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Multiple trait selection for maternal productivity in beef cattle

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Summary

The aim of this study was to develop a multiple trait genetic evaluation and selection tool for maternal productivity in beef cattle, particularly in the Hereford breed. Component traits of the maternal productivity index (MPI) were chosen on the basis of their potential to contribute to consistently weaning heavy calves over a sustained herd life, while controlling cow maintenance costs. (Co)variance components were estimated with a multiple trait model including direct and maternal birth weight, direct and maternal weaning weight, weight of the cow at the time her calf is weaned and survival, defined as the ability of a female to produce at least three calves given she became a dam. Although direct and maternal birth weight were included in the (co)variance parameters model, these traits were not included in the index. Estimates of heritability were 0.19, 0.18, 0.50 and 0.07 for direct and maternal weaning weight, cow weight, and survival, respectively. The correlation between direct and maternal components of weaning weight was −0.42. The genetic correlation estimated between direct weaning weight and cow weight was 0.85, while a low genetic correlation of −0.17 was estimated between maternal weaning weight and cow weight. Survival had a near zero (−0.01) genetic correlation with maternal weaning weight, but negative genetic correlations with direct weaning weight (−0.52) and cow weight (−0.48). The MPI was constructed as a linear function of derived economic weights multiplied by estimated breeding values for the four component traits from the model. Estimated economic values were $3.00, $2.70, $−0.49 and $2.39 for direct and maternal weaning weight, cow weight, and survival (expressed as a percentage), respectively. Relative economic weights were 0.30, 0.26, 0.17 and 0.27 for direct and maternal weaning weight, cow weight, and survival, respectively. A simulation study indicated that positive genetic trend would be expected in all component traits although increases in cow weight would be moderate.

Zusammenfassung

Selektion auf multiple maternale Produktivitätsmerkmale in Fleischrindern

Das Ziel der Arbeit war die Entwicklung eines Evaluierungs- und Selektionssystems für ein zusammengesetztes Merkmal maternaler Produktivität in Fleischrindern, speziell in Hereford. Die verwendeten Einzelmerkmale des maternalen Produktivitätsindexes basieren auf ihrem potentiellen Nutzen für die Produktion schwerer Absetzer bei langer Nutzungsdauer und gleichzeitiger Minimierung der Erhaltungskosten. Es wurden (Ko-)varianzkomponenten innerhalb eines zusammengesetzten Modells geschätzt, das direktes und maternales Geburtsgewicht, direktes und maternales Absetzgewicht, Gewicht der Kuh zum Absetzzeitpunkt und die Nutzungsdauer, welche als die Fähigkeit einer Kuh mindestens drei Kälber zu erzeugen definiert wurde, einbezieht. Obwohl direktes und maternales Geburtsgewicht als (Ko-)varianz Parameter berücksichtigt wurden, wurden diese Merkmale nicht mit in den Index einbezogen. Es wurden Schätzwerte für die Heritabilitäten von jeweils 0,19, 0,18, 0,50 und 0,07 für das direkte und maternale Absetzgewicht, Gewicht der Kuh und Nutzungsdauer, geschätzt. Die Korrelation zwischen direkten und maternalen Komponenten des Absetzgewichtes betrugen –0,42. Die genetische Korrelation zwischen dem direkten Absetzgewicht und dem Gewicht der Kuh betrug 0,85, während eine geringe Korrelation von –0,17 zwischen maternalem Absetzgewicht und Kuhgewicht geschätzt wurde. Die Nutzungsdauer zeigte keine Korrelation mit dem maternalen Absetzgewicht (−0,01), aber es wurden negative Korrelationen mit dem direkten Absetzgewicht (−0,52) und dem Gewicht der Kuh (−0,48) festgestellt. Der maternale Produktivitätsindex wurde als lineare Funktion der abgeleiteten ökonomischen Gewichte, multipliziert

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mit den geschätzten Zuchtwerten der vier Einzelmerkmale, konstruiert. Die geschätzten ökonomischen Werte waren 3,00$, 2,70$, 0,49$ und 2,39$, jeweils für direktes und maternales Absetztgewicht, Gewicht der Kuh und Nutzungsdauer (ausgedrückt als Prozentsatz). Die relativen ökonomischen Gewichtungen betrugen jeweils 0,30, 0,26, 0,17 und 0,27 für direktes und maternales Absetzgewicht, Gewicht der Kuh und Nutzungsdauer. Eine Simulationsstudie zeigt, dass ein positiver genetischer Trend in allen berücksichtigten Merkmalen zu erwarten ist, wobei die Zunahme des Gewichtes der Kühe mäßig bleibt.

Introduction

Maternal productivity of cows often refers to measurement of outputs in the beef production enterprise. The important output in a cow–calf system is the sale of weaned calves, but income is also derived from the salvage value of cull cows. Maternal productivity should also consider inputs, and as such is a composite trait influenced by several underlying cost components, including fertility, survival and mature size.

The Hereford breed has long been promoted as a maternal breed. Gallivan et al. (2000) reported that the Hereford cow was of average or better fertility, was moderate in size and milk production, had the ability to maintain body condition and was relatively efficient. It is generally accepted that the number and weights of calves weaned during the herd life of a cow determines her value in a cow–calf enterprise after adjustment for costs. Deland and Newman (1991) argued that lifetime productivity of cows is an important consideration in cow–calf production because the costs of maintaining breeding animals per progeny produced decreased with increasing numbers of progeny. Therefore, a profitable cow is one that remains in production beyond breakeven and into profitable parities. An organized genetic improvement programme for maternal ability requires definition of a breeding objective for use in selection of replacements.

The objectives of this study were: (i) to determine the key component traits affecting maternal productivity; (ii) estimate genetic and phenotypic parameters among the component traits; (iii) develop a multiple trait selection index procedure for maternal productivity and (iv) predict correlated genetic change in individual component traits as a result of selection for the maternal productivity index (MPI).

Materials and Methods

Data

Historical data on 3664 calves born to 186 sires and 886 dams during a 21-year (1964–1985) study conducted at the Onefour Research Substation near Manyberries, Alberta, were used to develop a multiple trait selection index for maternal productivity (MPI) in the Hereford breed. A description of the management of the experimental herds used for these analyses was given by Bailey et al. (1991).

Traits

Component traits were included in the MPI on the basis of their potential to contribute to high weaning weight with persistent production over a sustained herd life while considering costs. The MPI included direct (WWT_d) and maternal (WWT_m) weaning weight ($n = 3664$), cow weight at weaning (COWT, $n = 3609$) and the probability of having three or more calves given that a cow became a dam ($SURV_3$, $n = 751$). The definition of $SURV_3$ was derived from and similar to that of Snelling et al. (1995). Cow–calf producers derive a majority of their income from the sale of weaned calves, and both direct and maternal genetic effects on weaning weight were included in the MPI. To partially account for annual maintenance costs associated with raising a calf to weaning, COWT was included. The $SURV_3$ component was included in the MPI to account for reproductive consistency.

(Co)variance component and parameter estimation

Data used in these analyses came from an historical study designed to compare response to phenotypic selection for post-weaning gain on two post-weaning diets differing in energy level. Although only WWT_d, WWT_m, COWT and $SURV_3$ were included in the MPI, (co)variance components were estimated with a six-trait model that also included direct and maternal birth weight. For birth and weaning weights, the fixed effects portion of the model included diet, year of measurement, sex of calf and age of dam terms while the effect of sex was omitted in the model for COWT and $SURV_3$, which were sex-limited traits. In addition, the weaning weight model included age at weaning as a covariate.

An animal model was fit with derivative-free residual maximum likelihood (REML) procedures to estimate genetic components of (co)variance parameters (GRASER et al. 1987; BOLDMAN et al. 1995). In all cases, convergence was defined as the point where the variance of the simplex function was less than 10^{-9}. A full maternal model with permanent environmental effects was fit to weaning weight. In all analyses, at least three sets of (co)variance starting values were used to reduce the probability of local maxima solutions. Starting values for the multiple trait model were derived from univariate and bivariate model results.

Estimation of breeding values

Estimated breeding values (EBV) and estimates of correlations between true and index values were obtained for the four component traits using option four of the MTDFREML software (BOLDMAN et al. 1995). Estimates of genetic and residual (co)variance parameters from the multiple trait model were used to estimate heritabilities and genetic, phenotypic and environmental correlations. Sampling variances for heritability estimates were approximated using the formulae derived by FALCONER (1989).

Derivation of economic weights

The multiple trait model was based on weaning weight of calves, costs associated with the weight of the cow when her calf was weaned and the impact of genetic change in survival. The combined, or aggregate, genetic value (*T*) to be improved was then defined as:

$$T = v_1 BV_{WWT_d} + v_2 BV_{WWT_m} + v_3 BV_{COWT} + v_4 BV_{SURV_3}$$

where v_1, v_2, v_3 and v_4 represent net economic values derived independent of changes in other components. The MPI can then be defined as:

$$MPI = v_1 EBV_{WWT_d} + v_2 EBV_{WWT_m} + v_3 EBV_{COWT} + v_4 EBV_{SURV_3}$$

where EBV_i represents the estimated breeding value of the *i*th trait from a multiple trait analysis.

A gross value of \$3.00 kg^{-1} was used for WWT_d (ALBERTA AGRICULTURE, 1989). No reductions were included for extra maintenance requirements of cows because COWT was included in the model. Similarly, no adjustments were made for decreased fertility that may be associated with increased calf size because survival, whose main component is fertility, was included in the model.

The major contribution to the maternal component of weaning weight was assumed to be milk yield. Results from MILLER et al. (1999) for the effect of milk yield on gross margins (accounting for increased feed requirements) indicated that a net economic value of approximately 90% of the gross value for weaning weight would be appropriate, leading to a value of \$2.70 kg^{-1} for WWT_m.

The economic weight for COWT was based on the extra feed required by a heavier cow, reduced by the increased salvage value of that heavier cow. The estimated feed requirement for a 500 kg cow producing 5 kg day^{-1} milk is 12.3 kg day^{-1} (Alberta Agriculture 1989). This is approximately $[(12.3/500) \times 100]$ 2.46% of body weight. The feed associated with a 1 kg change in cow weight was therefore assumed to be 0.0246 kg day^{-1}. On an annual basis, this was (365×0.0246) 8.979 kg year^{-1}. At \$0.09 kg^{-1} (Alberta Agriculture 1989), the extra feed cost was \$0.81 kg^{-1} year^{-1}. The salvage value associated with cow weight was based on an estimated 25% replacement rate and a salvage value of \$1.28 kg^{-1} (Koots and Gibson 1998). Salvage revenue was then $(0.25 \times \$1.28)$ \$0.32 kg^{-1} year^{-1}. Net economic value was then (\$0.32 − \$0.81) \$−0.49 kg^{-1} year^{-1}.

The definition of survival used in this study was the probability that a female will have three or more calves given that she became a dam. An equivalence of survival to fertility was used to derive the relative economic weight of this component. Fertility rates of 81% for 2-year-old heifers and 90% for 3-year-old cows (Koots and Gibson 1998) resulted in the probability of having a third calf of $0.81 \times 0.90 = 0.729$. Increasing fertility by 1% gives a probability of 0.82×0.91, which is an increase of survival rate of 1.72% resulting from the increase of 1% in fertility. The value of a unit increase in survival was then estimated as 1.72 times that of one unit increase in fertility. Koots and Gibson (1998) using an economic model which also included cow weight, milk yield and growth rate estimated a value for cow fertility of \$14.72 per genetic SD. This economic value was assumed to be equivalent to $\$14.72 \times 1.72$, or \$25.30 per genetic SD of survival rate. With the estimated genetic SD reported here, the economic value for survival was then (\$25.30/10.6) 2.39% 2-39%$^{-1}$.

Combining EBV and corresponding economic values for each of the component traits into a linear function gives the index:

$$\text{MPI} = \$3.00\ \text{EBV}_{\text{WWT}_\text{d}} + \$2.70\ \text{EBV}_{\text{WWT}_\text{m}} - \$0.49\ \text{EBV}_{\text{COWT}} + \$2.39\ \text{EBV}_{\text{SURV}_3}$$

The relative importance of the four component traits was obtained by standardizing the derived economic weights by genetic SD as $v_i\sigma_{g(i)}$, where v_i and $\sigma_{g(i)}$ are the economic value and genetic SD of the i component trait, respectively.

Index simulation

A simulation approach was used to demonstrate the expected genetic change that would result from selection on the MPI and to show the impact of different amounts of data being available for its estimation. The simulation was based on selection of herd sires to improve aggregate breeding value for maternal productivity. The simulation included the possibilities of information on the sire's dam, the sire's progeny and grandprogeny for WWT, COWT and SURV_3 (WWT only for grandprogeny). Selection was assumed to be based on the MPI with economic values as described. A pedigree structure was assumed as shown in Fig. 1. The base simulation included information on 10 grandprogeny with records for weaning weight, 20 progeny with records for weaning weight, 10 progeny with records for cow weight, 10 progeny with records for SURV_3, and the dam of the sire with a record for weaning weight, cow weight and SURV_3, for a total of seven different sources of information across relatives. The expectations of (co)variances of observations and covariances of observations with genotype of sire were determined based on Van Vleck (1993).

Standard selection index approaches were used to calculate the accuracy of the index in evaluating the aggregate genotype and predictions of correlated changes in component traits. Variations in sources of information, amount of information and economic values were considered.

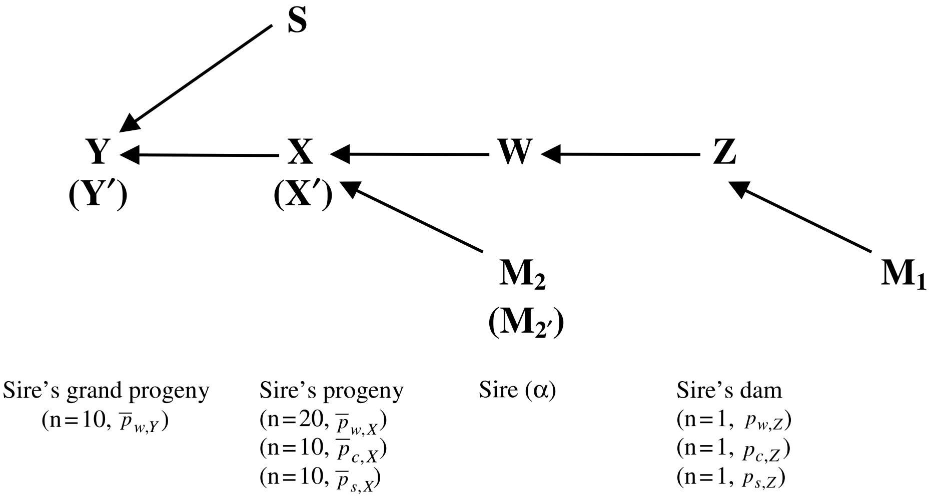

Fig. 1. Assumed pedigree and available records in the base simulation. W is the sire (α), Z is the sire's dam, M_1 is the sire's grand-dam, X are the sire's progeny produced by mating with unrelated dams (M_2), and Y are the sire's grand progeny produced by mating with unrelated sires (S). $M_{2'}$, X′ and Y′ denote direct ancestry. p or $\bar{p}$ are the single or average record values for the traits.

Results and discussion

Data summary. Table 1 contains a summary of the data used in this study. The average calf birth weight was 36 kg, average weaning weight, 177 kg and average cow weight at weaning was 496 kg. Survival, defined as the probability that a cow will produce three or more calves given that she became a dam was available on fewer animals and averaged 65% (on a percentage basis).

Variance components and genetic parameters. Estimates of genetic (co)variances and parameters are given in Table 2. Although not included in the final index, parameters for birth weight are given in addition to the four component traits of the MPI. For birth weight, estimates of direct and maternal heritability were 0.48 and 0.11, respectively, while estimates of direct and maternal heritability were 0.19 and 0.18 for weaning weight. The estimated direct heritability for weaning weight was slightly lower than the weighted mean value of 0.24, while the estimate for maternal heritability was equal to that reported by Koots et al. (1994a). The direct heritability estimate for survival was within the range of values reported by Snelling et al. (1995) for similarly defined survival traits.

In this study, the genetic correlation between direct and maternal weaning weight was −0.42 (Table 2). Koots et al. (1994b) summarized genetic correlation estimates published up to 1992 and reported an unweighted (weighted) average of −0.30 (−0.16) for the

Table 1. **Summary statistics for maternal productivity indicators included in the multiple trait model**

Component trait	*n*	Mean	SD
Birth weight (kg)	3664	36.2	4.7
Weaning weight (kg)	3664	177.4	27.9
Cow weight at weaning (kg)	3609	496.4	63.2
Survival (%[a])	751	64.7	47.8

[a]Survival defined as the probability of having three calves given that a female became a dam

Table 2. **Estimates of heritabilities, genetic (co)variances and genetic correlations among component traits**[a]

	BWT_d	BWT_m	WWT_d	WWT_m	COWT	$SURV_3$
h^{2b}	0.48 ± 0.02	0.11 ± 0.04	0.19 ± 0.04	0.18 ± 0.04	0.50 ± 0.07	0.07 ± 0.09
BWT_d (kg)	**8.4**	−0.09 ± 0.16	0.74 ± 0.02	−0.34 ± 0.09	0.67 ± 0.02	−0.82 ± 0.30
BWT_m (kg)	−0.4	**2.0**	0.09 ± 0.30	0.19 ± 0.27	−0.02 ± 0.27	0.41 ± 0.16
WWT_d (kg)	20.2	1.2	**88.5**	−0.42 ± 0.22	0.85 ± 0.02	−0.52 ± 0.56
WWT_m (kg)	−9.0	2.4	−3.6	**82.2**	−0.17 ± 0.15	−0.01 ± 0.34
COWT (kg)	64.7	−1.1	267.3	−52.0	**1120.5**	−0.48 ± 0.44
$SURV_3$ (%)	−24.0	6.0	−50.0	−1.0	−162.0	**113.0**

[a] BWT_d (WWT_d), direct birth (weaning) weight; BWT_m (WWT_m), maternal birth (weaning) weight; COWT cow weight at weaning (of her calf) and $SURV_3$, probability of having three or more calves given female became a dam. Genetic variances on the diagonal are in **bold**, genetic covariances below the diagonal, genetic correlations (± SE) above the diagonal

correlation of direct and maternal genetic effects for weaning weight. Van Vleck et al. (1996) reported estimates of genetic correlations between direct and maternal weaning weight of −0.46, −0.34, and −0.45 for calves born to 2, 3 and ≥ 4-year-old Hereford dams, respectively, in general agreement with the results of this study. Further, Dodenhoff et al. (1998) reported direct by maternal weaning weight genetic correlation estimates of −0.11 to −0.35 from selected and control lines of Hereford cattle using an animal model. DeMattos et al. (2000) reported direct by maternal genetic correlations of −0.42, −0.35 and −0.50, for Hereford populations in the United States, Canada and Uruguay, respectively.

The estimated genetic correlation between direct weaning weight and cow weight at weaning was 0.85, while the genetic correlation of cow weight at weaning with maternal weaning weight was low (−0.17). Koots et al. (1994b) reported an average estimate of 0.57 for the genetic correlation between direct weaning and mature cow weight. The genetic correlation between direct weaning weight and survival was −0.52 and that between maternal weaning weight and survival was near zero (−0.01). The genetic correlation between cow weight at weaning and survival was negative and moderately high (−0.48). Therefore, survival, as defined in this study, had uniformly negative genetic correlations with growth traits. Tanida et al. (1988) reported negative genetic correlations between longevity (survival from first calving to disposal) and weaning weight in the Hereford breed. Stewart and Martin (1981) also observed that the number of calves produced by a cow in her lifetime decreased with increasing mature weight in Angus and Milking Shorthorns. Consideration of cow size in voluntary culling decisions by producers is minor relative to reproductive soundness and conformation.

Table 3. **Estimates of phenotypic and residual (co)variances**[a] **among component traits**

	Birth weight	Weaning weight	Cow weight	Survival
$\sigma_P^{2\,b}$	17.5	468.2	2240.4	1501.3
Birth weight (kg)	**7.1**	7.3	2.8	3.0
x2592Weaning weight (kg)	27.6	**177.6**	−22.7	70.0
x2592Cow weight (kg)	34.8	−154.9	**394.2**	−48.0
Survival (%)	−2.0	2.0	−13.0	**1388.3**

[a] Residual variances on the diagonal are in **bold**, phenotypic covariances below the diagonal, residual covariances above the diagonal

[b] Phenotypic variance

Table 4. **Estimated phenotypic and residual correlations[a] among component traits**

Trait	Birth weight	Weaning weight	Cow weight	Survival
Birth weight (kg)		0.21 ± 0.08	0.05 ± 0.10	0.03 ± 0.11
Weaning weight (kg)	0.30		−0.09 ± 0.11	0.14 ± 0.10
Cow weight (kg)	0.18	−0.15		−0.07 ± 0.11
Survival (%)	−0.01	0.00	−0.01	

[a] Phenotypic correlations below the diagonal, residual correlations (± SE) above the diagonal

Estimates of phenotypic and residual (co)variances are reported in Table 3, while residual and phenotypic correlations are reported in Table 4. Among the traits used in the MPI, phenotypic and residual covariances and correlations were low ($r < 0.20$).

The estimated variance of the permanent environmental effects of dams, expressed as a proportion of phenotypic variance, was 0.01 for birth weight in this study, while the equivalent parameter for weaning weight was 0.33. The estimated correlation between permanent environmental effects on birth and weaning weights of offspring was 0.22.

Characteristics of the MPI. The MPI was constructed as a weighted linear combination of the multiple trait EBVs. There was a range from −\$96 to +\$89 for animals in the set of data analysed.

The actual and standardized weights for the EBVs are given in Table 5, along with the relative emphasis of individual component traits. From parameters and economic weights estimated here, the MPI will put 30% emphasis on WWT_d, 26% on WWT_m, 17% on COWT and 27% on $SURV_3$. The number of traits considered here and the limit on the scope of the selection programme to the production of a weaned calf make comparisons with studies considering carcass traits, such as MacNeil et al. (1994) and Koots and Gibson (1998), difficult. MacNeil et al. (1994) found relative economic values that were higher for female fertility than for direct or maternal weaning weight when considering weaning weight as the market endpoint. Cow weight had a negative economic value in their study and the relative value was approximately half that of direct and maternal weaning weight, similar to the current study. The study of Koots and Gibson (1998), which was the source of economic values for fertility in the current study, accounted for the population dynamics of the herd more completely than MacNeil et al. (1994), resulting in similar relative economic values for cow fertility and residual intake of mature cows.

Expected change in additive genetic value of component traits because of selection on the index. All component traits of the index would be expected to show positive genetic trend because of sire selection on the MPI for the information assumed

Table 5. **Derived economic weights and individual influence of component traits[a]**

Trait	Economic value v_i (\$)	Genetic SD (σ_g)	Standardised economic weight[b] (E)	Relative emphasis[c]
WWT_d (kg)	3.00	9.4	28.2	0.30
WWT_m (kg)	2.70	9.1	24.7	0.26
COWT (kg)	−0.49	33.5	16.4	0.17
$SURV_3$(%)	2.39	10.6	25.3	0.27

[a] WWT_d, direct weaning weight; WWT_m, maternal weaning weight, COWT, cow weight at weaning and $SURV_3$, probability of having three or more calves given a female became a dam (as a percentage)

[b] Standard economic weight, $E_i = v_i\sigma_{gi}$

[c] Relative influence on the index = $\left(E_i / \sum_{i=1}^{4} E\right)$

Table 6. **Accuracies and expected changes in additive genetic values of index component traits[a] as a result of sire selection**

	Base	No grand-progeny	Reduced survival information	Higher economic value for survival
Accuracy	0.51	0.36	0.47	0.48
Expected genetic change				
WWT_d (kg)	5.17	6.48	5.59	4.15
WWT_m (kg)	6.05	0.47	6.50	5.27
COWWT (kg)	10.85	17.49	11.74	8.25
$SURV_3$ (%)	3.75	5.50	1.86	5.08

[a] WWT_d, direct weaning weight; WWT_m, maternal weaning weight; COWT, cow weight at weaning and $SURV_3$, probability of having three or more calves given a female became a dam (as a percentage)

available in the base simulation (Table 6). All genetic covariances with survival in the simulation were taken at 10% of the values reported in Table 2 as a precaution against excessively high estimates of correlated response. The expected genetic changes are a function of the magnitude and sign of the genetic correlations among the component traits in the index as well as the economic values. Most noticeably, the economic value of mature cow weight was negative, yet the expected change in cow weight was positive. The expected change in cow weight for the base scenario was approximately 24% of the genetic SD, while expected change in direct weaning weight was approximately 44%. The extent of change in cow weight as a result of the positive genetic correlation with direct weaning weight was reduced but not removed by the negative economic value on cow weight.

The simulation demonstrates that without sufficient information on grand progeny (Y in the pedigree in Fig. 1), little genetic change would be expected in WWT_m (approximately 0.47 kg per generation). With sufficient information on grandprogeny, comparable increases in WWT_d and WWT_m (5.2 and 6.0 kg per generation, respectively) would be expected. Lack of information on Y also would lead to a larger genetic trend per generation in COWT (17.5 kg per generation) compared with when grandprogeny have records for weaning weight (10.8 kg per generation). Appropriate family structures are obviously needed to achieve genetic change in relationship to the relative economic values.

The accuracy of selection for the MPI decreased markedly with reduced information on grandprogeny (Table 6). The accuracy was decreased to a lesser extent if there were a reduced number of daughters with survival information, but the expected change in survival percentage was markedly reduced. Increasing the economic value of survival by 50% increased the expected genetic change from 3.8% in the base simulation to 5.1%. Expected changes in direct weaning weight and cow weight were reduced because of the negative genetic correlations between these traits and survival.

The maternal index as described can be implemented flexibly, with economic values changed in computations of index values as economic situations change. The assumption of linearity may be reasonable as long as the economic values are periodically re-estimated, which is an important consideration because the economic values are subject to population averages, especially for survival.

Implications

Selection for maternal productivity in beef cattle using an MPI incorporating EBV for direct and maternal weaning weight, cow weight and survival weighted by their independent economic values would be expected to result in positive genetic change for all component traits. This index would be of general use in varying production environments using economic weights reflecting those particular production environments.

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