Genetic evaluation of the ratio of calf weaning weight to cow weight[1,2,3]

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ABSTRACT: The phenotypic ratio of a calf's weaning weight to its dam's weight is thought to be an indicator of efficiency of the cow. Thus, the objectives of this research were to 1) estimate genetic parameters for the ratio of 200-d calf weight to mature-equivalent cow weight at weaning, its components, and other growth traits; and 2) evaluate responses to selection based on the ratio. Phenotypes evaluated were the ratio (100 kg/kg; n = 4,184), birth weight (kg; n = 5,083), 200-d weight (kg; n = 4,902), 365-d weight (kg; n = 4,626), and mature-equivalent cow weight at weaning (kg; n = 4,375). In 1989, a randomly selected and mated control line and a line selected for greater values of the ratio were established. Average generation intervals were 3.39 ± 0.05 and 3.90 ± 0.08 yr in the ratio selected line and control line, respectively. The ratio selection line (n = 895) accumulated approximately 4.7 SD more selection differential than the control line (n = 912) over 2.5 generations. Data were analyzed with a multiple-trait Gibbs sampler for animal models to make Bayesian inferences. Heritability estimates (posterior mean ± SD) for direct effects were 0.20 ± 0.03, 0.46 ± 0.04, 0.48 ± 0.03, 0.58 ± 0.04, and 0.76 ± 0.02 for ratio, birth weight, 200-d weight, 365-d weight, and cow weight, respectively. Estimates for heritability of maternal effects were 0.58 ± 0.05, 0.10 ± 0.02, 0.13 ± 0.02, and 0.10 ± 0.02 for ratio, birth weight, 200-d weight, 365-d weight, respectively. Significant response to selection was limited to maternal effects: 1.32 ± 0.38 ratio units per generation. As the ratio was a trait of the calf, estimated maternal genetic effects on the ratio contained both genetic effects due to dams that environmentally affected progeny performance and direct effects on the reciprocal of cow weight. In the control line, genetic trends in direct and maternal 200-d weight were –1.28 ± 0.91 and 0.62 ± 0.92 kg/generation, respectively, and the genetic trend in direct effects on cow weight was –5.72 ± 2.80 kg/generation. In the selection line, genetic trends in direct and maternal 200-d weight were 1.43 ± 0.79 and 2.90 ± 0.80 kg/generation and the genetic trend in cow weight was –2.79 ± 2.43 kg/generation. Significant correlated responses were observed in direct effects on birth weight and maternal effects on 365-d weight. Results contraindicate use of the ratio of calf weaning weight to cow weight as a selection criterion.

Key Words: Beef Cattle, Cow Indexes, Genetic Gain, Selection Responses

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Introduction

Nutritional cost of maintaining females is a substantial portion of input to a production unit (Fitzhugh, 1978). The phenotypic ratio of weaning weight of a calf to weight of its dam may be an indicator of efficiency, and Cunningham (1974) postulated a reasonable measure of economic utility of a commercial beef cow. The numerator indicates output, and the denominator indicates input through a commonly accepted association of cow weight and feed requirements. Dinkel and Brown (1978) evaluated this ratio as an indicator of efficiency and found little advantage of the ratio over weaning weight in predicting TDN consumed by cow and calf divided by the weaning weight of the calf. However, Davis et al. (1983) found cow weight correlated to efficiency, with smaller cows being more efficient in production of weaning weight. The relationship between cow size and efficiency may result from complementarity (Cartwright, 1970), although this basis also has been challenged (Dinkel, 1988).

To justify using a ratio to express information about two quantities, three conditions should be satisfied: 1) the relationship between components is linear; 2) the

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Table 1. Numbers of calves, generation numbers (G_n), and selection differentials accumulated over generations for weaning weight, cow weight, and their ratio reflecting selection applied, by year of birth and line

	Ratio line								Control line							
			200-d wt, kg		Cow wt, kg		Ratio				200-d wt, kg		Cow wt, kg		Ratio	
Year	No.	G_n	Sire	Dam	Sire	Dam	Sire	Dam	No.	G_n	Sire	Dam	Sire	Dam	Sire	Dam
1989	29	4.1	54.9	75.8	46.3	83.9	6.76	3.89	29	4.0	71.7	68.9	97.5	84.4	2.12	3.86
1990	50	4.1	40.8	64.9	15.0	68.0	8.83	3.66	52	4.1	52.6	61.7	86.1	64.0	1.73	3.19
1991	88	4.1	97.5	58.1	67.6	74.8	12.17	2.12	85	4.2	47.6	57.1	90.3	83.5	–0.12	1.37
1992	104	4.2	65.3	54.9	16.8	78.0	9.20	1.73	97	4.3	48.5	54.9	109.8	78.5	–1.36	1.91
1993	97	4.8	134.7	70.3	90.7	93.4	15.65	3.76	96	4.8	60.3	61.7	163.7	103.9	–4.16	1.58
1994	99	4.8	99.3	73.0	40.4	103.4	12.77	3.63	99	5.1	98.4	64.4	183.3	116.1	1.66	1.57
1995	93	5.5	129.7	94.8	44.9	112.0	20.82	7.42	110	5.4	68.0	70.8	121.6	147.0	1.07	0.38
1996	78	5.7	110.2	98.4	11.8	119.3	19.53	7.22	59	5.8	99.3	80.7	202.3	171.9	0.53	0.03
1997	63	6.1	149.2	113.9	102.5	125.6	19.55	10.65	58	6.1	83.9	83.0	147.0	168.7	3.35	1.14
1998	86	6.3	127.9	115.7	20.9	143.8	22.80	9.42	60	6.2	84.8	93.0	137.0	182.3	4.48	1.95
1999	99	6.5	133.4	113.9	29.5	121.6	22.67	10.98	115	6.3	83.0	86.1	138.8	194.1	3.84	–0.20
2000	77	6.6	153.3	130.2	54.9	116.6	24.09	15.23	116	6.3	96.6	88.9	160.1	197.3	4.52	0.03

intercept of the linear regression of numerator on denominator should be the origin; and 3) the variance of the ratio should increase with increasing values of numerator and denominator (Weil, 1962). In addition, a ratio of two normally distributed variables is not normally distributed (Fieller, 1932; Hinkley, 1969). Thus, concern was raised for the traditional concept of heritability of a ratio (Gunsett, 1987).

Despite theoretical issues with the ratio of calf weaning weight to cow weight, continuing interest in its use in selection and a need to improve the efficiency of beef production points to a need for genetic evaluation of this ratio and its components. Thus, the objectives of this research were to estimate genetic parameters for the ratio, its components, and other growth traits, and to evaluate responses to selection based on the ratio.

Materials and Methods

This research made use of a composite population of beef cattle (**CGC**) developed by USDA-ARS at Fort Keogh Livestock and Range Research Laboratory, Miles City, MT (Newman et al., 1993a,b). The general intent in forming the composite was to develop a strain of beef cattle with improved adaptation to the Northern Great Plains rangeland environment and greater potential profitability than existing breeds. The CGC population was initiated by mating Charolais (n = 14) and Tarentaise (n = 12) sires to Red Angus dams (n = 300). These foundation matings were made from 1979 to 1983. Subsequently (1981 to 1987), F_1 bulls were mated to F_1 females to produce progeny that were ½ Red Angus, ¼ Charolais, and ¼ Tarentaise. Animals of this breed composition were inter se mated in all subsequent generations. No additional germplasm has been introduced into CGC since the foundation matings. Thus, direct breed effects were stabilized in the F_2 generation, direct heterosis and maternal breed effects were stabilized in the F_3 generation, and maternal heterosis effects were stabilized in the F_4 generation. Additional details describing the formation of the CGC population can be found in Newman et al. (1993a).

In 1988, the population was divided randomly into three lines. Bulls for the first line were selected based on the index I = 365-d weight – 3.2(birth weight) (Dickerson et al., 1974). Response to selection for the index proposed by Dickerson et al. (1974) has been previously reported (MacNeil, 2003). Bulls for the second line were selected based on 100 times the ratio of their age-of-dam-adjusted 200-d weight to the coincident mature equivalent weight of their dam. Selection decisions were based on phenotypic performance within year. Virtually all selection pressure was applied to males, and most females were exposed for breeding as yearlings. Bulls for the third line were selected at random. All bulls were required to pass a breeding soundness examination as yearlings before being used for breeding.

In 1988 and 1989, the process of stabilizing the genetic composition of CGC was ongoing. Only cows belonging to generations subsequent to the F_2 contributed to the selection experiment. Hence, the numbers of calves in the control and ratio selection lines were less than the numbers of calves in subsequent years (Table 1). In 1989 and 1990, yearling heifers and bulls were sent to the U.S. Sheep Exp. Stn., Dubois, ID, for use with sheep in a mixed-species grazing trial. Mating occurred during the trial and all animals were returned to Miles City in late August. Thus, yearling heifers were mated to different bulls than the remainder of the cows in those years. Except during the mixed-species grazing trial, mating assignments were subject to the constraint that approximately equal numbers of like-aged females were assigned to each sire. In 1995 to 1997, a sample of cows was removed from the experiment (primarily from the control line) to initiate a project for mapping QTL (MacNeil and Grosz, 2002). Except as described below, four yearling bulls were used as sires in each line during each breeding season, with one sire from each line, selected at random, used the next year. In the control line: nine yearling bulls were used in the 1989 and 1990 breeding seasons and the same six bulls were used in the 1996 to 1998 breeding seasons; in the 1999 breeding season, four of the six bulls used in 1998 were used again, and the other two bulls used in 1998 were replaced by sons. In the ratio selection line, nine yearling bulls were used in the 1989 and 1990 breeding seasons, and in the 1992 and 1996 to 1999 breeding seasons, five yearling bulls were used each year. Increasing the number of bulls used per year, while decreasing the number of cows, allowed the effective population size of the control line to remain approximately equal to that of the ratio selection line during the latter years of this research. Within line, bulls selected for breeding were assigned to cows to avoid inbreeding of the progeny produced in the next generation.

At Fort Keogh Livestock and Range Research Laboratory, annual precipitation averages 34 cm, with 21 cm received from March to July. Average temperatures range from –9°C in January to 23°C in July. The terrain is broken badlands and plains rangelands that are typical of the northern Great Plains of the United States. Vegetation is predominantly western wheatgrass, blue grama, needle-and-thread, annual brome grasses, threadleaf sedge, greasewood, big and silver sagebrush, and fringed sagewort. Stocking rate on these rangelands is approximately 1 cow/14 ha, with supplemental feed required during winter.

A 45-d breeding season began on approximately June 15 of each year. Cows were exposed for breeding in single-sire pastures until approximately August 1, with the assignment to breeding pastures at random with respect to line. After the breeding season, cows were grouped by geographic proximity of the breeding herds into two larger herds, and grazed native rangeland until vegetation was covered by snow. Cows were weighed and pregnancy tested when their calves were weaned in early October. Nonpregnant females were culled. Cows and heifers were managed separately through winter, with approximately 1.4 kg of alfalfa pellets per animal provided daily when forage was available and hay fed when the forage was covered by snow. In preparation for calving, cows were moved to small pastures and fed approximately 9 kg of alfalfa hay per cow daily. As calving approached, first-calf heifers were observed periodically throughout the day. Older cows were observed only during daylight. Cow weights were adjusted to a mature (5-yr-old) equivalent basis using multiplicative adjustment factors derived from the data first in 1987 and subsequently in 1990. The adjustment factors were 1.197, 1.110, and 1.045 for 2-, 3-, and 4-yr-old cows, respectively.

Most calves were born during April and May of each year. Male calves were not castrated, and no creep feed was offered to the calves. Calves were weaned at an average age of approximately 180 d. After weaning, the calves were moved to a feedlot for a 140-d evaluation of postweaning growth. Before the test period began, the calves were allowed a pretest adjustment period of 2 to 4 wk following weaning. Bull calves were fed a diet that was formulated to support an average growth rate of 1.4 kg/d. The energy density of the diet was approximately 2.7 Mcal of ME/kg of DM, and the CP content was approximately 12% of DM. Primary ingredients in the diet were corn silage, barley, and a protein and mineral supplement. Heifer calves were fed to gain 0.8 kg/d. The approximate energy density and CP content of the diet were 2.4 Mcal of ME/kg of DM and 9% of DM, respectively. The calves were weighed on Monday and Wednesday of the weeks at the beginning and end of the postweaning test period, and the pairs of weights were averaged to calculate initial and final weights, respectively. Birth weight and gain from birth to weaning were adjusted for differences in age of dam following the results of Newman et al. (1993b). Weaning and yearling weights were then adjusted to age-constant bases as recommended by the BIF (1996).

Selection applied and turnover of generations were monitored for each line, separately. Individual selection differentials (ID) were computed for the ratio and component traits within year-sex-line subclasses based on the adjusted phenotypes. Cumulative selection differentials were calculated following the methodology of Newman et al. (1973), with differences in selection applied between sires and dams summarized by year-line subclass following Koch et al. (1994). Performance records were not available for the original purchased females and their contemporaries or for the purebred bulls used by AI and their contemporaries. Therefore, in calculating the cumulative selection differentials, the deviation of a phenotype of an individual from the contemporary group mean was assumed to be zero for all animals born before 1980. For an animal, the cumulative selection differential (CS) was calculated recursively as:

$$CS = ID + (CS_s + CS_d)/2$$

where CS_s = cumulative sire differential and CS_d = cumulative dam differential. The generation number (GN) of each animal was calculated similarly as:

$$GN = (GN_s + GN_d)/2 + 1$$

where GN_s and GN_d = generation numbers of the sire and dam, respectively (Brinks et al., 1964). Generation number also was assumed to be zero for all animals born before 1980.

Preliminary analyses to derive estimates of parameters of the prior distribution for a Bayesian analysis of these data were conducted using multiple-trait, derivative-free REML (Smith and Graser, 1986; Graser et al., 1987) methods as implemented by Boldman et al. (1995). Genetic parameters were estimated from phenotypes recorded from all animals born between 1980 and 2000. Pedigree information was extended to the founding purebreds, which were assumed to be unrelated. Earlier results indicated that year of birth, sex of calf, age of dam, and a variety of two-factor interactions among these traits affected birth, 200-d, and 365-d weights. Hence, contemporary groups for these traits were formed as year, sex, and age of dam subclasses for further analyses. Linear models for birth weight (kg; n = 5,083), 200-d weight (kg; n = 4,902), 365-d weight (kg; n = 4,626), and the ratio (100^{a}kg/kg; n = 4,184) were similar and included fixed contemporary groups and correlated random direct and maternal additive effects and uncorrelated random maternal permanent environmental effects of the dams. Cows ranged in age from 2 to 11 yr, with an average age of 3.6 yr. For cow weight (kg), contemporary groups were formed as year-age subclasses, with cows at least 5 yr of age being grouped together. A total of 1,433 cows had at least one recorded weight, and there were 4,375 observations over time. The linear model for cow weight included fixed contemporary group effects, random additive direct effects, and uncorrelated random permanent environmental effects to allow for repeated records of the cow. The same contemporary group effects were fitted in models for the ratio of 200-d weight to cow weight and 200-d weight. Multiple trait analyses, constructed using the models described above, allowed for correlations among the additive effects, the uncorrelated random effects, and the residual errors. This multiple-trait, derivative-free REML method involves maximizing the likelihood function (Λ) given the data and is equivalent to minimizing $-2 \log \Lambda$. Each analysis was assumed to have converged to a global maximum when the variance of $-2 \log \Lambda$ in the simplex was less than 10^{-10}, and the scaled parameter estimates changed by less than 0.01 in a reanalysis of the data using an updated starting value.

Final data analyses were conducted using a multiple-trait Gibbs sampler for animal models (VanTassell and Van Vleck, 1996). The linear models used for each trait were as described above. Inverted Wishart distributions, with shape parameter = 9, were used as prior distributions of the (co)variance components. For a univariate analysis of the ratio of weaning weight to cow weight and for a bivariate analysis of weaning weight and cow weight, initial Gibbs samples were obtained for chains run 20,000 rounds, saving every 20 rounds, and without discarding earlier rounds for burn-in. The Gibbsit program of Raftery and Lewis (1996) was used to evaluate the length of the burn-in period and thinning interval needed to obtain stationary chains of independent samples and to estimate the total number of Gibbs samples required for the cumulative distribution function of the 0.025 quantile to be estimated within ±0.0125, with a probability of 0.95 for all genetic parameters. The recommended burn-in periods were from 40 to 160 rounds. The thinning interval recommended by Gibbsit was consistently less than or equal to 20 rounds; however, it has been shown that the thinning intervals recommended by Gibbsit are not sufficiently large (Van Tassell and Van Vleck, 1996). Thus, final analyses were conducted using a conservative burn-in of 5,000 rounds, 50,000 rounds of post-burn-in Gibbs sampling, and a thinning interval of 100 rounds. In summarizing the Gibbs samples, results are reported as mean ± SD of the posterior Gibbs samples.

Results and Discussion

Generation numbers (Table 1) reflect the elapsed generations since the original foundation of CGC with purebred Red Angus, Charolais, and Tarentaise designated as generation 0. The average generation interval in the ratio line was 3.39 ± 0.05 yr. The average generation interval in the control line was 3.90 ± 0.08 yr. The difference between lines in average generation interval resulted from the greater repeated use of bulls over years in the control line beginning in 1996.

Selection differentials for calves born in the early years of this experiment resulted from selection applied during formation of the CGC composite population and stabilization of its breed composition. Initial differences in selection differentials between the ratio and control lines primarily reflect differences in individual deviations of the selected sires (Table 1). In the line selected for increased values of the ratio of calf weaning weight to weight of its dam at weaning, the total (sire + dam) indirect cumulative selection differential for 200-d weight increased by 153 kg (6.4 SD) from 1989 to 2000, whereas the direct cumulative selection differential increased by 28.67 ratio units (4.7 SD) over the same time period. However, the pattern of sire cumulative selection differentials for cow weight is remarkable and documents inconsistency in the indirect selection applied to cow weight through direct selection on the ratio of calf weaning weight to weight of its dam at weaning. Trends in the cumulative selection differentials for 200-d weight, cow weight, and their ratio were all significantly positive across years in the control line. Rogers et al. (2004) documented the increased risks that lighter cows and those that experience dystocia have of not being pregnant, and therefore being culled from this population. Thus, these positive trends of the selection differentials in the control may be compromised by small females failing to breed and/or calve successfully and from the relationship between the numerator and denominator of the ratio.

The mean estimate of phenotypic variance of the ratio of calf 200-d weight to cow weight in the posterior distribution was 37.6. Mean estimates of direct and maternal heritability for the ratio were 0.20 ± 0.03 and 0.58 ± 0.05, respectively. The estimated posterior mean of the genetic correlation between direct and maternal effects was −0.77 ± 0.04. Permanent environmental effects due to females and residual effects, on average, accounted for 23 ± 3% and 25 ± 2% of phenotypic variance, respectively. Distributions of the Gibbs sample estimates for each of these parameters are shown in Figure 1. No comparable partitioning of the variance of the ratio of calf weaning weight to cow weight was found in the literature. However, the strong genetic antagonism between direct and maternal genetic effects found here and the average posterior estimate of total heritability (Willham, 1972) of 0.10 ± 0.02 foretell of challenges in the genetic improvement of this trait through selection based on phenotype.

Trends in direct and maternal genetic effects on the ratio are presented in Figure 2 for both the selected

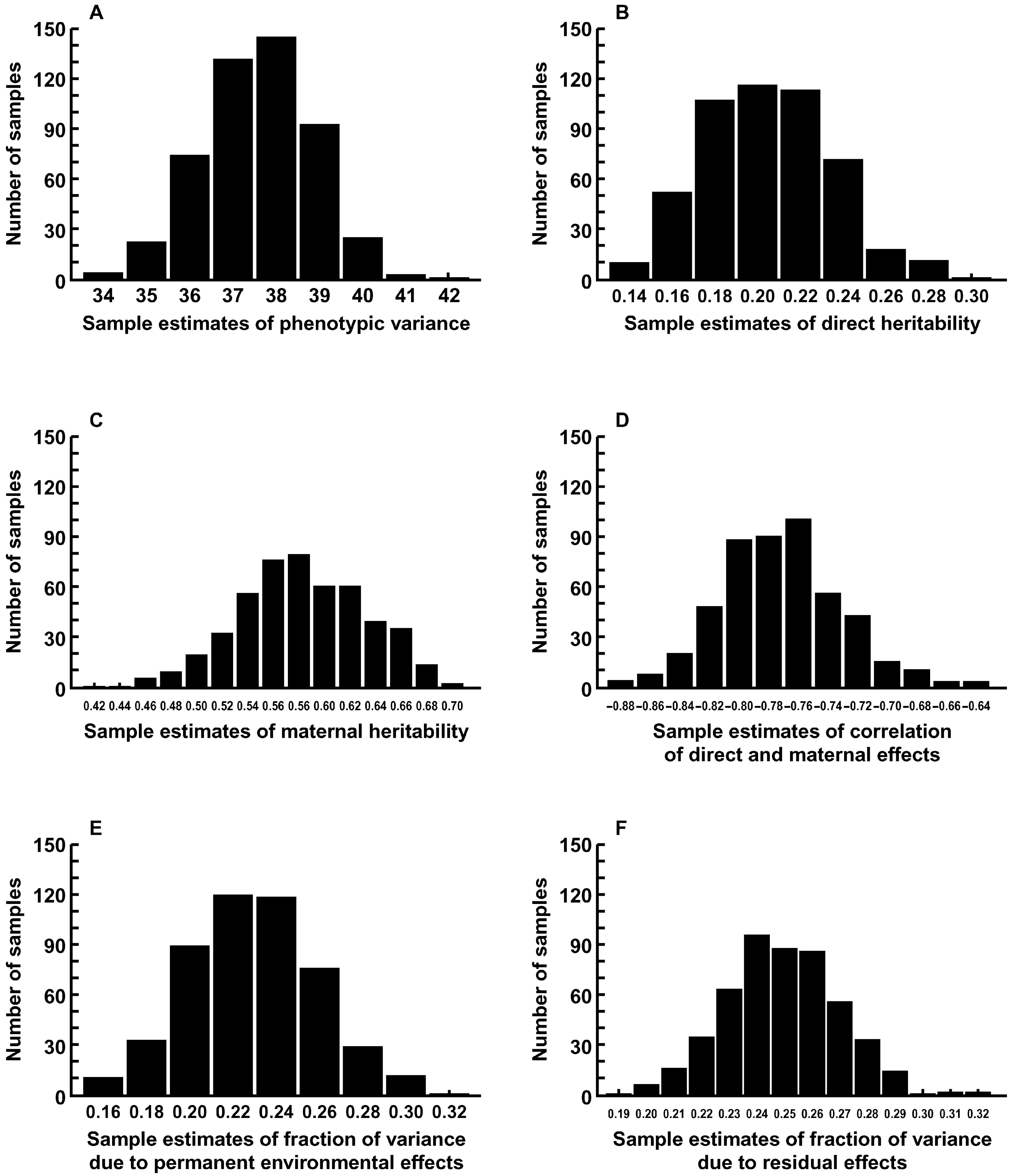

Figure 1. Marginal posterior distributions of Gibbs sample estimates of A) phenotypic variance (mean = 37.6), B) heritability of direct genetic effects (mean = 0.20), C) heritability of maternal genetic effects (mean = 0.58), D) genetic correlation between direct and maternal genetic effects (mean = –0.77), E) fraction of variance in the ratio explained by permanent environmental effects (mean = 0.23), and F) fraction of variance in the ratio explained by temporary environmental effects (mean = 0.25) on the ratio of calf 200-d weight to cow weight.

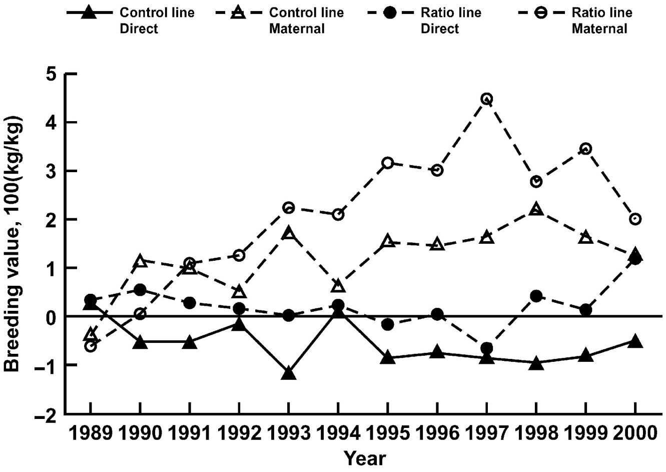

Figure 2. Trends in direct and maternal breeding values for the ratio of calf 200-d weight to mature-equivalent cow weight in the line selected for increased values of the ratio and a randomly selected control line.

and control lines. These trends result from the selection applied and from drift, which are inseparable in experiments without replicated lines, and from sampling error (Falconer, 1989). The posterior distribution of regressions of direct and maternal breeding values on generation number (–0.25 ± 0.23 and 0.52 ± 0.40, respectively) indicates no significant genetic change for the control line. For the ratio selection line, the regression of direct genetic effects on generation number (–0.02 ± 0.23) was not significant in the posterior distribution of the Gibbs sample estimates; however, the corresponding regression of maternal genetic effects on generation number (1.32 ± 0.38) indicated a significant positive genetic trend. As might be anticipated from the genetic trends, the ratio and control lines had diverged phenotypically by two ratio units at the end of the experiment (1998 to 2000).

The components of the ratio, calf 200-d weight and cow weight, were analyzed in a multiple-trait context to further dissect response to selection. Mean estimates of phenotypic variance for 200-d weight and cow weight in the posterior distribution were 564.0 and 2,906.8 kg^2, respectively. Heritability estimates for direct 200-d weight and cow weight derived from the posterior distributions of the Gibbs sample estimates of variance components were 0.48 ± 0.03 and 0.76 ± 0.02, respectively. The genetic correlation between direct effects was 0.91 ± 0.02. The estimate of heritability of maternal effects on 200-d weight was 0.13 ± 0.02. The heritability of maternal effects on cow weight was estimated to be essentially nil in preliminary REML analyses and was not pursued further. The heritability estimates for both components of the ratio differ from those reported by MacNeil (2003) for this population, with the estimated heritability of direct effect on 200-d weight being substantially greater than previously reported. The heritability estimates for direct effects on weaning weight and cow weight also were greater than the average estimates reported by Koots et al. (1994a), and the estimated genetic correlation between direct effects is also substantially greater than the average of literature estimates (Koots et al., 1994b). Selection for the ratio may be considered as selection to simultaneously increase 200-d weight and decrease cow weight. This selection is in opposition to the positive genetic correlation between the component traits. Thus, allele frequencies at those pleiotrophic loci that increase 200-d weight and decrease cow weight are expected to be changed rapidly toward fixation, whereas allele frequencies at loci with directionally similar effects on the component traits should be much less strongly influenced (Falconer, 1989). As a consequence, the genetic correlation between 200-d weight and cow weight in a line selected for the ratio may be more positive after a few generations of selection than before, thereby making long-term genetic change in the ratio more difficult. The theoretical effect on the genetic correlation has been tested experimentally several times, with decidedly mixed results (e.g., Sheridan and Barker, 1974; Archer et al., 2003). Estimates of genetic correlations of maternal effects on 200-d weight with the direct effects on either 200-d weight (–0.06 ± 0.09) or cow weight (–0.14 ± 0.08) were not significantly different from zero in these data. Permanent and temporary environmental effects associated with cows, either as repeated observations of weight of the cow when her calf was weaned or of weight of her calves at weaning, explained significant fractions of the phenotypic variance in both 200-d weight and cow weight (0.08 ± 0.02, 0.16 ± 0.01, 0.13 ± 0.02, and 0.28 ± 0.02, respectively). Correlations between permanent and temporary environmental effects were –0.49 ± 0.11 and 0.13 ± 0.03, respectively. The posterior mean of the phenotypic correlation between 200-d weight and cow weight was 0.20.

The regression of 200-d weight on cow weight after adjusting both weights for contemporary group effects was nonlinear ($P = 0.05$) and the y-intercept of the regression line was positive ($P < 0.01$), complicating interpretation of the ratio. Figure 3 illustrates the relationship between cow weight and 200-d weight of her calf as implied by the ratio vis à vis the relationship derived from the data via regression. Estimates of genetic trends in 200-d weight and cow weight for the control line and in response to selection on the ratio of 200-d weight to cow weight are shown in Figures 4 and 5, respectively. In the control line, the regressions of breeding value on generation number for direct and maternal 200-d weight were not significant (–1.28 ± 0.91 and 0.62 ± 0.92 kg/generation, respectively), and the regression of direct breeding value for cow weight on generation number was negative –5.72 ± 2.80 kg/generation. In the line selected for the ratio of calf 200-d weight to cow weight at weaning, the regressions of breeding value on generation number for direct and maternal effects on 200-d weight were 1.43 ± 0.79 and 2.90 ± 0.80 kg/generation, respectively, and the genetic trend in cow weight was not different from zero (–2.79 ± 2.43 kg/generation).

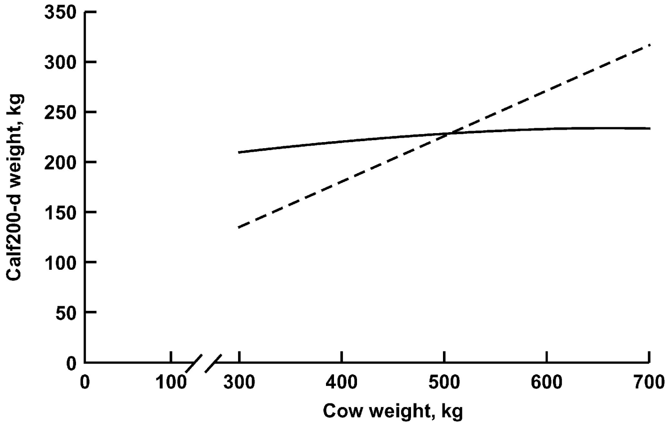

Figure 3. Relationships between 200-d weight of a calf and mature equivalent weight of the dam as measured by their phenotypic ratio (---) and by regression of calf weight on cow weight (—).

Because the ratio was considered a trait of the calf, the estimated maternal genetic effects on the ratio contain both genetic effects due to dams that environmentally affect performance of their progeny and direct genetic effects on the reciprocal of cow weight. Thus, the positive trend in maternal genetic effects on the ratio (Figure 2) observed in the selected line may arise from both the positive genetic trend in maternal effects on 200-d weight and the nonsignificant, but complimentary, negative trend in direct effects on cow weight. However, no maternal genetic trend was observed for the ratio in the control line, as the significant negative trend in direct effects on cow weight was offset in part by a nonsignificant positive trend in maternal effects on 200-d weight. Similar caution is relevant when interpreting parameter estimates relating other phenotypes to the ratio.

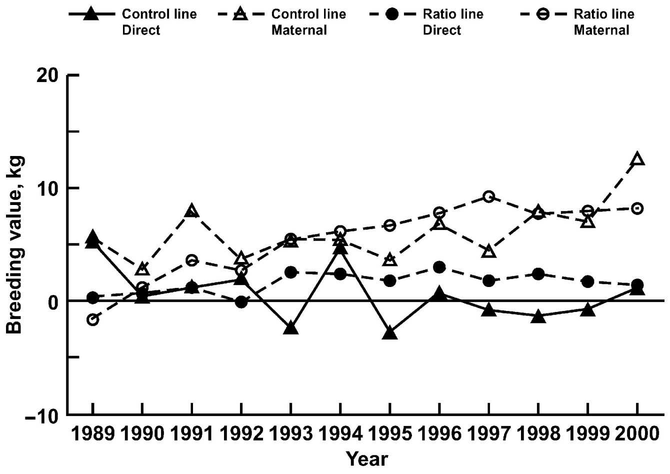

Figure 4. Trends in direct and maternal breeding values for calf 200-d weight in a line selected for increased values of the ratio of calf 200-d weight to mature-equivalent cow weight and a randomly selected control line.

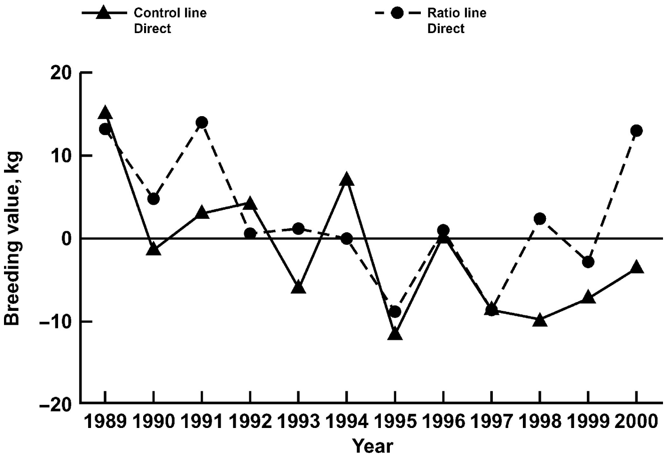

Figure 5. Trends in direct breeding values for mature-equivalent cow weight in a line selected for increased values of the ratio of calf 200-d weight to mature-equivalent cow weight and a randomly selected control line.

To further examine the relationships between the ratio and it components, additional bivariate analyses were conducted with the ratio and its numerator and denominator. When the relationship between the ratio and its 200-d weight was examined in these data, correlations between direct, permanent environmental, and residual effects were all large (0.95 ± 0.01, 0.82 ± 0.03, and 0.79 ± 0.02, respectively). The correlation between maternal effects was smaller, 0.53 ± 0.6, perhaps due in part to the negative covariance of maternal genetic effects on 200-d weight and direct effects on cow weight. The posterior mean phenotypic correlation between the ratio and its numerator was 0.62. Correlations of direct effects on cow weight with both direct and maternal effects on the ratio were –0.87 ± 0.02 and –0.80 ± 0.03, respectively. Likewise, the correlations between permanent and temporary environmental effects on cow weight and the ratio were also large and negative: –0.81 ± 0.04 and –0.55 ± 0.02, respectively. The correlation between direct effects on cow weight and the ratio, largely reflective of the corresponding correlation between direct effects on cow weight and 200-d weight, was 0.82 ± 0.02. Thus, the posterior mean phenotypic correlation between cow weight and the ratio was –0.62, which is approximately equivalent to that predicted following Sutherland (1965).

The mean estimate of phenotypic variance for birth weight in the posterior distribution was 32.0 kg^2. Estimates of heritability for direct and maternal genetic effects on birth weight were 0.46 ± 0.04 and 0.10 ± 0.02, somewhat greater and less than the corresponding average estimates from the literature reported by Koots et al. (1994a), and similar to those reported for this population by MacNeil et al. (2003). Genetic correlations between direct effects on birth weight and both direct and maternal effects on the ratio were large: 0.72 ± 0.05 and –0.60 ± 0.05, respectively. Genetic correlations of maternal genetic effects on birth weight with direct and

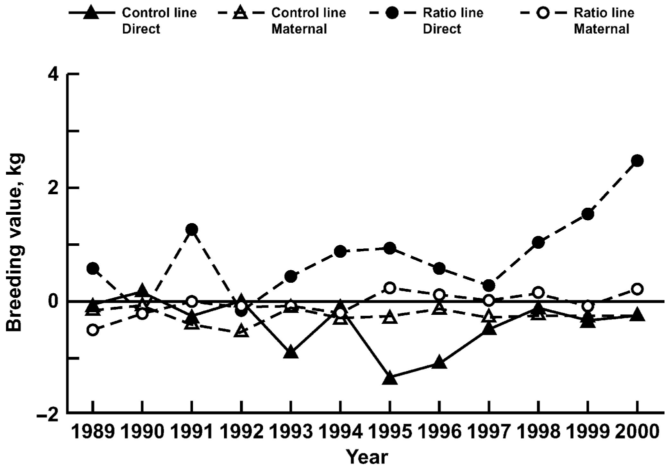

Figure 6. Trends in direct and maternal breeding values for birth weight in a line selected for increased values of the ratio of calf 200-d weight to mature-equivalent cow weight and a randomly selected control line.

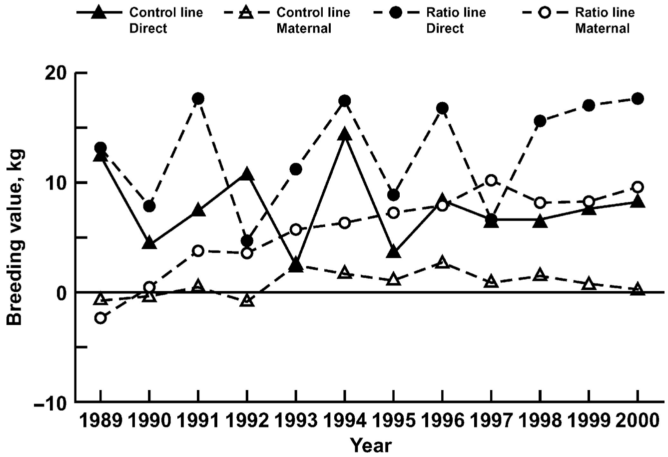

Figure 7. Trends in direct and maternal breeding values for calf 365-d weight in a line selected for increased values of the ratio of calf 200-d weight to mature-equivalent cow weight and a randomly selected control line.

maternal genetic effects on the ratio and with direct genetic effects on birth weight were small, 0.15 ± 0.11, –0.03 ± 0.10, and –0.05 ± 0.11, respectively. As in MacNeil et al. (2003), permanent environmental effects on birth weight due to dams were essentially nil, and temporary environmental effects accounted for 45 ± 3% of total variance. Correlations of permanent and temporary environmental effects on the ratio and birth weight were 0.19 ± 0.24 and 0.18 ± 0.04, respectively. Genetic trends in birth weight for the control line and in response to selection on the ratio of 200-d weight of the calf to the weight of its dam at weaning are shown in Figure 6. Only the regression of direct genetic effects on generation number in the selected line (0.13 ± 0.06 kg/generation) differed from zero.

The mean estimate of phenotypic variance for 365-d weight in the posterior distribution was 1,467 kg^2. Estimates of heritability for direct and maternal genetic effects on 365-d weight were 0.58 ± 0.04 and 0.10 ± 0.02. These estimates of the heritability of direct and maternal genetic effects on 365-d weight are greater than and similar to, respectively, the average of literature estimates reported by Koots et al. (1994a). Genetic correlations between direct effects on 365-d weight and both direct and maternal effects on the ratio were large, 0.87 ± 0.02 and –0.77 ± 0.03, respectively. Genetic correlations of maternal genetic effects on 365-d weight with direct effects on the ratio and on 365-d weight were both small, –0.13 ± 0.11 and –0.22 ± 0.09, respectively. However, the genetic correlation between maternal effects was sizeable, 0.48 ± 0.08, perhaps owing to the relative small variance in maternal genetic effects on 365-d weight. Permanent and temporary environmental effects on 365-d weight due to dams accounted for 0.06 ± 0.01 and 0.33 ± 0.03 of total variance, respectively. Correlations of permanent and temporary environmental effects on the ratio and 365-d weight were 0.82 ± 0.05 and 0.56 ± 0.03, respectively. Trends in direct and maternal genetic effects on 365-d weight resulting as correlated responses to selection for the ratio are shown in Figure 7. Only the regression of maternal genetic effects on generation number in the selected line (0.95 ± 0.32 kg/generation) differed from zero.

Use of Bayesian methods in this research was originally motivated by the anticipated nonnormal distribution of the ratio phenotype (Fieller, 1932; Hinkley, 1969) and the potential for differences in inference to result from using Bayesian vs. frequentist approaches (Blasco, 2001). However, means of the parameter estimates and their associated standard deviations from the posterior distribution of Gibbs samples were generally similar to those produced using REML, with standard errors approximated following Dodenhoff et al. (1988), either in preliminary analyses or reported previously by MacNeil (2003). The difference in heritability estimate for direct effects on 200-d weight reported here vs. the one reported by MacNeil (2003), 0.48 ± 0.03 vs.0.30 ± 0.04, is most striking. However, the present estimate was consistent with the preliminary REML results, and the difference between models used in the two REML analyses lies in mature-equivalent cow weight used as a correlated trait here vs. the function 365-d weight – 3.2(birth weight) used previously.

The ratio of calf weaning weight to cow weight is likely not the contemporary phenotype of choice on which to base a selection program. Its use arose during an era when genetic improvement programs were based on a culture of only measuring weights and trying to extract the most information from them. The ratio undoubtedly had and continues to have some intuitive appeal due to its ease of measurement and perceived relationship with efficiency. In this research, phenotypic selection for the ratio of a calf's 200-d weight to the mature equivalent weight of its dam resulted in a significant genetic trend being established for maternal effects on the ratio. In addition, significant correlated responses were observed in direct effects on birth weight, direct and maternal effects on 200-d weight, and maternal effects on 365-d weight. No significant genetic trend in mature equivalent cow weight was observed. However, a significant negative genetic trend in direct effects on cow weight was observed in the control line, and if this trend resulted from natural selection, rather than drift, it might be inferred that selection for the ratio would affect cow weight positively.

Implications

Selection for a ratio is complicated by shifting emphasis given to the component traits. Phenotypic selection for the ratio of calf weaning weight to cow weight is further complicated by measurement of the two component phenotypes on different individuals and the consequent confounding of direct and maternal genetic effects on these phenotypes. Thus, selection index procedures would seemingly yield a more defined criterion, with clear and consistent emphasis on the traits and their genetic components. Results of this experiment illustrated the complexity of anticipating response to selection when the criterion is a ratio.

Literature Cited

Archer, M. A., J. P. Phelan, K. A. Beckman, and M. R. Rose. 2003. Breakdown in correlations during laboratory evolution. II. Selection on stress resistance in Drosophila populations. Evolution 57:536–543.

BIF. 1996. Guidelines for Uniform Beef Improvement Programs. 7th ed. C. Bailey, ed. Beef Improv. Fed., Colby, KS.

Blasco, A. 2001. The Bayesian controversy in animal breeding. J. Anim. Sci. 79:2023–2046.

Boldman, K. G., L. A. Kriese, L. D. VanVleck, C. P. VanTassell, and S. D. Kachman. 1995. A Manual for use of MTDFREML. A set of programs to obtain estimates of variances and covariances (DRAFT). ARS, USDA, Washington, DC.

Brinks, J. S., R. T. Clark, N. M. Kieffer, and J. J. Urick. 1964. Estimates of genetic, environmental and phenotypic parameters in range Hereford females. J. Anim. Sci. 20:903. (Abstr.)

Cartwright, T. C. 1970. Selection criteria for beef cattle for the future. J. Anim. Sci. 30:706–711.

Cunningham, E. P. 1974. Breeding goals for beef cattle. Ann. Genet. Sel. Anim. 6:219–226.

Davis, M. E., J. J. Rutledge, L. V. Cundiff, and E. R. Hauser. 1983. Life cycle efficiency of beef production: II. Relationship of cow efficiency ratios to traits of the dam and progeny weaned. J. Anim. Sci. 57:852–866.

Dickerson, G. E., N. Künzi, L. V. Cundiff, R. M. Koch, V. H. Arthaud, and K. E. Gregory. 1974. Selection criteria for efficient beef production. J. Anim. Sci. 39:659–673.

Dinkel, C. A. 1988. The interaction of cow size with growth potential of the service sire. Can. J. Anim. Sci. 68:129–137.

Dinkel, C. A., and M. A. Brown. 1978. An evaluation of the ratio of calf weaning weight to cow weight as an indicator of cow efficiency. J. Anim. Sci. 46:614–617.

Dodenhoff, J., L. D. Van Vleck, S. D. Kachman, and R. M. Koch. 1988. Parameter estimates for direct, maternal, and grandmaternal effects for birth weight and weaning weight in Hereford cattle. J. Anim. Sci. 76:2521–2527.

Falconer, D. S. 1989. Introduction to Quantitative Genetics. 3rd ed. Longham Scientific and Technical, Essex, U.K.

Fieller, E. C. 1932. The distribution of the index in a normal bivariate population. Biometrika 24:428–440.

Fitzhugh, H. A. 1978. Animal size and efficiency, with special reference to the breeding female. Anim. Prod. 27:393–401.

Graser, H.-U., S. P. Smith, and B. Tier. 1987. A derivative free approach for estimating variance components in animal models by restricted maximum likelihood. J. Anim. Sci. 64:1362–1370.

Gunsett, F. C. 1987. Merit of utilizing the heritability of a ratio to predict genetic change of a ratio. J. Anim. Sci. 65:936–942.

Hinkley, D. V. 1969. On the ratio of two correlated normal random variables. Biometrika 56:635–639.

Koch, R. M., L. V. Cundiff, and K. E. Gregory. 1994. Cumulative selection and genetic change for weaning or yearling weight or for yearling weight plus muscle score in Hereford cattle. J. Anim. Sci. 72:864–885.

Koots, K. R., J. P. Gibson, C. Smith, and J. W. Wilton. 1994a. Analyses of published genetic parameter estimates for beef production traits. 1. Heritability. Anim. Breed. Abstr. 62:309–338.

Koots, K. R., J. P. Gibson, and J. W. Wilton. 1994b. Analyses of published genetic parameter estimates for beef production traits. 2. Phenotypic and genetic correlations. Anim. Breed. Abstr. 62:825–853.

MacNeil, M. D. 2003. Genetic evaluation of an index of birth weight and yearling weight to improve efficiency of beef production. J. Anim. Sci. 81:2425–2433.

MacNeil, M. D., and M. D. Grosz. 2002. Genome-wide scans for QTL affecting carcass traits in Hereford × composite double backcross populations. J. Anim. Sci. 80:2316–2324.

Newman, J. A., G. W. Rahnefeld, and H. T. Fredeen. 1973. Selection intensity and response to selection for yearling weight in beef cattle. Can. J. Anim. Sci. 53:1–12.

Newman, S., M. D. MacNeil, W. L. Reynolds, B. W. Knapp, and J. J. Urick. 1993a. Fixed effects in the formation of a composite line of beef cattle: I. Experimental design and reproductive performance. J. Anim. Sci. 71:2026–2032.

Newman, S., M. D. MacNeil, W. L. Reynolds, B. W. Knapp, and J. J. Urick. 1993b. Fixed effects in the formation of a composite line of beef cattle: II. Pre- and postweaning growth and carcass composition. J. Anim. Sci. 71:2033–2039.

Raftery, A. E., and S. M. Lewis. 1996. Implementing MCMC. Pages 115–130 in Markov Chain Monte Carlo in Practice. W. R. Gilks, D. J. Spiegelhalter and S. Richardson, ed. Chapman and Hall, London, U.K.

Rogers, P. L., C. T. Gaskins, K. A. Johnson, and M. D. MacNeil. 2004. Evaluating longevity of composite beef females using survival analysis techniques. J. Anim. Sci. 82:860–866.

Sheridan, A. K., and J. S. Barker. 1974. Two-trait selection and the genetic correlation. II. Changes in the genetic correlation during two-trait selection. Aust. J. Biol. Sci. 27:89–101.

Smith, S. P., and H.-U. Graser. 1986. Estimating variance components in a class of mixed models by restricted maximum likelihood. J. Dairy Sci. 69:1156–1165.

Sutherland, T. M. 1965. The correlation between feed efficiency and rate of gain, a ratio and its denominator. Biometrics 21:739–749.

Van Tassell, C. P., and L. D. Van Vleck. 1996. Multiple-trait Gibbs sampler for animal models: Flexible programs for Bayesian and Likelihood-based (co)variance component inference. J. Anim. Sci. 74:2586–2597.

Weil, W. B. 1962. Adjustment for size—A possible misuse of ratios. Am. J. Clin. Nutr. 11:249–252.

Willham, R. L. 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 35:1288–1293.