yield is due to cytoplasmic effects, heritability estimated from daughter on dam regression would be expected to be:

$$h_*^2 = .25 + 2(.05) = .35.$$

Bull Selection

If such a biased estimate of heritability from daughter on dam regression were to be used in evaluation of bulls, estimates of breeding value would be biased, and the accuracy of evaluation would be overestimated. For purposes of illustration, properties of the selection index (best linear prediction) for estimates of additive genetic values will be used. The accuracy of evaluation (correlation between the true additive genetic value and the selection index) from a progeny average is:

$$r_{TI_b} = [p/(p + \lambda)]^{.5}$$

where $\lambda = (4 - h^2)/h^2$ and p is number of effective daughters in sire's proof with each daughter in a different herd.

The expected genetic selection differential can then be estimated by:

$$\Delta G_b = i r_{TI_b} (h\sigma_x)$$

where ΔG_b is expected genetic selection differential for bulls with selection based on their progeny records, and i is standardized selection intensity factor (which for comparisons usually will be set equal to 1 in this study). When an inflated heritability is used, the expected but incorrect genetic selection differential will be increased because both r_{TI_b} and additive genetic standard deviation will be overestimated as:

$$r_{TI_b}^* = [p/(p + \lambda_*)]^{.5}$$

so that:

$$\Delta G_b^* = i r_{TI_b^*} (h^* \sigma_x)$$

The expected correlated response from regression of the bull's additive genetic value on his incorrect index can be used to estimate the actual genetic selection differential from use of an incorrect index assuming equal numbers of progeny per bull:

$$\Delta G_b = (\sigma_{G_b, I_b^*} / \sigma_{I_b^*}^2) (\sigma_{I_b^*}^2) (i) = (\sigma_{G_b, I_b^*} / \sigma_{I_b^*}) (i)$$

where I_b^* is selection index prediction of additive genetic value using overestimated heritability and ΔG_b is expected correlated response in true additive genetic value when using an incorrect index.

Expected genetic selection differentials in row 1 of Table 1 correspond to using correct heritability and can be compared to overestimates of selection differentials from using heritability estimates biased upwards by cytoplasmic variance. For example, with $p = 100$, true $h^2 = .25$ and cytoplasmic variance of 5% of phenotypic variance, the actual genetic gain would be 109 kg less (21%) than calculated with incorrect heritability but equal to what would be obtained if accurate heritability estimates were used. These calculations assumed all

bulls are evaluated with exactly 100 daughters; thus, bulls will be ranked the same no matter what heritability is. In practice, bulls usually will have slightly different numbers of daughters in first proofs and greatly different numbers of daughters after the first proof. The effect would be more bias in evaluations of bulls with few daughters than for bulls with many daughters.

Similar calculations for milk fat percent show that the actual genetic gain would be only 10% less than expected based on incorrect heritability. Again, no loss in actual genetic gain would occur, because in these calculations with equal numbers of daughters per bull, bulls would be ranked the same no matter what heritability is used.

Dam of Bull Selection

Biased heritability estimates may also affect selection of dams of future sires. For selection of these cows, emphasis is placed on their records. Cytoplasmic effects may cause some of the variance in production traits, and although a cow's cytoplasmic genes will be passed on to her offspring, her sons will not pass them on to their daughters. In this report, the index to select dams of bulls is calculated based on the cow's production record and her sire's proof:

TABLE 1. Calculated genetic selection differentials for bulls (ΔG_b^*) for milk yield and milk fat percent when overestimates of heritability are used. Row 1 entries are genetic selection differentials (ΔG_b) using correct heritability for milk yield (.25) and milk fat percent (.50).¹

Fraction of variance due to cytoplasmic effects ²	Apparent heritability		Number of daughters					
			10		50		100	
	Milk	Fat %	Milk	Fat %	Milk	Fat %	Milk	Fat %
.00	.25	.50	359	.16	497	.20	529	.21
.01	.27	.52	382	.17	522	.20	552	.21
.02	.29	.54	405	.17	545	.21	575	.21
.03	.31	.56	427	.18	567	.22	597	.22
.04	.33	.58	448	.18	598	.22	618	.22
.05	.35	.60	469	.19	610	.22	638	.23
Correlated genetic selection differentials (ΔG_b) when incorrect index is used			359	.16	497	.20	529	.21

¹ Phenotypic variance for milk = (1134)²; phenotypic variance for milk fat percent = (.3)².

² As fraction of phenotypic variance.

$$I_c = b_c X_c + b_s X_s$$

$$\Delta G_c^* = i r_{TI_c} (h^* \sigma_x)$$

where I_c is index value for the cow, b_c is selection index weight for X_c , her production record, and b_s is selection index weight for X_s , mean production records from sire's progeny test, the cow's paternal half-sisters. The equations to calculate the correct and biased selection index weights are shown in the Appendix.

The accuracy of evaluation is calculated as:

$$r_{TI_c} = (b_c + .25b_s)^{-.5}$$

where .25 is the numerator relationship of the cow to her paternal half-sisters. But, when an overestimate of heritability is used, the overestimate of accuracy is:

$$r_{TI_c}^* = (b_c^* + .25b_s^*)^{-.5}$$

The correct expected genetic selection differential for cows is:

$$\Delta G_c = i r_{TI_c} (h \sigma_x)$$

However, when the heritability and accuracy are biased by cytoplasmic variance, the expected selection differential is exaggerated:

To estimate the true genetic selection differential, which is obtained from selection using the incorrect index, the expected correlated response is found by regression of genotypic value on the index used:

$$\underline{\Delta G}_c = (\sigma_{G_c, I_c} / \sigma_{I_c}) (i)$$

Expected selection differentials with correct heritability are in row 1 of Table 2 and can be compared to overestimates of selection differentials from using overestimates of heritability. The lower part of Table 2 gives the expected correlated selection differentials for additive genetic value if selection is based on incorrect heritability. For example, if the number of paternal half-sisters is 100, and cytoplasmic effects cause 5% of phenotypic variance, $\Delta G_c^* = 452$ kg and $\underline{\Delta G}_c = 344$ kg, but if correct indexes with true heritability are used, $\Delta G_c = 349$ kg. Thus, if an incorrect index is used when heritability is incorrect because 5% of the phenotypic variance is due to cytoplasmic variance, the correlated selection differential is only 1.4% less than that which would have been obtained if the correct index were used. This loss is not

TABLE 2. Calculated inaccurate genetic selection differentials for cows (ΔG_c^*) with one record and records of paternal half-sibs for milk yield or milk fat percent when overestimates of heritability (h^2) are used. Row 1 entries are expected genetic selection differentials using correct heritabilities for milk (.25) and for milk fat percent (.50).

Fraction of variance due to cytoplasmic effects	Apparent h^2		Number of paternal half-sibs					
			10		50		100	
	Milk	Fat %	Milk	Fat %	Milk	Fat %	Milk	Fat %
.00	.25	.50	315	.16	342	.16	349	.16
.01	.27	.52	337	.16	363	.16	370	.17
.02	.29	.54	360	.17	385	.17	391	.17
.03	.31	.56	382	.17	406	.18	411	.18
.04	.33	.58	404	.18	426	.18	432	.18
.05	.35	.60	426	.18	447	.19	452	.19
Correlated true selection differentials (ΔG_c) in cows when incorrect index is used.								
.01	.27	.52	314	.16	342	.16	349	.16
.02	.29	.54	314	.16	341	.16	348	.16
.03	.31	.56	314	.16	341	.16	347	.16
.04	.33	.58	314	.16	339	.16	346	.16
.05	.35	.60	313	.16	338	.16	344	.16

very significant, but a problem of perception is that if inflated heritability is used in the calculations, expected gain is much greater (nearly 30% for this example) than that which is possible.

For milk fat percent, the potential genetic gain that would be lost is relatively much smaller than that for milk yield, because cytoplasmic variance constitutes a smaller proportion of the total genetic variance.

Effect of Ignoring Cytoplasmic Variance During Selection

If cytoplasmic variance is ignored during selection when correct heritability and cytoplasmic variance are known, total genetic gain (nuclear and cytoplasmic) might be less than is potentially possible.

Assume, for example, that heifers are selected for production on the basis of their dams' records and their sires' proofs by using the index to select for $g_c + t$ (sum of additive genetic merit and cytoplasmic effect for cow c):

$$I_c = b_d X_d + b_s X_s$$

where I_c is index value of cow; b_d is selection index weight for X_d , the dam's record; and b_s is selection index weight for X_s , the average of records of sire's daughters (cow's paternal half-sisters). Equations used to determine selection weights are shown in the appendix. The index weights are used to calculate the accuracy of selection:

$$r_{TI_{g+t}} = \frac{[b_d(.5h^2\sigma_x^2 + \sigma_t^2) + b_s(.25h^2\sigma_x^2)]}{(h^2\sigma_x^2 + \sigma_t^2)^{.5}}$$

The expected genetic (nuclear plus cytoplasmic) selection differential is:

$$\Delta G_{g+t} = i r_{TI_{g+t}} (h^2\sigma_x^2 + \sigma_t^2)^{.5}$$

However, if selection is for only direct inheritance, the covariance between X_d and g_c is $.5h^2\sigma_x^2$ rather than $.5h^2\sigma_x^2 + \sigma_t^2$ so that the selection index weights are different, b_d^* and b_s^* . Then $r_{TI_g} = \{[b_d^*(.5)h^2 + b_s^*(.25)h^2]/h^2\}^{.5}$ and $\Delta G_g = i r_{TI_g} (h\sigma_x)$, which will be smaller than ΔG_{g+t} if there is variation due to cytoplasmic effects.

This selection differential really is not an accurate estimate of the true genetic selection differential when cytoplasmic variance is ignored during selection because cows with superior cytoplasmic genes are still likely to be selected. As in the previous case with incorrect heritability, the expected total genetic selection differential can be estimated by correlated response through regression of the genotype ($g + t$) on the index to be used:

$$\Delta G_{g+t} = (\sigma_{G,I}/\sigma_I) (i)$$

The expected values are outlined in the Appendix.

When the cytoplasmic effects contribute 5% to total phenotypic variance for milk yield but are ignored and number of paternal half-sisters is 100 (see Table 3): $\Delta G_{g+t} = 331$ kg, $\Delta G_g = 300$ kg, and $\Delta G_{g+t} = 327$ kg. Thus, if a selection program uses correct heritability but does not consider cytoplasmic effects, the expected selection differential is 327 kg of milk compared with 331 kg for a selection program that considers additive effects of both chromosomal and cytoplasmic genes.

When calculations are done for milk fat percent, the loss due to ignoring cytoplasmic effects is even less significant because heritability is high and the nuclear genes contribute a larger proportion of total variation than for milk yield.

Effect of Selection for Cytoplasmic Effects on Genetic Progress

Of the four paths of selection, only in path of dam to cow will cytoplasmic effects be passed to descendants. That selection path usually is associated with low intensity of selection and less accuracy as compared to the other paths. Genetic progress per year at equilibrium usually is stated to be equivalent to the sum of genetic selection differentials for the four paths of selection divided by the sum of the corresponding generation intervals. However, in the case of cytoplasmic effects, genetic gain per year must be estimated by a slightly different method since cytoplasmic genes are only transmitted maternally:

$$\begin{aligned} \Delta G/\text{yr} &= \frac{\Delta SS + \Delta DS + \Delta SD + \Delta DD_g + \Delta DD_t}{L_{SS} + L_{DS} + L_{SD} + L_{DD} + L_{DD}} \\ &= \Delta G_g/\text{yr} + \Delta G_t/\text{yr} \end{aligned}$$

where $\Delta G/\text{yr}$ is estimated genetic gain per year; L_{SS} is generation interval for sires of bulls (assumed in the following example to be 9.9 yr); L_{DS} is generation interval for dams of bulls (assumed to be 6.9 yr); L_{SD} is generation interval for sires of cows (assumed to be 9.0 yr); L_{DD} is generation interval for dams of cows (assumed to be 4.2 yr); ΔSS is genetic selection differential for sires of bulls, assumed for the example to be with $\sigma_g = [.25(1134)^2]^{.5} = 567$; $(2.4)(.9)(567) = 1225$ kg; ΔDS is genetic selection differential for dams of bulls, assumed to be $(2.0)(.65)(567) = 737$ kg; ΔSD is genetic selection differential for sires of cows, assumed to be $(2.2)(.8)(567) = 998$ kg. (For the example calculations of genetic selection differentials, values for i and r_{TI} were chosen based on selection of AI sires with high intensity and accuracy, and dams of sires with a great deal of intensity after about three lactation records. Calculations also assume correct heritability, .25, is used.)

The ΔDD_g is genetic selection differential due to additive effects of nuclear genes of dams of cows which will depend on whether selection considers cytoplasmic effects; ΔDD_c is genetic

selection differential due to cytoplasmic effects of dams of cows which also will depend on whether selection considers cytoplasmic effects. The top 90% ($i = .2$) will be selected except when sexed semen or embryo transfer examples are examined.

If for this example, cytoplasmic effects account for 5% of phenotypic variance but are ignored during selection,

$$\Delta G/\text{yr} = \frac{1225 + 737 + 998 + (.2)(300)}{9.9 + 6.9 + 9.0 + 4.2} + \frac{(.2)(27)}{4.2} = 101.95 \text{ kg}$$

If cytoplasmic effects cause 5% of the phenotypic variance and are considered during selection:

$$\Delta G/\text{yr} = \frac{2960 + (.2)(297)}{30} + \frac{(.2)(34)}{4.2} = 102.26 \text{ kg (Table 4)}.$$

Therefore, based on this example, unless selection intensity of dams can be greatly increased,

TABLE 3. Expected genetic selection differentials (ΔG) for selection of heifers for additive genetic value plus cytoplasmic value for milk yield and milk fat percent from dam's record and records of paternal half-sisters.

Fraction of variance due to cytoplasmic effects	Number of paternal half-sisters					
	10		50		100	
	Milk	Fat %	Milk	Fat %	Milk	Fat %
.00	229	.11	286	.12	300	.13
.01	236	.11	292	.13	305	.13
.02	243	.11	298	.13	311	.13
.03	251	.12	304	.13	318	.13
.04	259	.12	311	.13	324	.13
.05	268	.12	318	.13	331	.14
Expected selection differentials for additive genetic value plus cytoplasmic effect (ΔG) for milk yield and milk fat percent if cytoplasmic effects are ignored during selection.						
.00	229	.11	286	.12	300	.13
.01	235	.11	292	.13	305	.13
.02	243	.11	298	.13	311	.13
.03	249	.12	303	.13	316	.13
.04	257	.12	309	.13	322	.13
.05	264	.12	314	.13	327	.14

TABLE 4. Total (genetic plus cytoplasmic) gain per year for milk yield (kg) and milk fat percent when selection in dam of cow path is for nuclear and cytoplasmic effects.

Fraction of variance due to cytoplasmic effects	Number of paternal half-sisters					
	10		50		100	
	Milk	Fat %	Milk	Fat %	Milk	Fat %
	Selection of top 90% of cows					
.00	100	.02	101	.02	101	.02
.01	101	.02	101	.02	101	.02
.02	101	.02	101	.02	101	.02
.03	101	.02	102	.02	102	.02
.04	102	.02	102	.02	102	.02
.05	102	.02	102	.02	102	.02
	Selection of top 10% of cows					
.00	112	.02	115	.02	116	.02
.01	115	.02	118	.02	118	.02
.02	118	.02	121	.02	121	.02
.03	122	.02	123	.03	124	.03
.04	126	.03	127	.03	127	.03
.05	129	.03	130	.03	130	.03

any significant benefit by selection for cytoplasmic effects in addition to selection of nuclear effects seems unlikely.

Sexing of semen, however, would reduce the number of cows needed as dams to 45% ($i = .88$) so that;

$$\Delta G/\text{yr} = \frac{2960 + (.88)(297)}{30} + \frac{(.88)(34)}{4.2}$$

$$= 114.50 \text{ kg}$$

Embryo transfer could further increase selection intensity by decreasing the necessary number of dams of replacement heifers to 10% ($i = 1.755$), so that:

$$\Delta G/\text{yr} = \frac{2960 + (1.755)(297)}{30} + \frac{(1.755)(34)}{4.2}$$

$$= 130.25 \text{ kg (Table 4)}.$$

Embryo transfer and selection directed toward improvement of nuclear and cytoplasmic genetic effects could result in genetic gain per year of 130 kg of milk or 28 kg more than would be possible without the use of embryo transfer and selection for nuclear plus cytoplasmic effects. Assuming \$.15 profit/kg of

milk produced, this would result in an increased net genetic value of \$4.20/yr, so that many years would be required to cover the cost of embryo transfer.

A reviewer has pointed out that because of lack of segregation and recombination, variation due to cytoplasmic effects is likely to be reduced due to selection so that the formula may not hold true after one generation.

CONCLUSIONS

Even if cytoplasmic effects cause a bias in the heritability estimate and an overestimate of expected response or if cytoplasmic effects are ignored during selection, there is very little effect on genetic gain. Selection index weights are less accurate than they could be, but the effect on selection response is only slightly less than optimum. However, if cytoplasmic effects cause a very large proportion of the phenotypic variance or selection on dams of cows is intense, conclusions from an analysis as described here by example might be different. These results assume no interaction between cytoplasmic effects and nuclear additive genetic effects. If the interaction is linear with additive genetic effects and is known, then the method of this

paper can be extended to consider the interactions.

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REFERENCES

- 1 Anderson, S., A. T. Bankier, B. G. Barrell, M.H.L. deBruijn, A. R. Coulson, J. Drouin, I. C. Eperon, D. P. Nierlich, B. A. Roe, F. Sanger, P. H. Schreier, A.J.H. Smith, R. Staden, and I. G. Young. 1982. Complete sequence of human and bovine mitochondrial DNA. Page 5 in *Mitochondrial genes*. P. Slonimski, P. Borst, and G. Attarci, ed. Cold Spring Harbor Laboratory.
- 2 Bell, B. R., B. T. McDaniel and O. W. Robison. 1985. Effects of cytoplasmic inheritance on production traits of dairy cattle. *J. Dairy Sci.* 68: 2038.
- 3 Bosemark, N. O. 1981. The use of cytoplasmic inheritance in plant breeding. *Acta Agric. Scand.* 23(Suppl.):71.
- 4 Huizinga, H. A., S. Korver, B. T. McDaniel, and R. D. Politiek. 1986. Maternal effects due to cytoplasmic inheritance in dairy cattle. Influence on milk production and reproduction traits. *Livest. Prod. Sci.* 15:11.
- 5 Kennedy, B. W. 1986. A further look at recent evidence for cytoplasmic inheritance of production traits in dairy cattle. *J. Dairy Sci.* 69:3100.
- 6 Powell, R. L., H. D. Norman, and R. M. Elliot. 1981. Accuracy of genetic indexes of cows from adding relatives. *J. Dairy Sci.* 64:838.
- 7 Reed, P. D., and L. D. Van Vleck. 1987. Lack of evidence of cytoplasmic inheritance in milk production traits of dairy cattle. *J. Dairy Sci.* 70:837.
- 8 Robison, O. W., B. T. McDaniel, and E. J. Rincon. 1981. Estimation of direct and maternal additive and heterotic effects from crossbreeding experiments in animals. *J. Anim. Sci.* 52:44.
- 9 Seykora, A. J., and B. T. McDaniel. 1983. Heritabilities and correlations of lactation yields and fertility in Holsteins. *J. Dairy Sci.* 66:1486.
- 10 Van Vleck, L. D., and G. E. Bradford. 1965. Comparison of heritability estimates from daughter-dam regression and paternal half-sib correlations. *J. Dairy Sci.* 48:1372.
- 11 Van Vleck, L. D., and G. E. Bradford. 1966. Genetic and maternal influences on the first three lactations of Holstein cows. *J. Dairy Sci.* 49:45.

APPENDIX

Calculation of Correlated Response When Incorrect Heritability Used for Selection of Bulls from Daughter Records

$$\begin{aligned}\Delta G_b &= (\sigma_{G_b, I_b^*} / \sigma_{I_b^*}^2) (\sigma_{I_b^*}) (i) \\ &= (\sigma_{G_b, I_b^*} / \sigma_{I_b^*}) (i)\end{aligned}$$

where σ_{G_b, I_b^*} is covariance of additive genetic value of bull and index from his progeny average obtained using incorrect heritability. This covariance has expected value:

$$b^* (.5) h^2 \sigma_x^2$$

where b^* is biased weight for progeny average and .5 is relationship of bull with his progeny; $\sigma_{I_b^*}^2$ is variance of inaccurate index based on bull's progeny with an expected value of:

$$b^* \sigma_x^2 [1 + (p - 1)h^2/4] / p$$

Calculation of Selection Index Weights to Predict a Cow's Additive Genetic Value from her Record and the Average of p Paternal Half-Sisters

The selection index equations can be written as:

$$\begin{aligned}\sigma_x^2 b_c + .25h^2 \sigma_x^2 b_s &= h^2 \sigma_x^2 \\ .25h^2 \sigma_x^2 b_c + \sigma_x^2 [(1 + (p - 1)h^2/4)/p] b_s &= .25h^2 \sigma_x^2\end{aligned}$$

If cytoplasmic effects bias the estimate of heritability, then incorrect weights are due to use of h_*^2 rather than h^2 in the selection index equations.

Calculation of Correlated Genetic Selection Differential When Incorrect Heritability (h_*^2) is Used to Determine the Index Weights

$$\Delta G_c = (\sigma_{G_c, I_c^*} / \sigma_{I_c^*}) (i)$$

where σ_{G_c, I_c^*} is covariance of true genetic value and incorrect index with an expected value of $b_c^* (h^2 \sigma_x^2) + b_s^* (.25) (h^2 \sigma_x^2)$.

$\sigma_{I_c^*}^2$ = variance of the index, which has expected value:

$$\begin{aligned}E(b_c^* X_c + b_s^* X_s)^2 &= \\ E(b_c^2 \sigma_x^2 X_c^2 + b_s^2 \sigma_x^2 X_s^2 + 2b_c^* b_s^* (\sigma_{X_c, X_s}))\end{aligned}$$

which equals:

$$\begin{aligned}b_c^2 \sigma_x^2 + b_s^2 \sigma_x^2 [(1 + (p - 1)h^2/4)/p] \\ + 2(.25) b_c^* b_s^* h^2 \sigma_x^2\end{aligned}$$

Calculation of Index to Predict Additive Genetic Value Plus Cytoplasmic Effect for a Heifer from Her Dam's Record and Average of p of Her Paternal Half-Sisters

The index weights are estimated from:

$$\sigma_x^2 b_d = .5h^2 \sigma_x^2 + \sigma_t^2$$

$$\sigma_x^2 b_s [(1 + (p - 1)h^2/4)/p] = .25h^2 \sigma_x^2$$

where h^2 is correct heritability and σ_t^2 is cytoplasmic variance.

Expected Genetic Selection Differential for Additive Genetic Value Plus Cytoplasmic Effects when Selection is for Additive Genetic Value Plus Cytoplasmic Effects

$$\Delta G = (\sigma_{G,I}/\sigma_I)(i)$$

which except for i equals.

$$\frac{(.5b_d h^2 \sigma_x^2 + .25b_s h^2 \sigma_x^2 + b_d \sigma_t^2)}{\{b_d^2 \sigma_x^2 + b_s^2 \sigma_x^2 [(1 + (p - 1)h^2/4)/p]\}^{.5}}$$

Calculation of Expected Additive Genetic Selection Differential when Selection of Heifers is for Additive Genetic Plus Cytoplasmic Effects

$$\Delta DD_g = (\sigma_{G_g,I}/\sigma_I)(i)$$

where $\sigma_{G_g,I}$ = covariance of nuclear additive genetic effects with index, with expected value:

$$.5b_d h^2 \sigma_x^2 + .25b_s h^2 \sigma_x^2$$

and σ_I^2 = variance of index that has expected value:

$$b_d^2 \sigma_x^2 + b_s^2 \sigma_x^2 [(1 + (p - 1)h^2/4)/p]$$

Calculation of Expected Selection Differential for Cytoplasmic Effects when Selection of Heifers is for Additive Genetic Plus Cytoplasmic Effects

$$\Delta DD_t = (\sigma_{G_t,I}/\sigma_I^2)(\sigma_I)(i)$$

where $\sigma_{G_t,I}$ = covariance of cytoplasmic genes with index, with an expected value of $b_d \sigma_t^2$.