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Genetic and Economic Implications of Fetal Effects on the Dam

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ABSTRACT

The genetic model for fetal effect on production of the dam is described, and studies on genetic and economic implications are reviewed. The effect on production from the sire of the cow has 1.58 to 3.02 times as much economic value as the effect from the sire of the fetus. The use of mate records in evaluating a sire in addition to daughter records could increase economic gain from selection by 1 to 2% depending on the variation from sire of fetus. Mate records alone do not appear valuable for sire selection. About 1% of the variation in milk yield appears to be due to the effect of sire of fetus as indicated by a summary of various estimates and from consideration of the data and methods used to obtain the estimates. The correlation between effects of sire of fetus and sire of cow appears to be nearly zero. A method of joint evaluation of bulls as sires of cows or as sires of fetuses is described.

INTRODUCTION

Skjervold and Fimland (16) reported a measurable effect of the sire of the fetus on subsequent production of the sire's mates for a substantial set of data. Some readers' interpretations were that the sire of the fetus accounted for 10% of the variation in subsequent milk production of the mother when, in fact, about 1% was associated with the sire of the fetus. The confusion resulted from the correlation of .10 between the sire of the fetus and production of the mother and probably contributed to the considerable interest in studying effects from sire of the fetus. Skjervold and Fimland (16) stated that work by Tucker (19) had led to their analyses. The physiological basis and evidence for such an effect are reviewed by others (2, 4, 18) and will not be discussed here.

The first report of data from the United States by Adkinson et al. (1) indicated sire of the fetus accounted for 8 to 10% of the variance of milk production. Data sets (1) of all lactation records were not as likely to have service sires randomly distributed across herds and sires of cows as the data set of first lactation records used by Skjervold and Fimland (16). Results from other studies have been within the range of the two original papers and will be discussed in a later section.

Skjervold and Fimland (16) suggested that such an effect may require altering methods of selection of dairy sires. The two most obvious changes are: 1) use of production of the mates for early preliminary proofs of the bull, and 2) deliberate selection of bulls to increase production of their mates. Thus, there are essentially three genetic and economic questions that need to be answered. All require development of a model that takes into account interrelationships between direct and fetal effects of various relatives in dairy cattle selection — primarily sire of the cow, sire of the fetus, the cow that is the mother of the fetus and mate of the sire of fetus, and fetus. The questions are: 1) what are the parameters for variances from fetal effects and for covariances between fetal and direct effects, 2) what is the economic value of increased production from genetic fetal effects relative to that from direct genetic effects, and 3) what are the expected responses in genetic fetal and direct effects from selection by mates' records, progeny records, or both? The answers to those questions to a great extent will dictate whether and how current sire evaluation procedures should be modified. The first question will be discussed last since a number of diverse estimates are now available.

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THE MODEL

The genetic model is an example of an embedded trait – the phenotype of one trait is included in the measurement of another trait, which will be called the direct trait (23, 24). The embedded trait may have a genetic component but is an environmental effect for the measured direct trait. In fact, the model discussed by Van Vleck (20) for fetal effects is a special case of such models proposed by Willham (24) that usually have been applied to maternal effects.

The model, ignoring all other fixed and random effects, is

$$P_x = g_x + f_w + e_x + e_w \qquad [1]$$

for a record on animal x initiated by the birth of fetus w. In the usual model $P = G + E$, G is the direct genetic effect of x for production, g_x, and E contains f_w, the effect of the fetal genes of w for production of x, and e_w, the fetal environmental effects as well as e_x, the other environmental effects associated with the record. Figure 1 diagrams these effects for animal x that carried fetus w and for animal y that carried fetus z. For sire evaluation, three terms in Figure 1 will be of interest: g_{x_s} and f_{x_s}, the direct and fetal genetic effects of the sire of the cow making a record, and f_{w_s}, the fetal genetic effect of the mate of the cow that is the sire of the fetus that affects the record of the cow.

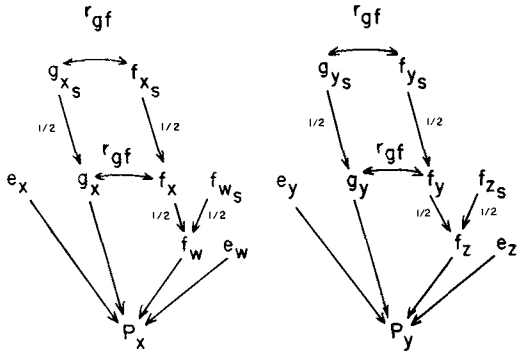

Figure 1. Diagram of direct genetic and environmental effects (g_x and e_x) and fetal genetic and environmental effects (f_w and e_w) on the phenotypic record of animal, x, carrying fetus, w. x_s is the sire of x, w_s is the sire of the fetus, and, of course, x is the dam of the fetus. A similar diagram is given for any potential relative, y, carrying fetus, z. Adapted from (20).

The models for records on x and y can be used to determine the genetic contributions to the covariance between any pair of relatives x and y having fetuses w and z (20, 24). If only additive direct and fetal genetic effects are considered, the genetic parts of the covariance between P_x and P_y can be written as

$$\text{Cov}(g_x + f_w, g_y + f_z) = a_{xy}\sigma_g^2 + a_{wz}\sigma_f^2 + (a_{xz} + a_{yw})\sigma_{gf}$$

where the a's are additive (numerator) relationships, σ_g^2 and σ_f^2 are additive genetic variances for direct and fetal effects, and σ_{gf} is the corresponding additive genetic covariance. Table 1 gives the make-up of the covariances between various relatives. The important point is that in a sire evaluation model that contains effects of sire of cow and sire of fetus (equation [2]), variances of those effects are the same as the covariances between paternal sibs having different mates ($\sigma_s^2 = \sigma_g^2/4 + \sigma_f^2/16 + \sigma_{gf}/4$) and between groups of unrelated cows that carried fetuses by the same sire ($\sigma_t^2 = \sigma_f^2/4$).

$$P_{ijk} = s_i + t_j + r_{ijk} \qquad [2]$$

where s_i is the effect of the sire of the cow, t_j is the effect of the sire of the fetus, and r_{ijk} is the residual effect for the record of the kth daughter of the ith sire having been mated to the jth bull. What is important and apparent from the variance components, the diagram, and the necessary correspondence between equations [1] and [2] is that $s_i = g_i/2 + f_i/4$, and $t_j = f_j/2$. Thus, selection as now for s_i is actually selection for one-fourth of the fetal genetic effect of the sire as well as the expected one-half of the direct genetic effect of the sire since the sire of the cow is also the maternal grandsire of the fetus. The implication of this confounding will become apparent in discussion of responses expected from selection. Next, however, the economic values of direct and fetal genetic effects will be discussed.

ECONOMIC VALUE

An often difficult problem in selection for more than one trait is assignment of relative

TABLE 1. Coefficients of additive genetic variances for direct effects, σ_g^2, for fetal effects, σ_f^2, and of additive genetic covariance between direct and fetal effects, σ_{gf}, for the covariance between various relatives and combinations of sires of fetuses.[a]

Animals with records	Sire of fetus	Coefficient of σ_g^2	Coefficient of σ_f^2	Coefficient of σ_{gf}
Daughter-dam	Daughter not from service sire of dam	1/2	1/8	1/2
Daughter-dam	Daughter from service sire of dam	1/2	1/2	5/4
Full sibs	Different	1/2	1/8	1/2
Full sibs	Same	1/2	3/8	1/2
Paternal or maternal sibs	Different	1/4	1/16	1/4
Paternal or maternal sibs	Same	1/4	5/16	1/4
Maternal sibs	Sire of x is service sire of y	1/4	3/16	1/2
Unrelated	Same	0	1/4	0

[a]These covariances also may include other more likely components due to effects such as direct dominance and maternal additive. Adapted from (20).

economic values to the traits. Such assignment in many cases is arbitrary. For the fetal trait embedded in the phenotype of another trait, assignment of economic values is less arbitrary since there is only one marketable trait which is the result of both direct and fetal effects. In fact, the first impression would be that both the direct and fetal effects have equal value. That impression is true only at the market and not necessarily at the time of selection of a sire.

The reason economic values may be different at selection for direct and fetal effects is the time between mating and when the effects are marketed. The fetal effect can be expressed in the mate either during gestation of the fetus or more likely immediately after the birth of the calf — a period of no more than 9 mo from mating. However, the direct effect does not become expressed until the calf, a female, begins to produce about 3 yr later. In addition, there is about twice as great a chance the fetal effect will be expressed, since expression of the direct effect of the sire through the calf requires the calf be a heifer, be alive, and survive to freshen. The direct effect, however, will be expressed in each of the heifer's lactations. Chances of survival, probability of descendants production, discount rate, and predicted investment period all need to be considered.

The procedure of Everett (5), developed for calculating the expected discounted return for a fresh heifer, can be adapted to determine the relative economic value of direct and fetal effects (21), which accounts for gene flow, age adjusted production, and the factors listed above. Whether the fetal effect influences more than the lactation initiated by the birth of the calf or also influences the lactation the fetus is carried also will affect relative economic values. If only production in the subsequent lactation is affected, then Table 2 gives the relative economic values for several discount rates and investment periods. The economic values are weights to be given to the usual estimate of the effect of sire of cow, which includes a

TABLE 2. Ratio of economic weight for the usual sire of cow effect ($g/2 + f/4$) to the weight for the fetal sire effect ($f/2$) for five discount rates and four investment periods.

Years in investment period	Discount rate .06	.08	.10	.12	.14
5	1.05	1.00	.94	.89	.84
10	2.24	2.04	1.87	1.71	1.58
15	2.77	2.47	2.21	1.99	1.81
20	3.02	2.65	2.34	2.09	1.88

TABLE 3. Expected response in selection of sires for direct and fetal genetic effects from records of 40 daughters and 200 mates of the sire for equal economic weight for direct and fetal genetic effects.[a]

Genetic Variance			Using daughter and mate averages		Using daughter averages only		Using mate averages only	
g	f	Corr'n	Δg	Δf	Δg	Δf	Δg	Δf
.24	.02	.3	.41	.06	.42	.05	.10	.10
		.0	.40	.02	.41	.02	.00	.10
		−.3	.40	−.01	.41	−.02	−.10	.10
.24	.04	.3	.40	.11	.42	.08	.12	.16
		.0	.39	.07	.41	.03	.00	.16
		−.3	.38	.01	.40	−.02	−.12	.16
.24	.08	.3	.38	.19	.42	.13	.13	.25
		.0	.36	.14	.40	.07	.00	.25
		−.3	.34	.07	.39	.00	−.13	.25
.24	.16	.3	.36	.31	.41	.21	.14	.38
		.0	.31	.26	.39	.13	.00	.38
		−.3	.26	.20	.38	.04	−.14	.38

[a]To obtain absolute rather than relative expected response multiply by product of selection intensity factor and phenotypic standard deviation.

quarter of a fetal genetic effect and to the estimate of the effect of sire of fetus.

Except for a short investment period when direct genetic effects would not have time to be expressed, weights for the effect of sire of cow are from 1.58 to 3.02 times those for the effect of sire of fetus. These would be the weights to apply in practice. From a technical point of view, these ratios ignore the contribution of the genetic fetal portion of the effect of sire of cow so that the economic value for the fetal effect is larger than shown in Table 2. If the components are separated, the relative weights are about 1:1 for the 10% discount rate and an investment of 10 yr. In any case, the fetal effect, in most situations, has more relative economic weight than any trait of the dairy cow other than milk yield. The final importance of the effect, however, also depends on the relative variances of direct and fetal effects as well as in the expected responses of the two components to selection.

EXPECTED RESPONSES TO SELECTION

Both Skjervold and Fimland (16) and Adkinson et al. (1) suggested that records of mates may be useful in sire selection either for early proving of bulls on their mates' subsequent production or for use in improving production of their mates. Selection index theory was applied by Van Vleck (22) to calculate expected responses in the direct and fetal genetic effects for both cow and bull selection. Only bull selection will be discussed here. The example chosen assumed each bull would have 200 mates and 40 daughters with records. Several heritabilities of direct and fetal effects were used in connection with three genetic correlations. Three sets of economic values also were used, but only equal weighting will be presented here, which corresponds to the ratio for 10% and 10 yr. Table 3 lists the relative expected responses in direct and fetal genetic effects for heritability of the direct component of .24.

The striking feature of Table 3 is how little extra total economic response ($\Delta g + \Delta f$) can be expected from using mate records in addition to daughter records. The potential, however, slightly increases when a larger portion of the variation in production is from fetal genetic effects. As expected, more of the expected total response consists of fetal genetic effect when records of mates are used in addition to daughter records.

Using mate records as a preliminary proof

for a young sire does not appear desirable as shown on the right side of Table 3. The total response depends on the genetic correlation between direct and fetal effects. With a positive correlation of .30 and a heritability of direct effects of .24, the total expected response per generation would be from about one-half to two-thirds that from daughter records alone for σ_f^2 = .04 and .08. Only with a reasonably high positive genetic correlation would mate records seem to be useful as a preliminary production proof. As the fraction of variance of production records accounted for by fetal genetic effects increases, the value of mate records also increases. The importance also depends, as with any multiple trait selection procedure, on good estimates of the genetic covariance between traits, which are often difficult to obtain. The genetic variance of fetal effects and covariance between direct and fetal genetic effects are critical in determining the genetic importance of the fetal effect.

ESTIMATES OF PARAMETERS

Evidence for the component of variance in milk production from genetic fetal effects is contradictory. This component has been estimated from the component of variance for sire of fetus, which as shown earlier would be one-fourth of the fetal genetic variance. The results for several studies are summarized in Table 4.

The preponderance of evidence suggests that the sire of fetus accounts for no more than 1% of the variation in milk yield so that the total fetal genetic component may account for 4% of the variability. Estimates that are larger generally have come from analyses of data in which nonrandom association of the sire of fetus with herds or daughters of certain sires is possible and when the method of analysis does not account for such associations. The random mating implicit in the data from Norway and New Zealand would preclude such associations. The US data of Adkinson et al. (1) and that of Johnson and Van Vleck (7) are likely to have been afflicted with such nonrandomness. The estimates of Adkinson et al. (1), in particular, from a random model that does not account for association between herds and service sires or service sires and sires of cows, are much too large to be biologically possible. Multiplying by four suggests 40% of the variation in production of a cow is accounted for by her fetus. Such large proportions indicate the possibility of confounding or association as a reason for inflating the estimates. The succession of estimates by Johnson and Van Vleck (6, 7) illustrate the point. The more likely the method of estimation is to account for nonrandom associations or the more random the data, the smaller the estimate. The estimate of .8% from the Method 3 procedure as compared to 2.7% from Method 1 is particularly revealing. The Method 3 procedure treated all other effects in the model as fixed except for the component being estimated, which should account for any nonrandom association of sire of fetus with either effects of herd-year-season or sire of cow. An even smaller estimate of .001% was obtained from a Method 3 analysis of over 7,000 first lactation records in which random mating of service sire would be expected (unpublished). Thus, the estimates of Skjervold and Fimland (16) and Wickham (unpublished) from random data and the Method 3 analyses, which account for the nonrandomness, agree. When the Florida Jersey data (1, 14) were reanalyzed with effects of sire of cow considered fixed to eliminate any effect from nonrandom mating of service sires, the estimate of the variance from effect of sire of fetus dropped to 1.1% (Wilcox, 1979, personal communication), which tends to confirm the tentative conclusion that about 1% of the variation in production is accounted for by genetic effects of the sire of the fetus.

ESTIMATION OF GENETIC COVARIANCES BETWEEN EFFECTS OF SIRE OF COW AND SIRE OF FETUS

Estimates of the covariance between the direct and fetal genetic effects are even more difficult to interpret. Skjervold and Fimland (16) and Adkinson et al. (1) reported correlations between effects of sire of cow and sire of fetus of about zero. Taylor et al. (17) used a set of data obtained as a by-product of an efficiency of production experiment and found large negative correlations between effects of sire of cow and sire of fetus of −.32 to −.52. Conversion of these estimates to correlations between direct and fetal effects is difficult because some of the correlations involved proofs and others simple averages.

Johnson and Van Vleck (8, unpublished) attempted to estimate covariances between

TABLE 4. Component of variance from effects of sire of fetus.

Study	Data	Method of estimation	Percentage of phenotypic variance
Skjervold and Fimland (16)	4 years 48,852 first lactations 256 to 357 test sires/year Norwegian Red	Method 1	1.0
Adkinson et al. (1)	7 years 27,200 all lactations 2080 numerically identified sires Holstein	Method 1	8.2
	7 years 3,731 all lactations 432 numerically identified sires Jersey	Method 1	11.8
Wickham (unpublished)	1 year 3,364 ⩾ second lactations 15 AI sires Holstein	MINQUE	.9
	1 year 4,223 ⩾ second lactations 32 AI sires Jersey	MINQUE	1.1
Johnson and Van Vleck (6, 7, unpublished)	8 years 64,195 second lactations 4,110 registered sires Holstein	Method 1	3.8
	8 years 50,199 second lactations 1,334 AI sires Holstein	Method 1	3.0
	8 years 10,519 second lactations 761 connected AI sires Holstein	Method 1	2.7
	Same	Method 3	.8
	3 years 7,257 first lactations 281 connected AI sires Holstein	Method 3	.001

effects of sire of cow and sire of fetus from various sources and then to approximate the genetic correlation between direct and fetal effects. From a correlation of .01 computed between Northeast AI Sire Comparisons and estimates of second lactation effects of sire of fetus, an approximation was −.12 for the genetic correlation between direct and fetal effects. For first lactations, the variance component for sire of fetus (.001%) was too small

to obtain reasonable estimates of the genetic correlation. If, however, an arbitrary 1% for the variance component associated with service sire was used, an estimate of the genetic correlation was −.13 from solutions for effects of sire of cow and sire of fetus on bulls with 12 or more daughters and mates. A similar procedure using estimates in the literature indicates the genetic correlation between direct and fetal effects is probably small and, perhaps, slightly negative. The genetic covariance between direct and fetal effects as well as their genetic variances are needed to evaluate sires for direct and fetal effects.

JOINT EVALUATION OF SIRES OF COWS AND SIRES OF FETUSES

The evaluation procedure is a combination of that for a single trait and for multiple traits (11), since only the direct trait is measured and the other is embedded. As developed by Johnson and Van Vleck (unpublished), the procedure is as follows. The model in matrix form is

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Z}_1\mathbf{s} + \mathbf{Z}_2\mathbf{t} + \mathbf{e},$$

where $\mathbf{y}$ is the vector of observations, β is a vector of fixed effects such as herd-year-season and genetic groups, $\mathbf{X}$ is a matrix of zeros and ones describing which fixed effects are included in each observation, $\mathbf{s}$ is a vector of effects of sires of cows, $\mathbf{Z}_1$ is a matrix of zeroes and ones describing the sires of the cows, $\mathbf{t}$ is a vector of effects of sires of fetuses, $\mathbf{Z}_2$ is a matrix of zeroes and ones describing the sires of the fetuses which affect the records, and $\mathbf{e}$ is a vector of residual effects. Except for the fixed effects, the equation for the model is the same as that described in equation [2]. For simplicity all sires can be included in $\mathbf{s}$ and all in $\mathbf{t}$.

$$E[\mathbf{y}] = \mathbf{X}\beta$$

$$\text{Var}\begin{bmatrix}\mathbf{s}\\ \mathbf{t}\\ \mathbf{e}\end{bmatrix} = \mathbf{V} = \begin{bmatrix}\mathbf{C}_{ss} & \mathbf{C}_{st} & \mathbf{O}\\ \mathbf{C}'_{st} & \mathbf{C}_{tt} & \mathbf{O}\\ \mathbf{O} & \mathbf{O} & \mathbf{R}\end{bmatrix},$$

where $\mathbf{C}_{ss} = \sigma_s^2\mathbf{A}$, $\mathbf{C}_{st} = \sigma_{st}\mathbf{A}$, $\mathbf{C}_{tt} = \sigma_t^2\mathbf{A}$, and $\mathbf{R} = \sigma_e^2\mathbf{I}$, $\mathbf{A}$ is the matrix of numerator (additive) relationships among the sires, $\mathbf{I}$ is the identity matrix, σ_s^2 is the variance of effects of sire of cow, σ_t^2 is the variance of effects of sire of fetus, σ_{st} is the covariance between the effect of a sire on his daughters and the effect through his fetus on his mates, and σ_e^2 is the variance of residual effects. Let

$$\sigma_e^2\mathbf{V}^{-1} = \begin{bmatrix}\mathbf{W}_{ss} & \mathbf{W}_{st} & \mathbf{O}\\ \mathbf{W}'_{st} & \mathbf{W}_{tt} & \mathbf{O}\\ \mathbf{O} & \mathbf{O} & \mathbf{I}\end{bmatrix}$$

The mixed model equations are

$$\begin{bmatrix}\mathbf{X}'\mathbf{X} & \mathbf{X}'\mathbf{Z}_1 & \mathbf{X}'\mathbf{Z}_2\\ \mathbf{Z}'_1\mathbf{X} & \mathbf{Z}'_1\mathbf{Z}_1+\mathbf{W}_{ss} & \mathbf{Z}'_1\mathbf{Z}_2+\mathbf{W}_{st}\\ \mathbf{Z}'_2\mathbf{X} & \mathbf{Z}'_2\mathbf{Z}_1+\mathbf{W}'_{st} & \mathbf{Z}'_2\mathbf{Z}_2+\mathbf{W}_{tt}\end{bmatrix}\begin{bmatrix}\hat{\beta}\\ \hat{\mathbf{s}}\\ \hat{\mathbf{t}}\end{bmatrix} = \begin{bmatrix}\mathbf{X}'\mathbf{y}\\ \mathbf{Z}'_1\mathbf{y}\\ \mathbf{Z}'_2\mathbf{y}\end{bmatrix}$$

Some columns of $\mathbf{Z}_1$ may contain all zeroes since some sires may not have daughters with production (10). Similarly some columns of $\mathbf{Z}_2$ may be null. Let

$$\sigma_e^2\begin{bmatrix}\sigma_s^2 & \sigma_{st}\\ \sigma_{st} & \sigma_t^2\end{bmatrix}^{-1} = \begin{bmatrix}v_{11} & v_{12}\\ v_{12} & v_{22}\end{bmatrix}$$

Then $\mathbf{W}_{ss} = v_{11}\mathbf{A}^{-1}$, $\mathbf{W}_{st} = v_{12}\mathbf{A}^{-1}$, and $\mathbf{W}_{tt} = v_{22}\mathbf{A}^{-1}$. If β is made up of herd-year effects and group effects for sires of cows and fetuses, the usual procedure would be to absorb the herd-year-season equations into the sire equations. If effects of sire groups are included in the model, the group equations can be made up from the sire equations after absorption, and finally $\mathbf{W}_{ss}$, $\mathbf{W}_{st}$, and $\mathbf{W}_{tt}$ would be added as indicated. One constraint would be required on the group equations for sires of cows, and one constraint also would be needed for the group equations for sires of fetuses.

Johnson and Van Vleck (unpublished) used models in which grouping was not included and compared solutions for sire and service sire effects from a model which jointly estimated effects with solutions from models in which the other type of sire effect was ignored. The data included 7,257 first lactation records of daughters of 424 Holstein sires which had been mated to 281 sires of fetuses. The correlation between solutions for effects of sire of cow for the two methods was near unity (.999) for 305-day ME

milk production and nearly as high (.972) for effects of sire of fetus. The maximum change in evaluations of sire of cow was 13.3 kg and in evaluations of sire of fetus was 33.8 kg, which reflects genetic variances of the two traits. Thus, little improvement in evaluation of sires of cows would be expected by considering the sire of fetus.

CONCLUSIONS

Genetic and economic implications of the effect of sire of fetus do not seem important. Some new methodology, however, has been developed that may be applicable to other biological systems. Association between sire of fetus and other effects is apparent in the sets of records where random mating could not be imposed. The consequences of this nonrandomness for sire evaluation should be studied, and if important, methods for accounting for the nonrandomness should be developed.

Reports by physiologists, e.g., Bolander et al. (3), have indicated differences in circulating bovine placental lactogen (the implied cause of fetal effect) in dairy and beef cows that have been interpreted as correlated with milk production. Studies with litter-bearing animals have suggested a dosage effect of placental tissue, which is genetically the same as that of the fetus. Skjervold (15), in a cross fostering study with mice, found a positive relationship between number of fetuses and subsequent production. Hayden et al. (9) reported that hand-milked does bearing twins and triplets had 27% and 47% more production than mothers of single kids. Placental lactogen was correlated (.23 and .69) with total weight of the fetuses and with subsequent milk yield. These results suggest that if there is an effect of sire of fetus, it may be associated with mass of placental tissue through differences in calf size. Estimates of production of Holstein heifers bred to bulls of different breeds seem to follow this pattern, although birth weights were not obtained (unpublished). Florida studies (Wilcox, 1979, personal communication) indicate a positive curvilinear relationship between calf birth weight and milk yield for both Holsteins and Jerseys. The implication is that larger calves and longer gestation lengths induce more subsequent production. Yet selecting for larger calves is clearly not desirable because of potential losses due to calving difficulty (12).

Although genetic implications seem relatively unimportant, the possibility of a dosage effect indicates that physiological management to increase placental lactogen may have the potential to increase mammary growth and production.

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