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Bayesian analysis of selection for greater weaning weight while maintaining birth weight in beef cattle¹

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ABSTRACT: An experimental Hereford herd established in 1960 was used from 1986 to 2006 to select for increased weaning weight (W) without increasing birth weight (B). Data were B and W collected over the 47 yr from 2,124 calves. Including ancestors, the pedigree file had 2,369 animals. Selection was practiced only in males. In the first stage (1986 to 1993), mass-selected bulls were chosen with the index $I = B + 9374.76 \text{ RDG}$ (relative daily gain). From 1994 to 2006, the selection criterion for bull i was $I_i = \text{BLUP}_i(\text{WD}) - 2.33 \text{ BLUP}_i(\text{BD})$, where the BLUP were for the direct BV of B (BD) and W (WD), respectively. Predictions were obtained from a 2-trait animal model with B having only BD, and W with WD and WM (maternal additive effects). Selection response was estimated using a Bayesian approach by means of the Gibbs sampler for a 2-trait animal model including BD, BM (maternal BV for B), WD, and WM. Estimated heritabilities for BD, BM, WD, and WM were 0.40, 0.23, 0.05, and 0.23,

respectively. The correlation between BD and BM was close to zero (0.01), and between WD and WM was positive (0.37). The correlation between BD and WD was 0.07, and between BM and WM was 0.58. The 2 methods used to estimate selection response gave similar results. In both periods BD decreased, whereas BM increased. The reduction of BD due to selection was slightly larger in the second period than in the first one. The regression of BV for W increased due to selection in both stages, but selection response was 21.6% larger from 1986 to 1992 than from 1993 to 2006. The maternal effect, WM increased more than 3 times compared with WD in the first period, but ended up being almost the same value as WD in period 2. The Bulmer effect was manifested by the decrease in magnitude of all (co) variance components during selection. It is concluded that selection to increase BW at weaning in beef cattle, although not increasing BW at birth, was moderately effective.

Key words: beef cattle, Bulmer effect, restricted selection

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INTRODUCTION

Because selection goals in beef cattle involve multiple traits that are correlated, the definition of the selection criteria often requires selecting 2 traits in directions that are opposite to their correlation: antagonistic selection (MacNeil, 2003; Bennett, 2008). Dickerson et al. (1974) pioneered this development by proposing

the index yearling weight minus 3.2 times birth weight (**B**). Selection experiments reported by MacNeil et al. (1998), MacNeil (2003), and Bennett (2008), are examples of the antagonistic selection approach to increase economic efficiency of beef production. There are no experimental reports of selection for weaning weight (**W**) while restricting B, a selection goal that focuses on improving maternal productivity without increasing calving difficulty.

Ideally, selection experiments should include a control line to precisely estimate selection response (Sorensen et al., 2003). However, due to cost restrictions, some selection experiments in beef cattle were conducted with no control line (Mrode, 1988). In the absence of a control line, selection response is measured by genetic trend in the selected line. It is in this situation of little information in the data that the Bayesian approach

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becomes helpful because it can handle estimation of the distribution of selection response (Sorensen et al., 1994). Moreover, the Bayesian approach also becomes useful to infer the trajectory of elements of the additive covariance matrix during the course of selection (Sorensen et al., 2001), which is affected by the build up of inbreeding and by the generation of negative linkage disequilibrium (Bulmer, 1971). The objective of this research was to estimate direct and maternal genetic trends in B and W, from an experimental herd of beef cattle selected for greater W while restricting B. A second goal was to infer the trajectory of the elements of the additive covariance matrix during selection. To accomplish these objectives, we followed the Bayesian approach.

MATERIALS AND METHODS

All experimental procedures involving the use of animals were conducted in accordance with the *Manual de Procedimientos sobre el Bienestar Animal (Handbook of Procedures for Animal Welfare)* of SENASA (National Service of Animal Health) of Argentina.

Data

The experimental herd was maintained at Balcarce Experimental Station, National Institute of Agricultural Technology, INTA, Balcarce, Province of Buenos Aires, Argentina (37° 45' S latitude, 58° 18' W longitude, 130 m above sea level). The weather is temperate and humid with an average annual temperature of 15°C and an average annual rainfall of 890 mm. Cattle grazed pastures composed of *Lolium multiflorum*, *Dactylis glomerata*, *Bromus catharticus*, *Trifolium repens*, and *Trifolium pratense*. Grass production is seasonal with the largest peak in spring and a smaller peak during the fall. Since the beginning of the selection experiment in 1986, services were by natural mating. All cows that were visually detected in heat were mated in pens with an individual bull. From 1960 to 1985, matings were made to some bulls from the herd and several purchased purebred bulls without using a formal selection criterion. The use of bulls from outside the herd was intensified before the beginning of the experiment to increase variability and to decrease the level of inbreeding. The service season was from mid-October to mid-December. This was followed by a clean-up period of 1 mo on single sire pastures. Weaning was in March (fall) at an average age of 180 d. Bull and heifers were first bred as 2-yr-olds. The approximate herd size was 100 cows and 4 bulls.

Selection Protocols

Directional selection was practiced only on males, with some culling of females due to insufficient BW at first service. Only those males having both parents identified and absence of horns were candidates for selec-

tion. Out of the 4 bulls used in the herd, 2 were 3 yr old and 2 were 4 yr old at the time of replacement. Every year, the 2 older bulls were replaced with the 2-yr-old males having the largest value of the selection index. From 1986 to 1993, bulls were selected by the index $I_i = B_i + 9,374.76 \text{ RDG}_i$. For bull i , B_i is its birth weight and RDG_i is its relative daily BW gain from birth to weaning calculated as the regression of the logarithm of BW on age at measure, any animal having a minimum of 5 and a maximum of 8 BW measurements during the period from B to W. The index was obtained by Melucci et al. (1983), and the goal was to increase relative ADG from birth to weaning without increasing BW at birth. It should be mentioned that the estimated additive correlation between RDG and B at that time was negative. From 1994 to 2006, the selection criterion was $X_i = \text{BLUP}_i(\text{WD}) - 2.33 \text{ BLUP}_i(\text{BD})$. The BLUP were for the direct BV of B (BD) and W (WD), respectively. The index was calculated by Melucci (1995) using the methodology proposed by Lin (1990). Predictions were obtained from a 2-trait animal model for B with BV for direct effects only (BD), and W with direct (WD) and maternal (WM) additive effects. Each selected bull was mated to a group of cows with the smallest average relationship.

The data set included all records since the formation of the herd in 1960, to 2006. There were phenotypic observations on 2,124 animals, all having B and W. The calves were the progeny of 105 bulls and 760 cows. Including all ancestors, the pedigree file consisted of 2,369 animals. The index of pedigree completeness (MacCluer et al., 1983) was equal to 0.89. Inbreeding coefficients were calculated with the software ENDOG version 4.5 (Gutiérrez and Goyache, 2005).

Analysis of Data

Let \mathbf{y}_B and \mathbf{y}_W be the vectors of B and W records, respectively. Then, data were analyzed using the following 2-trait model:

$$\begin{bmatrix} \mathbf{y}_B \\ \mathbf{y}_W \end{bmatrix} = \begin{bmatrix} \mathbf{X}_B & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_W \end{bmatrix} \begin{bmatrix} \boldsymbol{\beta}_B \\ \boldsymbol{\beta}_W \end{bmatrix} + (\mathbf{I}_2 \otimes \mathbf{Z}_D) \begin{bmatrix} \mathbf{a}_{BD} \\ \mathbf{a}_{WD} \end{bmatrix} + (\mathbf{I}_2 \otimes \mathbf{Z}_M) \begin{bmatrix} \mathbf{a}_{BM} \\ \mathbf{a}_{WM} \end{bmatrix} + \begin{bmatrix} \mathbf{0} \\ \mathbf{Z}_E \mathbf{e}_M \end{bmatrix} + \begin{bmatrix} \mathbf{e}_B \\ \mathbf{e}_W \end{bmatrix}, \quad [1]$$

where \mathbf{I}_2 is an identity matrix of order 2, and \mathbf{X} , \mathbf{Z}_D , \mathbf{Z}_M , and \mathbf{Z}_E are incidence matrices that relate records to the vectors of fixed effects ($\boldsymbol{\beta}_B$ and $\boldsymbol{\beta}_W$), direct BV (\mathbf{a}_{BD} and \mathbf{a}_{WD}), maternal BV (\mathbf{a}_{BM} and \mathbf{a}_{WM}), and maternal environmental effects (\mathbf{e}_M), respectively. Error terms for B and W are \mathbf{e}_B and \mathbf{e}_W , respectively. Fixed effects for B were sex, age of dam (4 classes), and contemporary groups (103 classes), whereas for W the same effects

were included, plus the integer covariate age of calf (in days). Breeding values were assumed to be distributed as

$$\begin{bmatrix} \mathbf{a}_{BD} \\ \mathbf{a}_{BM} \\ \mathbf{a}_{WD} \\ \mathbf{a}_{WM} \end{bmatrix} \sim N \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_{A_{BD}}^2 & \sigma_{A_{BD-BM}} & \sigma_{A_{BD-WD}} & \sigma_{A_{BD-WM}} \\ \sigma_{A_{BD-BM}} & \sigma_{A_{BM}}^2 & \sigma_{A_{BM-WD}} & \sigma_{A_{BM-WM}} \\ \sigma_{A_{BD-WD}} & \sigma_{A_{BM-WD}} & \sigma_{A_{WD}}^2 & \sigma_{A_{WD-WM}} \\ \sigma_{A_{BD-WM}} & \sigma_{A_{BM-WM}} & \sigma_{A_{WD-WM}} & \sigma_{A_{WM}}^2 \end{bmatrix} \right) \quad [2]$$

$$\otimes \mathbf{A} = \mathbf{G}_0 \otimes \mathbf{A}$$

where \mathbf{G}_0 is the 4×4 additive covariance matrix among the traits, and \mathbf{A} is the additive relationship matrix.

A normal density is also assumed for maternal environmental effects, such that

$$\mathbf{e}_M \sim N \left(\mathbf{0}, \sigma_{E_M}^2 \right). \quad [3]$$

Error terms were distributed as follows:

$$\begin{bmatrix} \mathbf{e}_B \\ \mathbf{e}_W \end{bmatrix} \sim N \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \mathbf{I} \otimes \begin{bmatrix} \sigma_{E_B}^2 & \sigma_{E_{BW}} \\ \sigma_{E_{BW}} & \sigma_{E_W}^2 \end{bmatrix} \right). \quad [4]$$

Estimation of Variance Components

The covariance components in [2], [3], and [4] were estimated using a Bayesian procedure by means of a Gibbs sampling algorithm, as described in section 13.4 of Sorensen and Gianola (2002). The only difference with their multiple-trait algorithm was the use of a normal prior for the vectors β_B and β_W , with a covariance matrix reflecting independent and identically distributed elements having a large variance (108). The idea was to reflect high uncertainty on the prior distribution of the fixed effects (Cantet et al., 2004), whereas the posterior distribution is proper (Hobert and Casella, 1996). Conditionally on the additive genetic covariance components, the prior distribution for BV was as in [2]. The prior density for the vector \mathbf{e}_M was as in [3]. For the covariance components, prior inverted Wishart distributions were used for \mathbf{G}_0 and \mathbf{R}_0 , and a scaled inverted chi-square density for $\sigma_{E_M}^2$.

A single chain Gibbs sampler was run to draw 210,000 samples, and the first 10,000 iterates were discarded due to burn-in. The Bayesian Output Analysis (BOA version 1.1.5; Smith, 2005) package was used to calculate the autocorrelations for all lags from 1 to 200. Mean, mode, median, SD, and 95% high posterior den-

sity (95% HPD) interval were then calculated with BOA for all parameters from the individual marginal posteriors, under the free software *R* (<http://www.r-project.org/>).

Trajectory of Genetic Covariance Due to Selection

The procedure of Sorensen et al. (2001) was employed to infer the trajectory of \mathbf{G}_0 during the course of selection. In doing so, animals were classified into generations using their generation numbers (\mathbf{g} , Brinks et al., 1961) as follows:

$$g \text{ of the individual} = \frac{g \text{ of the sire} + g \text{ of the dam}}{2} + 1. \quad [5]$$

The g of founder individuals were set to 1, and then the above formula was used on the 2,369 animals in the pedigree file. Overlapping generations were then transformed to discrete generations by setting, for example, every value between 3.0 and 3.99 to 3, and from 5.0 to 5.99 to 5, and so on. This resulted in the 2,369 animals classified in 7 generations with 253, 566, 491, 359, 259, 224, and 217 individuals in generations 1 to 7, respectively. Now, let $a_{it(d)}$ be the additive genetic value for genetic effect t of animal i ($i = 1, \dots, 2,369$) in discrete generation d ($d = 1, \dots, 7$). Then, Sorensen et al. (2001) observed that the jk element ($j, k = BD, BM, WD, \text{ and } WM$) of the genetic covariance matrix in generation d is equal to

$$\sigma_{A_{jk(d)}} = \frac{1}{n_d} \sum_{i=1}^{n_d} a_{ij(d)} a_{ik(d)} - \left(\sum_{i=1}^{n_d} a_{ij(d)} \right) \left(\sum_{i=1}^{n_d} a_{ik(d)} \right). \quad [6]$$

At each iteration of the Gibbs sampler, formula [6] was used to calculate the 10 different elements of each of all 7 $\mathbf{G}_{0(d)}$ matrices.

Response to Selection

Two methods were used to estimate selection response as linear combinations of the BV: 1) regression of the BV averages on generation coefficients, and 2) mean BV across generations. Both methods were estimated for all 4 sets of BV, using the Bayesian procedure of Sorensen et al. (1994) by means of the Gibbs sampler.

RESULTS

Inbreeding

The average inbreeding was 0.0164 ± 0.0345 , with values ranging from 0 to 0.2805. The evolution of in-

Table 1. Posterior statistics for additive genetic (co)variances (kg²)

Parameter ¹	Mean	Median	Mode	SD	95% HPD ²	h^2 or r_G
$\sigma_{A_{BD}}^2$	8.444	8.383	9.156	1.505	6.073; 11.043	$h_{BD}^2 = 0.40$
$\sigma_{A_{BD-BM}}$	0.071	0.099	0.422	0.809	-1.308; 1.354	$r_G = 0.01$
$\sigma_{A_{BD-WD}}$	1.193	1.057	-0.507	3.842	-4.845; 7.796	$r_G = 0.07$
$\sigma_{A_{BD-WM}}$	1.474	1.583	-1.063	4.443	-5.995; 8.634	$r_G = 0.04$
$\sigma_{A_{BM}}^2$	4.817	4.787	4.368	0.794	3.577; 6.168	$h_{BM}^2 = 0.23$
$\sigma_{A_{BM-WD}}$	7.020	6.984	5.125	2.617	2.757; 11.374	$r_G = 0.60$
$\sigma_{A_{BM-WM}}$	14.558	14.389	12.300	3.593	8.991; 20.748	$r_G = 0.58$
$\sigma_{A_{WD}}^2$	28.081	26.293	20.821	11.56	12.992; 50.128	$h_{WD}^2 = 0.05$
$\sigma_{A_{WD-WM}}$	22.206	22.826	16.062	14.817	-3.266; 45.876	$r_G = 0.37$
$\sigma_{A_{WM}}^2$	128.109	124.591	110.952	39.264	70.626; 99.021	$h_{WM}^2 = 0.23$

¹ $\sigma_{A_{BD}}^2$ = additive variance for direct effects of birth weight; $\sigma_{A_{BD-BM}}$ = additive covariance between direct and maternal effects for birth weight; $\sigma_{A_{BD-WD}}$ = additive covariance between direct effects of birth and weaning weight; $\sigma_{A_{BD-WM}}$ = additive covariance between direct effects of birth weight and maternal effects of weaning weight; $\sigma_{A_{BM}}^2$ = additive variance for maternal effects of birth weight; $\sigma_{A_{BM-WD}}$ = additive covariance between maternal effects of birth weight and direct effects of weaning weight; $\sigma_{A_{BM-WM}}$ = additive covariance between maternal effects of birth and weaning weight; $\sigma_{A_{WD}}^2$ = additive variance for direct effects of weaning weight; $\sigma_{A_{WD-WM}}$ = additive covariance between direct and maternal effects for weaning weight; $\sigma_{A_{WM}}^2$ = additive variance for maternal effects of weaning weight; r_G = additive correlation between direct and maternal effects for weaning weight.

²95% HPD = 95% high posterior density interval.

breeding with the generations of selections is displayed in Figure 1.

Estimates of the (Co)Variance Components

Posterior statistics (mean, median, mode, SE, and 95% HPD intervals) for the additive genetic (co)variance components are displayed in Table 1, whereas similar statistics for error (co)variances are shown in Table 2. Posterior means and medians tended to agree,

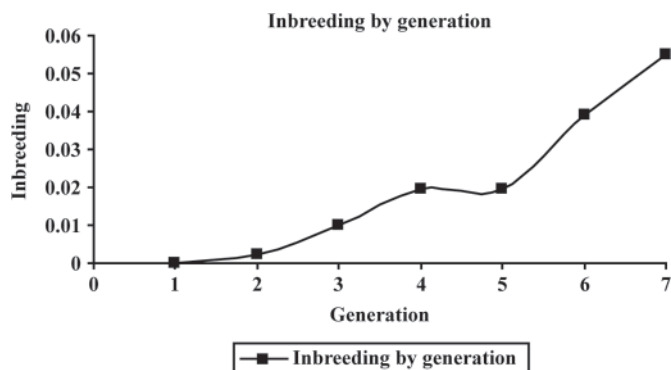


Figure 1. Inbreeding by generation.

whereas posterior modes were somewhat different from the other 2 statistics. Heritabilities and genetic correlations were then estimated using posterior means. Only the 95% HPD intervals of $\sigma_{A_{BM-WD}}$, $\sigma_{A_{BM-WM}}$, and $\sigma_{e_{B-W}}$ did not include 0. Whereas the estimates of h_{BD}^2 , h_{BM}^2 , and h_{WM}^2 were close to the average of published values, the estimate of h_{WD}^2 was much less (0.05). Surprisingly, the estimate of the genetic correlation between WD and WM displayed a positive sign and had a sizeable magnitude ($r_G = 0.37$). The correlation between BD and BM was close to zero ($r_G = 0.01$).

Estimates of the (co)variance components assessing the effects of selection can be seen in Table 3, where the trajectories of all of the different elements of $\mathbf{G}_{0(d)}$ are inferred across generations. Notice that all (co)variances decrease in magnitude through time. The precision of the estimated variances was greater than the precision of the estimated covariances.

Response to Selection

The linear regressions of BV on generation coefficients are displayed in Table 4. The average means of BV across generations are shown in Figure 2. In both periods BD decreased, whereas BM increased. The reduction of BD due to selection was slightly larger in

Table 2. Posterior statistics for error (co)variances (kg²)

Parameter ¹	Mean	Median	Mode	SD	95% HPD ²
$\sigma_{E_M}^2$	58.240	58.079	36.321	23.842	18.577; 97.973
$\sigma_{E_B}^2$	7.789	7.793	7.620	0.824	6.415; 9.145
$\sigma_{E_{B-W}}$	26.122	26.126	24.538	2.673	21.756; 30.521
$\sigma_{E_W}^2$	311.946	311.771	317.587	14.568	288.268; 336.196

¹ $\sigma_{E_M}^2$ = maternal environmental variance; $\sigma_{E_B}^2$ = error variance for birth weight; $\sigma_{E_{B-W}}$ = error covariance between birth and weaning weight; $\sigma_{E_W}^2$ = error variance for weaning weight.

²95% HPD = 95% high posterior density interval.

the second period than in the first. The regression of BV for WD increased due to selection in both periods, but selection response was 21.6% larger from 1986 to 1992 than from 1993 to 2006. The maternal component WM increased more than 3 times when compared with WD in the first period, but ended up having almost the same magnitude as WD in the second period. Whereas the 95% HPD intervals for the regression of BD on generation coefficients did not include 0 in both periods and WM in the first period, the 95% HPD of BM and WD included 0 in both periods and WM in the second period.

DISCUSSION

The results of the current experiment show that selection for greater BW at weaning in beef cattle, although not increasing BW at birth, is achievable. The genetic trends for WD and WM in both periods are positive, whereas the trend for B seems to be null as the trend for BD is negative and the trend for BM is positive (though maternal effects are expressed one generation of selection later). Melucci and Mezzadra (2002) analyzed the same experiment up until 2001 using the same 2-trait model as the one employed to calculate the BLUP in the second period: B with the BD component only and W with WD and WM effects. They found a positive trend for W and no change for B. Overall, the magnitude of observed trends is moderate. This may partly be explained by the size of the estimated direct additive variances for B and W (see below), partly by the fact that selection was practiced only in males, and finally by the small size of the herd so that the actual selection pressure in bulls was low.

There have been 3 selection experiments with beef cattle using an antagonistic selection objective (MacNeil et al., 1998; MacNeil, 2003; Bennett, 2008). In those experiments, the trait selected in the upward direction was yearling weight, whereas B (or calving difficulty, a trait positively correlated with B) was selected in the downward direction. However, in the mostly pastoral beef production system that predominated in Argentina up until the increase in the use of feedlots in the last decade, greater yearling weights or mature weights were

economically undesirable as the time to finish a large steer on grass increases. Therefore, W was chosen as the trait that was selected upward because it is economically important for the cow-calf operation (Melucci et al., 1983). The genetic trends observed in our research for the first period of selection were -0.355 , 0.222 , 0.574 , and 1.861 kg per generation, for BD, BM, WD, and WM, respectively. The fact that the response for WM was more than 3 times the corresponding value for WD may be due to the index used and to the larger value of the estimated h_{WM}^2 (0.23) when compared with h_{WD}^2 (0.05) and the positive correlation between them ($r_G = 0.37$). Selecting for greater RGD “would have relatively little effect on mature size” (Fitzhugh, 1976) and might have increased WM because calves with the greatest BW gain from birth to weaning tended to be selected, the progeny of cows with greater maternal ability. For BD, BM, WD, and WM, the genetic changes in average BV during the second stage were -0.396 , 0.251 , 0.472 , and 0.474 kg per generation, respectively. The values estimated for the genetic trends for BD and BM are intermediate to those obtained by MacNeil et al. (1998), MacNeil (2003), and Bennett (2008), whereas genetic trends for WD and WM were less than in previous research. A comparison of our results with these experiments is somewhat handicapped by differences in the selection criteria, plus the fact that their results were expressed as differences from a control line. In all experiments, including ours, most selection occurred on the bull side, with some culling of females based on selection targets occurring in the experiment reported by Bennett (2008). The control line of MacNeil et al. (1998) was mass-selected for increased yearling weight. In the case of the experiment by Bennett (2008), the control line was selected for similar growth rate after birth as the index line. It would have been desirable (Mrode, 1988; Sorensen et al., 2003) to include a control line in our experiment, but facilities were not available. MacNeil et al. (1998) performed a 2-stage selection experiment in Herefords by independent culling levels for below-average B and high yearling weight. They obtained a small decrease in BD (-0.052 kg per generation) and a small increase in BM (0.177 kg per generation). MacNeil (2003) reported a selection ex-

Table 3. Posterior means of the (co)variance components (kg^2) across generations (Monte Carlo SE are in parentheses)

Generation	n	Parameter ¹									
		$\sigma_{A_{BD}}^2$	$\sigma_{A_{BD-BM}}$	$\sigma_{A_{BD-WD}}$	$\sigma_{A_{BD-WM}}$	$\sigma_{A_{BM}}$	$\sigma_{A_{BM-WD}}$	$\sigma_{A_{BM-WM}}$	$\sigma_{A_{WD}}^2$	$\sigma_{A_{WD-WM}}$	$\sigma_{A_{WM}}^2$
1	253	9.09 (1.7)	0.06 (0.9)	1.51 (4.1)	1.03 (4.81)	5.18 (0.9)	7.63 (2.91)	15.51 (3.76)	29.5 (12.39)	22.67 (15.45)	133.37 (40.35)
2	566	10.17 (1.67)	-0.57 (0.92)	0.88 (4.29)	-1.32 (4.81)	5.00 (0.85)	7.34 (2.73)	14.29 (3.45)	28.56 (11.57)	20.75 (14.6)	127.52 (37.45)
3	491	8.1 (1.34)	-0.32 (0.79)	1.19 (3.56)	0.22 (3.96)	5.05 (0.85)	7.37 (2.65)	14.17 (3.42)	27.81 (11.13)	20.2 (13.58)	121.67 (34.96)
4	359	7.2 (1.2)	-0.07 (0.69)	1.44 (3.2)	-0.19 (3.74)	4.52 (0.78)	6.47 (2.36)	11.91 (3.27)	25.57 (10.14)	15.78 (12.52)	111.65 (34.09)
5	259	7.16 (1.2)	-0.35 (0.73)	1.2 (3.18)	-0.08 (3.62)	4.24 (0.76)	6.13 (2.25)	10.73 (3.02)	24.65 (9.7)	14.26 (11.43)	100.19 (29.69)
6	224	6.14 (1.09)	-0.23 (0.65)	1.24 (2.83)	1.03 (3.41)	3.91 (0.72)	5.49 (2.12)	11.51 (3.27)	23.12 (9.1)	15.49 (12.36)	111.04 (35.35)
7	217	6.65 (1.21)	-0.04 (0.75)	1.74 (3.14)	0.19 (4.08)	3.88 (0.78)	5.44 (2.2)	11.68 (3.63)	23.04 (9.39)	15.14 (12.83)	112.06 (38.5)

¹ $\sigma_{A_{BD}}^2$ = additive variance for direct effects of birth weight; $\sigma_{A_{BD-BM}}$ = additive covariance between direct and maternal effects for birth weight; $\sigma_{A_{BD-WD}}$ = additive covariance between direct effects of birth and weaning weight; $\sigma_{A_{BD-WM}}$ = additive covariance between direct effects of birth weight and maternal effects of weaning weight; $\sigma_{A_{BM}}$ = additive variance for maternal effects of birth weight; $\sigma_{A_{BM-WD}}$ = additive covariance between maternal effects of birth weight and direct effects of weaning weight; $\sigma_{A_{BM-WM}}$ = additive covariance between maternal effects of birth and weaning weight; $\sigma_{A_{WD}}^2$ = additive variance for direct effects of weaning weight; $\sigma_{A_{WD-WM}}$ = additive covariance between direct and maternal effects for weaning weight; $\sigma_{A_{WM}}^2$ = additive variance for maternal effects of weaning weight.

Table 4. Posterior means (kg) of the regression of breeding values on generation coefficients at the 2 selection periods followed by 95% high posterior density intervals¹

Period	BD			BM			WD			WM		
	Mean	SE	95% HDI	Mean	SE	95% HDI	Mean	SE	95% HDI	Mean	SE	95% HDI
1986 to 1992	-0.355	± 0.216	(-0.712; -0.004)	0.222	± 0.180	(-0.072; 0.518)	0.574	± 0.556	(-0.323; 1.502)	1.861	± 0.927	(0.358; 3.397)
1993 to 2006	-0.396	± 0.172	(-0.681; -0.116)	0.251	± 0.167	(-0.018; 0.531)	0.472	± 0.446	(-0.247; 1.214)	0.474	± 0.878	(-0.961; 1.932)

¹BD = birth weight direct effects; BM = birth weight maternal effects; WD = weaning weight direct effects; WM = weaning weight maternal effects.

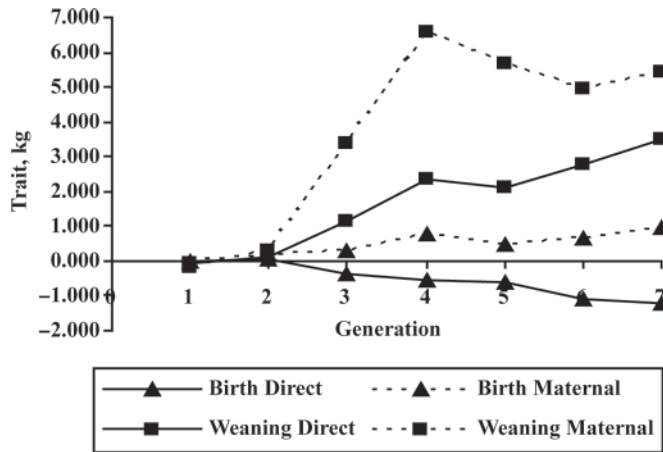


Figure 2. Posterior means (kg) of the breeding value averages per generation.

periment with a composite population using the selection index proposed by Dickerson et al. (1974): yearling weight minus 3.2 B. The regressions of estimated BV on generation coefficients were 0.45 for BD and 0.04 for BM. The estimated genetic correlation between BD and yearling weight was 0.71, indicating a strong antagonistic effect when attempting not to increase B. In comparison, the genetic correlation between BD and WD in our study was much less (additive correlation between direct and maternal effects for weaning weight, $r_G = 0.07$). Using 7 different purebred and composite populations, Bennett (2008) informed the results of selecting for decreased 2-yr-old heifer calving difficulty score and greater WM and yearling weight, using a procedure that mimics the restricted and desired BW gains index of Brascamp (1984). If one considers the values at the beginning and at the end of the selection period from Figure 2 of Brascamp (1984), and after 1.56 generations of selection, the resulting genetic trends are -1.09 and 2.69 kg per generation for BW at birth and weaning, respectively. Selection pressures, measured as the ratio of number of selected bulls divided by the number of males calves born in the experiment, were similar across experiments: 0.078 (MacNeil et al., 1998), 0.086 (MacNeil, 2003), 0.100 (Bennett, 2008), and 0.096 (current experiment). Also, selection accuracy was probably greater in the experiment of Bennett (2008), because the selection was based on BLUP from a multiple trait animal model. MacNeil et al. (1998), MacNeil (2003), and the first stage of the current research used mass selection on precorrected data. In the second period of the current research, BLUP of BV from multiple trait animal models with maternal effects were used, so the accuracy was probably similar to the one from the experiment by Bennett (2008) and greater than the other 2.

When compared with most other literature estimates, the values of heritabilities and genetic correlations are close to the average except for 2 peculiarities: 1) the

low value of h^2_{WD} (0.05); 2) the positive correlation between WD and WM ($r_G = 0.37$). Meyer (1993) found more frequent negative estimates of $\sigma_{A_{WD-WM}}$ in field data than in those data sets that originated from experimental herds. Whether this is due to more uniform management of experimental animals, or to lack of preferential treatment in the case of experimental data, remains to be seen. The SE of the estimated covariance components are reasonable, and whereas the HPD 95% interval of $\sigma_{A_{WD}}^2$ does not include 0, it is marginally within the interval for $\sigma_{A_{WD-WM}}$. Moreover, the number of calves per cow, a key element to disentangle direct from maternal effects, was equal to 2.79, which is similar to the value of 2.87 from the experiment by MacNeil et al. (1998). Therefore, there seems to be enough information in the data set for the (co)variance components to be reasonably well estimated. Thus, the larger value of h^2_{WM} than h^2_{WD} and the positive genetic correlation between WD and WM may also explain in part the larger genetic trend for WM than for WD, when the latter was the genetic component directly selected for, as explained above.

Of particular interest in this experiment is the measurement of the dynamics of the additive genetic covariance matrix during the course of selection. The Bayesian methodology set forth by Sorensen et al. (2001) allowed estimating the individual covariance components at each of the 7 generations. The procedure requires that selection be ignorable (Sorensen et al., 2001), which is taken care of because all data collected in the experiment were used in the analysis (data based selection). A look at the estimates in posterior means of the (co)variance components across generations indicates that all variances and covariances decreased in magnitude as selection generations progressed, thus evidencing the Bulmer effect (Bulmer, 1971). As expected, the decreasing trend was more consistent for the variances of BV of the traits directly selected for (BD and WD) than for those that were indirectly selected (BM and WM). Whereas the use of expression (9.30) in Bulmer (1985; with $h^2 = 0.05$, and a selection intensity in males of 2.135 from $\alpha = 0.042$: the theoretically smallest male selection ratio) produced a reduction in the magnitude of $\sigma_{A_{WD}}^2$ to 96% of its original value after approximately 7 generations of selection; the estimated change was 78.1% of the initial value. Corresponding figures for $\sigma_{A_{BD}}^2$ were 83.1 and 73.1%. We were not able to detect any other research report about a selection experiment where the Bulmer effect has been measured under a multiple trait setting.

Selection of beef cattle to increase BW at weaning, although not increasing BW at birth, is feasible. To achieve such a selection goal, commercial breeders can take advantage of national genetic evaluations to select bulls from sire summaries with an index such as the one used here.

LITERATURE CITED

- Bennett, G. L. 2008. Experimental selection for calving ease and postnatal growth in seven cattle populations. I. Changes in estimated breeding values. *J. Anim. Sci.* 81:2093–2102.
- Brascamp, E. W. 1984. Selection indices with constraints. *Anim. Breed. Abstr.* 52:645–654.
- Brinks, J. S., R. T. Clark, and F. J. Rice. 1961. Estimation of genetic trends in beef cattle. *J. Anim. Sci.* 20:903. (Abstr.)
- Bulmer, M. G. 1971. The effect of selection on genetic variability. *Am. Nat.* 105:201–211.
- Bulmer, M. G. 1985. *The Mathematical Theory of Quantitative Genetics*. Clarendon Press, Oxford, UK.
- Cantet, R. J. C., A. N. Birchmeier, and J. P. Steibel. 2004. Full conjugate analysis of normal multiple traits with missing records using a Generalized Inverted Wishart. *Genet. Sel. Evol.* 36:49–64.
- 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.
- Fitzhugh, H. A. 1976. Analysis of growth curves and strategies for altering their shape. *J. Anim. Sci.* 42:1036–1051.
- Gutiérrez, J. P., and F. Goyache. 2005. A note on ENDOG: A computer program for analyzing pedigree information. *J. Anim. Breed. Genet.* 122:172–176.
- Hobert, J. P., and G. Casella. 1996. The effect of improper priors on Gibbs sampling in hierarchical linear mixed model. *J. Am. Stat. Assoc.* 91:1461–1473.
- Lin, C. Y. 1990. A unified procedure of computing restricted best linear unbiased prediction and restricted selection index. *J. Anim. Breed. Genet.* 107:311–315.
- MacCluer, J., B. Boyce, L. Dyke, D. Weitzkamp, A. Pfenning, and C. Parsons. 1983. Inbreeding and pedigree structure in Standardbred horses. *J. Hered.* 74:394–399.
- 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., J. J. Urlick, and W. M. Snelling. 1998. Comparison of selection by independent culling levels for below-average birth weight and high yearling weight with mass selection for high yearling weight in line 1 Hereford cattle. *J. Anim. Sci.* 76:458–467.
- Melucci, L. M. 1995. Estimación de un índice genético restringido para crecimiento predestete en bovinos para carne. Resúmenes 1° Jornada Argentino-Chilena de Genética. XXVI Congreso Argentino de Genética y XXVIII Reunión Anual de la Sociedad de Genética de Chile. Bariloche 22–26 Octubre 1995. Argentina.
- Melucci, L. M., and C. A. Mezzadra. 2002. Respuesta a la selección por crecimiento en ganado Hereford. Actas XXXI Congreso Argentino de Genética. *J. Basic Appl. Genet.* XV(Suppl.):129. (Abstr.)
- Melucci, L. M., M. C. Miquel, and H. A. Molinuevo. 1983. Índices de selección para crecimiento en bovinos para carne. *Producción Anim.* 10:417–426.
- Meyer, K. 1993. Covariance matrices for growth traits of Australian Polled Hereford cattle. *Anim. Prod.* 57:37–45.
- Mrode, R. A. 1988. Selection experiments in beef cattle. Part I. A review of design and analysis. *Anim. Breed. Abstr.* 56:67–73.
- Smith, B. J. 2005. Bayesian Output Analysis Program (BOA), Version 1.1.5. The University of Iowa. <http://www.public-health.uiowa.edu/boa> Accessed Mar. 23, 2005.
- Sorensen, D. A., R. L. Fernando, and D. Gianola. 2001. Inferring the trajectory of genetic variance in the course of artificial selection. *Genet. Res.* 77:83–94.
- Sorensen, D. A., and D. Gianola. 2002. *Likelihood, Bayesian, and MCMC Methods in Quantitative Genetics*. Springer-Verlag, New York, NY.
- Sorensen, D. A., B. Gulbrandsen, and J. Jensen. 2003. On the need for a control line in selection experiments: A likelihood analysis. *Genet. Sel. Evol.* 35:3–20.
- Sorensen, D. A., C. S. Wang, J. Jensen, and D. Gianola. 1994. Bayesian analysis of genetic change due to selection using Gibbs sampling. *Genet. Sel. Evol.* 26:333–360.

References

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