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Genetic parameters for six measures of length of productive life and three measures of lifetime production by 6 yr after first calving for Hereford cows¹

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ABSTRACT: Genetic parameters for length of productive life given the opportunity (LPL|O), measured as days between first calving and disposal conditioned on one of six opportunity groups, L1 through L6 (e.g., L2 is length of productive life in days given the opportunity to live 2 yr after first calving), and lifetime production (LP), measured as the number of calves born (NB), number of calves weaned (NW), and cumulative weaning weight (CW) by 6 yr after first calving, were estimated using records of 1,886 Hereford cows from a selection experiment with three selected lines and a control line. Weaning weights were adjusted to 200 d of age and for sex and age of dam. Estimates of heritability and genetic and environmental correlations were obtained by restricted maximum likelihood with bivariate animal models, with year of birth of cow as a fixed effect and direct genetic and residual as random effects. Genetic trends were estimated by regressing means of estimated breeding values by year of birth and line on birth year. Estimates of heritability (SE) for LPL|O ranged from 0.05 (0.01) to 0.15 (0.03). Estimates of genetic correlations (SE) among LPL|O ranged from 0.74 (0.14) to 1.00 (0.00), and estimates of environmental

correlations ranged from 0.67 (0.05) to 0.98 (0.01). Estimates of heritability (SE) for NB, NW, and CW were 0.17 (0.05), 0.21 (0.06), and 0.18 (0.01). Estimates of genetic correlations (SE) among NB, NW, and CW ranged from 0.96 (0.02) to 0.99 (0.01). Estimates of environmental correlations (SE) ranged from 0.93 (0.01) to 0.99 (0.01). Estimates of genetic correlations for L6 with NB, NW, and CW were near 1.00 (0.09). Estimates of environmental correlations (SE) ranged from 0.57 (0.03) to 0.60 (0.03). Estimates of genetic change per year (SE) for L6 were low for all lines and ranged from -3.53 (2.09) to 4.63 (2.11) d/yr. Genetic trends for NB and NW were negligible for all lines. Genetic trends for CW were low and ranged from -2.81 (1.67) to 3.29 (1.76) kg/yr. Differences in genetic trends between selected lines and control were not significant ($P > 0.05$). Estimates of environmental trends (SE) over all lines were -104.00 (25.48) d/yr, -0.26 (0.02) calves/yr, -0.25 (0.02) calves/yr, and -55.10 (15.63) kg/yr, for L6, NB, NW, and CW, respectively. Selection for LPL|O or LP could be successful in a breeding program, but may be relatively slow due to the low magnitude of heritability and extended generation interval.

Key Words: Beef Cattle, Longevity, Selection

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Introduction

Length of productive life of a beef cow is a complex trait that reflects the performance of a cow over her total herd life, which is determined principally by her fertility, maternal ability, health (ability to avoid involuntary culling), and survival of herself and her calves.

Length of productive life is a trait that affects overall profitability and is an important component of efficiency in beef production.

Selection for length of productive life would be practical only with indicators of length of productive life which can be obtained early in life and which show genetic variation (Burnside and Wilton, 1970). The importance of length of productive life for economic value was outlined by Rendel and Robertson (1950). Longer productive life may increase profits by 1) decreasing annual cost of replacements of cows, 2) increasing herd production through an increase in proportion of cows in higher-producing age groups, 3) decreasing the number of replacements to be reared, and therefore allowing an increase in size of the productive herd, and 4) increasing voluntary culling.

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Weight of weaned calves per female accumulated over a lifetime is a comprehensive measure of fertility (pregnancy and calving rate), maternal ability (weaning rate), milking capacity (weaning weight), and cow survival (ability of the cow to delay culling or death), which has been proposed as an integral measurement of lifetime production (Tanida et al., 1988).

The objectives of this study were to 1) estimate genetic parameters for six measures of length of productive life and three measures of lifetime production evaluated to 6 y after calving, and 2) estimate genetic and environmental trends for these measures of length of productive life and lifetime production for a control and three selected lines of Hereford cows.

Materials and Methods

The Project

Data were from the Nebraska Agric. Exp. Stn. Project 40-002 entitled "Effect of selection for weaning weight, yearling weight, and muscling in beef cattle," in cooperation with the Roman L. Hruska U.S. Meat Animal Research Center (USMARC) (Koch et al., 1974a,b; 1994). Data used were from animals born from 1964 through 1980.

The Population

The three selection lines were established in 1960 by randomly allocating 325 cows from 14 Hereford herds to the weaning weight line (**WWL**), the yearling weight line (**YWL**), and the index line based on yearling weight and muscle score (**IXL**). The 42 foundation sires used from 1957 to 1963 were from 11 of the same 14 herds as the cows and from two other herds (Koch et al., 1974a,b; 1994).

The cattle were maintained at Fort Robinson Beef Cattle Research Station, Crawford, NE, until 1971, when they were moved to USMARC, near Clay Center, NE. The projected herd size of 150 breeding females per line was reached by 1964 and maintained until the end of the experiment. Approximately 225 foundation cows and other cows from the three selection lines that had been replaced were artificially inseminated with semen from seven of the foundation sires from 1968 through 1971 to provide the basis for a control line. In 1971, the control line (**CTL**) was established from 20 representative sons and heifer calves from matings with the 225 cows (Koch et al., 1974a,b; 1994).

Selection in WWL was based on weight adjusted to 200 d of age. Selection in YWL was based on weight at 452 d (approximately 15 mo of age) for bulls and at 550 d (approximately 18 mo of age) for heifers. Selection in IXL was based on an index giving equal emphasis to muscle score and yearling weight when both were expressed in standard measure. Selection of heifers in IXL from birth years 1960 through 1965 was based on yearling weight alone. Originally, only bulls were

evaluated for muscle score, but beginning in the 1966 birth year, heifers were also evaluated for muscle score and were selected for an index of muscle score and yearling weight until the end of the experiment (Koch et al., 1974a,b; 1994). Selection continued through matings to produce the 1982 calf crop.

Bulls were selected at 2 yr of age. Through 1970, two bulls were chosen from each year of birth and used to sire calves when 3, 4, and 5 yr old. After 1970, three 2-yr-old bulls were selected each year to be used for 2 yr (i.e., they sired calves when 3 and 4 yr of age. Bulls were removed from service early only because of breeding unsoundness. To minimize inbreeding, no more than two sons of a given sire or dam were selected (Koch et al., 1974a,b; Koch et al., 1994). Heifers born in 1964 and later were bred to calve at 2 yr of age. All heifers were exposed to bulls. Selection was practiced only among those that were pregnant. Through 1970, the top 25 heifers from each line were selected based on their line. After 1970, the top 35 heifers were selected. After 1973, essentially all pregnant heifers were kept in the herd. Cows were removed without regard to progeny performance based on the following criteria (Koch et al., 1974a,b; 1994): 1) not pregnant at weaning time; 2) serious unsoundness (e.g., cancer eye, chronic bloat, broken teeth); 3) failure to raise a live calf for two consecutive years; and 4) older cows were removed if, after Criteria 1 through 3 were applied, too many cows were still left.

Exceptions for Criteria 1 and 3 were made only when additional cows were needed to maintain the herd size.

For each breeding season, mating sires were randomly assigned to females within each age and line, except that half-sib or more closely related matings were avoided. The 60-d breeding season was generally during the months of June and July.

All lines were maintained as one herd except during the breeding season. The herd calved only in the spring. Calves were weaned together each year when the average age was about 200 d (Koch et al., 1974a,b; 1994).

Analysis of Length of Productive Life and Lifetime Production

Analysis of length of productive life requires that only observations from complete cohorts can be used (Schons et al., 1985; Tanida et al., 1988). Although a female receives a length of productive life observation when she leaves the herd, that observation cannot be used until all her contemporaries have left the herd. However, some of the drawbacks can be overcome using the concept of opportunity groups (Hudson and Van Vleck, 1981), which offer considerable flexibility in specification of length of productive life.

Length of productive life (**LPL|O**) was defined as the number of days a cow survived in the next N years given that she was alive at first calving and had the opportunity to stay in the herd at least N years. Opportunity, in this case, is determined by when the selection

experiment was terminated. A cow born 3 yr before termination of data collection and calving at 2 yr of age would have the opportunity to live only 1 yr. Length of productive life was defined for six different opportunity groups: **L1**, **L2**, **L3**, **L4**, **L5**, and **L6**, where, for example, L1 is the length of productive life in days in the next year of a cow that was alive at first calving and had the opportunity to live at least 1 yr longer. Lifetime production (**LP**) was defined in three ways (all corresponding to opportunity group, L6): 1) total number of calves born by 6 yr after first calving (**NB**); 2) total number of calves weaned by 6 yr after first calving (**NW**); and 3) total weaning weight in kilograms of all calves (adjusted to 200-d, and for sex and age of dam), by 6 yr after first calving (**CW**).

Records of a cow qualified for inclusion only if the cow calved as a 2 yr old. The NB excluded abortions and twins, and therefore is equivalent to total number of single calves born alive or dead. A total of 1,886 cows had records for longevity analysis (WWL, 507; YWL, 506; IXL, 485; and CTL, 388).

Genetic parameters were estimated using a two-trait animal model with data pooled from all lines. For all traits, the model included year the cow was born as a fixed effect and animal direct genetic as a random effect. The two-trait animal model was as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} X_1 & 0 \\ 0 & X_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 \\ 0 & Z_2 \end{bmatrix} \begin{bmatrix} u_1 \\ u_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where y_1 = an $n_1 \times 1$ vector of observations for Trait 1, y_2 = an $n_2 \times 1$ vector of observations for Trait 2, b_1 = a vector of fixed effects for Trait 1, b_2 = a vector of fixed effects for Trait 2, u_1 = a vector of random animal direct genetic values for Trait 1, u_2 = vector of random animal direct genetic values for Trait 2, e_1 = an $n_1 \times 1$ vector of random residual effects for Trait 1, e_2 = an $n_2 \times 1$ vector of random residual effects for Trait 2, and X, Z = known incidence matrices relating the observations to fixed and random effects, respectively.

The first and second moments of the model are assumed to be:

$$E \begin{bmatrix} y_1 \\ y_2 \\ u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} X_1 b_1 \\ X_2 b_2 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} \text{ and } \text{Var} \begin{bmatrix} u_1 \\ u_2 \\ e_1 \\ e_2 \end{bmatrix} = \begin{bmatrix} G_0 \otimes A & 0 \\ 0 & R_e \end{bmatrix}$$

where A = Wright's numerator relationship matrix:

$$G_0 = \begin{bmatrix} \sigma_{u1}^2 & \sigma_{u1u2} \\ \sigma_{u1u2} & \sigma_{u2}^2 \end{bmatrix}$$

σ_{u1}^2 = additive genetic variance for Trait 1, σ_{u2}^2 = additive genetic variance for Trait 2, σ_{u1u2} = additive genetic covariance between Trait 1 and Trait 2:

$$R_e = \begin{bmatrix} \sigma_{e1}^2 I_1 & 0 & 0 \\ 0 & R_0 \otimes I_2 & 0 \\ 0 & 0 & \sigma_{e2}^2 I_3 \end{bmatrix}, R_0 = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma_{e2}^2 \end{bmatrix},$$

σ_{e1}^2 = residual variance for Trait 1, σ_{e2}^2 = residual variance for Trait 2, σ_{e1e2} = residual covariance between Traits 1 and 2, I_1 = an identity matrix with order, number of animals with records only for Trait 1, I_2 = an identity matrix with order, number of animals with records for both traits, I_3 = an identity matrix with order, number of animals with records only for Trait 2.

For pairwise analyses with no missing values (e.g., L6 with NB, NW, and CW [$n_1 = n_2$]), I_1 and I_3 will collapse into I_2 (i.e., $R_e = R_0 \otimes I_2$).

Estimates of genetic parameters were obtained using a multiple trait derivative-free algorithm to obtain restricted maximum likelihood estimates with MTDFREML (Boldman et al., 1995) for combinations of traits with equal number of observations and, an AIREML algorithm (Kachman, 2001) with MATVEC (Wang, et al., 2002) for combinations of traits with unequal number of observations. Starting values for the estimates of (co)variance components were from the literature (Tanida et al., 1988, Morris et al., 1993, Arthur et al., 1994). The simplex algorithm was stopped when the variance of the function values (i.e., $-2\log L$ with L = likelihood given y) in the simplex was less than 1×10^{-6} . Once the convergence criterion was reached, fresh restarts from those estimates were continued until $-2\log L$ differed by less than 1×10^{-2} between successive restarts. The (co)variance components attained from the last restart were used for estimating breeding values.

Standard errors were obtained directly from MTDFREML program for the two-trait analyses for NB, NW, CW, and L6 because they had the same number of observations using the average information matrix. Due to a restriction in the MTDFREML program, standard errors for the estimates of parameters for multiple-trait analyses cannot be calculated when there are missing observations. Therefore, an AIREML algorithm (Kachman, 2001) was used with MATVEC (Wang, et al., 2002) to obtain the information matrix at convergence from the two-trait analyses for the six measures of length of productive life. Standard errors were estimated using the "delta method" and the average information matrix at convergence (Searle et al., 1992).

Genetic trends were estimated by regressing averages of estimated breeding values by year of birth and line on birth year. The environmental trend was estimated by regressing the solutions for birth year on birth year. Genetic and environmental trends were estimated only for L6, NB, NW, and CW.

Table 1. Summary of statistics unadjusted for model effects for each measure of length of productive life^a

Trait	No.	Mean	SD	CV, %	Minimum	Maximum
L1	1,886	334	81	24	4	365
L2	1,728	625	213	34	4	730
L3	1,566	894	350	39	4	1,095
L4	1,394	1,152	475	41	4	1,460
L5	1,224	1,445	554	38	4	1,825
L6	1,095	1,660	683	41	4	2,190

^aLN is the number of days a cow survived in the next N years given that she was alive at first calving and had the opportunity to live up to N yr longer.

Results and Discussion

Table 1 summarizes the number of observations and descriptive statistics for different definitions of length of productive life. Phenotypic means and unadjusted standard deviations for length of productive life ranged from 334 ± 81 for L1 to $1,660 \pm 663$ d for L6.

Table 2 contains descriptive statistics for NB, NW, and CW. Phenotypic means were 3.72 ± 2.07 , 3.22 ± 2.07 , and 637 ± 437 for NB, NW, and CW (kg), respectively. These values are comparable to previous reports (Cundiff et al., 1992; Arthur et al., 1993).

Estimates of Genetic Parameters

Table 3 summarizes estimates of heritability and genetic and environmental correlations for measures of length of productive life from two-trait analyses. Estimates of heritability were low, ranging from 0.05 for L1 to 0.15 for L6. Estimates of heritability increased with increasing years of opportunity. Averages of estimates over all two-trait analyses were 0.05, 0.08, 0.08, 0.10, 0.12, and 0.15 for L1, L2, L3, L4, L5, and L6, respectively. The increase in estimates of heritability with increase in length of opportunity group may be due to longer periods for genetic differences to be expressed.

Estimates of heritability are within the range of estimates found in the literature for beef cattle (Tanida et al., 1988; Arthur and Makarechian, 1992; van der Westhuizen et al., 2001). Tanida et al. (1988) reported estimates of heritability for length of productive life (age between first calving and disposal) in Hereford cows of 0.26 (SE = 0.08) from paternal half-sib analysis and 0.16 (0.08) from daughter-dam regression. Estimate of heritability by Arthur and Makarechian (1992) was 0.18 (0.14). Later, Arthur et al. (1994) reported an

estimate of heritability of 0.22 (0.01). An estimate of heritability for length of productive life measured as number of mating years by Morris et al. (1993) was 0.13 (0.08). In South Africa, van der Westhuizen et al. (2001) reported an estimate of heritability for length of productive life of 0.08.

Estimates of genetic correlations were in the range of 0.74 to 1.00 for L1 with L6, for L2 with L3, and L4 with L5, respectively, as would be expected from the part-whole relationships. The estimates of genetic correlations tended to decrease with each added 1-yr increments between the opportunity groups. Thus, for analyses of L1 with L2, L3, L4, L5, and L6, estimates of genetic correlations were 0.89, 0.83, 0.83, 0.76, and 0.74, respectively. The pattern was similar for the other combinations of LPL|O. Similarly, estimates of environmental correlations were high with a range between 0.67 to 0.98, for L1 with L6, and for L5 with L6, respectively. Thus, for analyses of L1 with L2, L3, L4, L5, and L6, estimates of environmental correlations were 0.91, 0.81, 0.71, 0.70, and 0.67, respectively. As with the estimates of genetic correlations, estimates of environmental correlations decreased with each additional 1-yr increment between opportunity groups. The pattern was similar for the other combinations of LPL|O.

Table 4 summarizes results from two-trait analyses for estimates of genetic parameters for length of productive life to 6 y after first calving (L6) and lifetime production defined as NB, NW, or CW by 6 y after first calving. Estimates of heritability for L6, NB, NW, and CW ranged from low to medium. The estimates of heritability averaged 0.15, 0.17, 0.21, and 0.18 for L6, NB, NW, and CW, respectively. These estimates are similar to those reported by Arthur and Makarechian (1992), Arthur et al. (1994), and Morris et al. (1993).

Table 2. Summary of statistics unadjusted for model effects for NB, NW, and CW by 6 yr after first calving

Trait ^a	No.	Mean	SD	CV, %	Minimum	Maximum
NB	1,095	3.72	2.07	56	1	6
NW	1,095	3.22	2.15	67	0	6
CW	1,095	637	437	69	0	1,414

^aNB = number of calves born; NW = number of calves weaned; CW = cumulative weaning weight (kg).

Table 3. Estimates (and standard errors) of heritability, genetic and environmental correlations for length of productive life for several opportunity groups^{a,b}

Trait 1	Trait 2	σ_{p1}^2	σ_{p2}^2	h_1^2	h_2^2	r_g	r_e
L1	L2	5,409	36,367	0.05 ± 0.01	0.08 ± 0.02	0.89 ± 0.07	0.91 ± 0.00
	L3	5,414	95,103	0.05 ± 0.01	0.08 ± 0.02	0.83 ± 0.09	0.81 ± 0.01
	L4	5,412	186,932	0.05 ± 0.01	0.09 ± 0.03	0.83 ± 0.11	0.71 ± 0.03
	L5	5,413	335,316	0.05 ± 0.01	0.13 ± 0.03	0.76 ± 0.13	0.70 ± 0.03
	L6	5,417	487,090	0.05 ± 0.01	0.15 ± 0.03	0.74 ± 0.14	0.67 ± 0.05
L2	L3	36,349	101,485	0.07 ± 0.02	0.08 ± 0.02	1.00 ± 0.00	0.96 ± 0.01
	L4	36,341	199,485	0.08 ± 0.02	0.09 ± 0.02	0.98 ± 0.01	0.89 ± 0.01
	L5	36,335	361,968	0.08 ± 0.02	0.12 ± 0.03	0.96 ± 0.01	0.84 ± 0.01
	L6	36,342	523,308	0.08 ± 0.02	0.15 ± 0.03	0.90 ± 0.03	0.80 ± 0.04
L3	L4	93,535	186,993	0.08 ± 0.02	0.09 ± 0.02	0.99 ± 0.01	0.97 ± 0.01
	L5	93,799	338,251	0.08 ± 0.02	0.12 ± 0.03	0.98 ± 0.01	0.93 ± 0.02
	L6	94,523	503,981	0.08 ± 0.02	0.15 ± 0.03	0.93 ± 0.03	0.88 ± 0.03
L4	L5	163,222	347,143	0.10 ± 0.02	0.12 ± 0.03	1.00 ± 0.00	0.98 ± 0.01
	L6	163,850	436,696	0.09 ± 0.02	0.15 ± 0.03	0.97 ± 0.01	0.94 ± 0.01
L5	L6	331,317	466,243	0.12 ± 0.03	0.15 ± 0.03	0.99 ± 0.01	0.98 ± 0.01

^aLN is the length of productive life in days of a cow that was alive at first calving and had the opportunity to live up to N yr longer.

^b σ_{p1}^2 = estimate of phenotypic variance for Trait 1; σ_{p2}^2 = estimate of phenotypic variance for Trait 2; h_1^2 = estimate of heritability for Trait 1; h_2^2 = estimate of heritability for Trait 2; r_g = estimate of genetic correlation; r_e = estimate of environmental correlation.

Tanida et al. (1988) reported estimates of heritability for Hereford cows from daughter-dam regression and from paternal half-sib analyses for total number of calves weaned per cow of 0.16 (0.08) and 0.22 (0.08), respectively. Estimates of heritability for length of productive life (time between first calving and disposal) for Hereford cows were 0.26 (0.08) from half-sib analysis and 0.16 (0.08) from daughter-dam regression (Tanida et al., 1988). Estimates of heritability by Arthur and Makarechian (1992) were 0.18 (0.13) for LPL|O and 0.28 (0.14) for lifetime number of calves weaned. Morris et al. (1993) reported estimates of heritability of 0.13 (0.08), 0.11 (0.08), and 0.15 (0.08) for LPL|O, NB, and NW, respectively. Arthur et al. (1994) reported an estimate of heritability of 0.22 (0.01) for LPL|O and 0.24 (0.02) for lifetime NW.

Estimates of the genetic and environmental correlations are high, ranging from 0.96 to 1.00 and from 0.56

to 0.99, respectively. These estimates are within the range found in the literature (Tanida et al., 1988; Arthur and Makarechian, 1992). For Hereford cows, Tanida et al. (1988) reported estimates of genetic and phenotypic correlations between length of productive life measured as time between first calving and disposal date of 0.98 and 0.96, respectively. Similarly, estimates of genetic and phenotypic correlations for Angus cows were 1.05 (estimated from Henderson's Method III) and 0.96, respectively. Arthur and Makarechian (1992) reported estimates of genetic and phenotypic correlations between length of productive life measured as time between first calving and disposal date and number of calves weaned of 0.81 (0.13) and 0.90, respectively. Estimates of genetic and phenotypic correlations between length of productive life and cumulative weaning weight were 0.82 (0.13) and 0.89, respectively (Arthur and Makarechian, 1992). Estimates of genetic and phe-

Table 4. Estimates (and standard errors) of heritability, genetic and environmental correlations for NB, NW, CW (kg) and L6 (d), by 6 yr after first calving^{a,b}

Trait 1	Trait 2	σ_{p1}^2	σ_{p2}^2	h_1^2	h_2^2	r_g	r_e
L6	NB	466,564	3.68	0.15 ± 0.03	0.17 ± 0.05	1.00 ± 0.09	0.60 ± 0.03
	NW	466,733	4.08	0.15 ± 0.03	0.21 ± 0.06	1.00 ± 0.07	0.56 ± 0.03
	CW	466,359	163,968	0.15 ± 0.03	0.18 ± 0.01	1.00 ± 0.07	0.57 ± 0.03
NB	NW	3.63	4.02	0.16 ± 0.05	0.21 ± 0.05	0.99 ± 0.01	0.94 ± 0.01
	CW	3.62	162,370	0.17 ± 0.05	0.18 ± 0.01	0.96 ± 0.02	0.93 ± 0.01
NW	CW	4.03	162,137	0.20 ± 0.06	0.17 ± 0.01	0.98 ± 0.01	0.99 ± 0.01

^aNB = number of calves born; NW = number of calves weaned; CW = cumulative weaning weight; L6 = length of productive life for cows with opportunity to live at least 6 yr after first calving.

^b σ_{p1}^2 = estimate of phenotypic variance for Trait 1; σ_{p2}^2 = estimate of phenotypic variance for Trait 2; h_1^2 = estimate of heritability for Trait 1; h_2^2 = estimate of heritability for Trait 2; r_g = estimate of genetic correlation; r_e = estimate of environmental correlation.

Table 5. Estimates and standard errors of genetic and environmental trends per year for L6, NB, NW, and CW^{a,b}

Trait	Genetic				Environmental
	WWL	YWL	IXL	CTL	
L6	1.34 ± 1.99	-3.53 ± 2.09	-2.05 ± 1.76	4.63 ± 2.11	-104.00 ± 25.48
NB	0.01 ± 0.01	-0.01 ± 0.01	-0.01 ± 0.01	0.02 ± 0.01	-0.26 ± 0.02
NW	0.00 ± 0.01	-0.01 ± 0.01	-0.01 ± 0.01	0.02 ± 0.01	-0.25 ± 0.02
CW	1.24 ± 1.52	-2.81 ± 1.67	-0.66 ± 1.37	3.29 ± 1.76	-55.10 ± 15.63

^aDifferences in genetic trend between selected lines and CTL were not significant ($P > 0.05$); NB = number of calves born; NW = number of calves weaned; CW = cumulative weaning weight (kg); L6 = length of productive life (d) for cows with opportunity to live up to 6 yr after first calving.

^bWWL = weaning weight line; YWL = yearling weight line; IXL = index line for yearling weight and muscle score; CTL = control line.

notypic correlations between number of calves weaned and cumulative weaning weight were 1.00 (0.01) and 0.99 (Arthur and Makarechian, 1992).

Estimates of Genetic and Environmental Changes

Table 5 summarizes estimates of genetic and environmental changes per year for L6, NB, NW, and CW. The environmental trends were significantly negative for all traits. The genetic trends were not different from zero for NB and NW. Although none was statistically significant, estimates of genetic change for CW were 1.24, -2.81, -0.66, and 3.29 kg/yr for WWL, YWL, IXL, and CTL, respectively. The estimates of genetic change for L6 were 1.34, -3.53, -2.05, and 4.63 d/yr for WWL, YWL, IXL, and CTL, respectively, but only the change in CTL was significantly different from zero. No statistically significant differences were found between the selected lines (WWL, YWL, and IXL) and CTL ($P < 0.05$) for any of the traits. Unfortunately, a lack of research exists about previous estimates of genetic and environmental correlations between measures of length of productive life with different opportunity groups and lifetime production.

The small genetic changes for L6, NB, and NW with time are not surprising because of the small estimates of heritability and because direct selection was not applied for these traits. The small genetic change for CW is more surprising given the estimates of response to selection for weaning weight in the WWL and the estimates of correlated response in the YWL and IXL reported previously (Koch et al., 1994). The genetic model used in this study and results from the terminal phase of the selection experiment may be helpful in interpretation of this result. In the terminal phase of the experiment response to selection was partitioned into direct and maternal components for weaning weight and yearling weight (Koch et al., 2004) by evaluating differences between reciprocal crosses of each selection line with the control line. In the current study, CW is treated as a trait of the dam, so estimates of breeding value for weaning weight (CW) include half the direct breeding values plus all the maternal breeding values. Direct effects transmitted from sire to offspring would be asso-

ciated primarily with residual variance in the present analysis, as progeny of a cow in successive years were usually produced by different sires due to rerandomization of males and females mated each year and the pattern of sire replacement. For weaning weight, estimates of direct genetic response were: 12.3, 11.0, and 7.9 kg for WWL, YWL, and IXL, respectively. Estimates of maternal genetic response were: 1.2, -3.2, and 7.0 kg for WWL, YWL, and IXL, respectively (Koch et al., 2004). Estimates of genetic change shown (Table 5) would tend to correspond to maternal effects, for which estimates of genetic trend were small.

Implications

Selection for length of productive life given different opportunities to be alive (additional years after first calving), and lifetime production measured as number of calves born, number of calves weaned, and cumulative weaning weight by 6 yr after first calving would be possible, but would be expected to be slow due to low estimates of heritability and possible lengthening of the generation interval. The high estimates of genetic correlations among measures of length of productive life (various opportunity groups) indicate that length of productive life measured through 1 yr after first calving predicts productive life through 6 yr after first calving with reasonable accuracy. High genetic correlations among these measures of productivity traits suggest that any of the measures could be used to select for improving productive life. Selection for weights at weaning and yearling ages had little genetic effect on any measure of lifetime production.

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