

CORRELATED RESPONSES IN GROWTH AND
MATERNAL ABILITY OF SHORTHORN CATTLE
SELECTED FOR YEARLING WEIGHT.

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of
Graduate Studies
The University of Manitoba
by
Corinna Jasienczyk

In Partial Fulfillment of the
Requirements for the Degree
of
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OF SHORTHORN CATTLE SELECTED FOR YEARLING WEIGHT

BY

CORINNA JASIENCZYK

A Thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in
partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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ABSTRACT

Jasiencyk, Corinna L. M.Sc., The University of Manitoba, October 1992. Correlated Responses in Growth and Maternal Ability of Shorthorn Cattle Selected for Yearling Weight. Major Professor; Gary H. Crow.

Mixed-model methodology (also known as the animal model) was used to estimate breeding values of Shorthorn cattle for postweaning gain, direct weaning weight, and the maternal component of weaning weight, in a population selected for high yearling weight. The Shorthorn population consisted of a select line and an unselected control line, and represented 10 years of selection. In the studies by Newman et al. (1973) and Olthoff et al. (1990b), the control line was used to measure the yearly environmental changes (control-line method) in order to estimate the genetic responses of yearling weight and its correlated traits in the select line. In this thesis, the lines are analyzed together and separately: to compare the animal model results and conclusions to those of the control-line method for the genetic and environmental trends; to investigate the effectiveness of mixed-model methodology when a control is not available, as is typically the case in the livestock industry employing this method; and to investigate the sensitivity of the results to assumed genetic parameters by varying the genetic correlation between weaning weight and postweaning gain (+.5 or -.1), the environmental correlation between weaning weight and postweaning gain (+.2 or -.2), and the direct-maternal genetic correlation of weaning weight (+.5, 0.0, or -.5).

The genetic trends in postweaning gain, direct weaning weight, and maternal weaning weight were, respectively, 2.52 kg yr⁻¹, 1.16 kg yr⁻¹, and 0.30 kg yr⁻¹ when the lines were analyzed together. The genetic trend in yearling weight was constructed from the sum of its parts and was 4.53 kg yr⁻¹. Compared to the control-line method of Olthoff et al. (1990b), these results were, for yearling weight, postweaning gain, and direct weaning weaning weight, 96%, 92%, and 63% of the corresponding control-line genetic trend estimates. (The maternal weaning weight trend could not be calculated by the control-line method.) When only the select-line data were analyzed, the genetic trends for yearling weight, postweaning gain, direct weaning weight, and maternal weaning weight were, respectively, 3.07 kg yr⁻¹, 2.07 kg yr⁻¹, 1.17 kg yr⁻¹, and 0.30 kg yr⁻¹. These results are also less than those estimated by the control-line method.

The effect of the assumed genetic correlations on the genetic trends was investigated. Trends in postweaning gain and direct weaning weight were primarily influenced by the assumed genetic correlation between weaning weight and postweaning gain, and trends in maternal weaning weight, by the assumed direct-maternal correlation for weaning weight.

Results indicated more variability in postweaning gain genetic trend and the environmental effect than in weaning weight. The ranking of ten sires and ten yearling bulls for estimated breeding values for the three correlated traits varied with the twelve assumed parameter combinations, and also depended on whether the select line was analyzed alone or with the control line. The ranking was least variable for postweaning gain. The mixed-model methodology seemed to be least effective in

separating the genetic and environmental components when a trait has a large environmental component in its phenotypic response.

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I would like to thank Dr. G.H. Crow for his guidance and constructive criticism throughout my program of study. I wish to acknowledge the financial support for this study by Agriculture Canada under the Agri-Food Agreement, a subsidiary agreement of the Canada-Manitoba Economic and Regional Development Agreement. Finally, I would like to dedicate this thesis to my family and friends for their support and encouragement.

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LIST OF ABBREVIATIONS

- for weaning weight (direct and maternal) and postweaning gain

WWD = direct component of weaning weight

WWM = maternal component of weaning weight

WWPE = permanent maternal environment component of weaning weight

PWG = direct component of postweaning gain

| Breeding values | Environment | Phenotype |
|-------------------|------------------|------------------|
| G_{WWD} | E_{WW} | P_{WW} |
| G_{WWM} | E_{WWPE} | |
| G_{PWG} | E_{PWG} | P_{PWG} |
| Variances | | |
| $V_{G:WWD}$ | $V_{E:WW}$ | $V_{P:WW}$ |
| $V_{G:WWM}$ | $V_{E:WWPE}$ | |
| $V_{G:PWG}$ | $V_{E:PWG}$ | $V_{P:PWG}$ |
| Covariances | | |
| $COV_{G:WWD,WWM}$ | $COV_{E:WW,PWG}$ | $COV_{P:WW,PWG}$ |
| $COV_{G:WWD,PWG}$ | | |
| Correlations | | |
| $r_{G:WWD,WWM}$ | $r_{E:WW,PWG}$ | $r_{P:WW,PWG}$ |
| $r_{G:WWD,PWG}$ | | |
| $r_{G:PWG,WWM}$ | | |
| Heritabilities | | |
| h^2_{WWD} | | |
| h^2_{WWM} | | |
| h^2_{PWG} | | |

INTRODUCTION

Most farm livestock evaluation programs currently use mixed-model methodology (eg. Quaas and Pollak, 1980) to estimate breeding values for traits of interest. This method simultaneously estimates the environmental and genetic components, and can estimate breeding values of all individuals for all traits, regardless of whether there is an actual observation or not. This is accomplished by using the genetic relationships among individuals (eg. sire, dam). Maternal ability, for example, is a trait of the dam expressed only in the weaning weight of her calf (Hohenboken, 1985a) but maternal breeding values for sires can be estimated through records on their dams, daughters, and sisters. Implicit in this methodology is prior knowledge of the variances and covariances among the random effects of the model for all traits (Schaeffer and Wilton, 1981). The variances and covariances are calculated from genetic parameters obtained from the literature or from population analysis. In either case, they are subject to error. The dependence of the estimated breeding values on the assumed genetic parameters needs to be better understood to ensure that selection is based on information that is as accurate as possible. One way of assessing the effectiveness and accuracy of the mixed-model methodology is to compare the results and conclusions obtained to a more traditional method, such as the use of an unselected control population to measure the environmental trend, and, by subtraction from a selected population maintained contemporaneously, the genetic trend can be estimated.

One of the livestock populations in which mixed-model methodology is used is beef cattle. Traditionally, selection studies have focused on growth traits, especially weaning weight and yearling weight, because they are economically important, respond to selection, and are easily measured (see reviews by Mrode, 1988a,b; Barlow, 1978). More recently, interest has shifted to total herd productivity, including maternal ability of the dam and its relationship with growth. The use of mixed-model methodology has, in part, facilitated this shift.

This thesis investigates the correlated responses in postweaning gain and in the direct component of weaning weight, and in the maternal component of weaning weight to yearling weight selection, and uses the mixed-model methodology. The results and conclusions are compared to those obtained from the control-line method - Newman et al. (1973) for the direct response to yearling weight selection and Olthoff et al. (1990b) for the correlated responses.

The objectives are:

1. To evaluate selection response in the growth and maternal components of weaning weight and the growth component of postweaning gain for a population of beef Shorthorn cattle in a yearling weight selection experiment conducted at the Agriculture Canada Research Station in Brandon, Manitoba, Canada.
2. To compare the selection response estimated from mixed-model methodology and the control-line method, which compares yearly mean phenotypes of the select and control lines. The mixed-model methodology is applied to the two lines separately and combined.

3. To determine the sensitivity of the selection response estimated from mixed-model methodology to the assumed values of the genetic correlation between the direct and maternal components of weaning weight, and the genetic and environmental correlations between weaning weight and postweaning gain.

LITERATURE REVIEW

Growth

Individual growth patterns are largely a function of differences in mature weight and rate of maturing (Taylor, 1985) but also reflect genetic differences due to breed and sex, and the unique set of environmental conditions affecting each individual, such as herd of origin, year of birth, and maternal effect (Brown et al., 1972b). Consequently, individuals measured at a specific chronological age are not likely to be at the same developmental age, or degree of maturity. Eighteen-month weight of females and 13-month weight of males, for example, has been suggested as describing the same developmental stage (Nwakalor et al., 1986).

The growth pattern is a sigmoid-shaped curve. In beef cattle, rate of growth increases from conception to about 6 months of age, is essentially linear from 6 months to about 18 months of age, then declines from 18 months to maturity (5 to 7 years) (Fitzhugh, 1976). Measurements of growth are commonly taken at specific chronological ages corresponding to the production cycle. Calves are usually weaned on the same day and a correction factor for weaning age applied to records before analysis so that all records are adjusted to a common age basis (typically 200d.). These measures, for example, weaning weight (6 to 8 months), yearling weight or long yearling

weight (13 to 18 months), preweaning gain, and (or) postweaning gain, can be used to select replacement stock and to cull excess stock.

The growth of the calf prior to weaning is dependent upon the milk production of its dam and, if available, supplemental feed (creep-feeding), to meet its genetic growth potential. After weaning, the calves may be placed on a feedlot or pasture performance test for increased postweaning gains or high final weights (12 to 18 months) (e.g., Alenda and Martin, 1987). Bulls are often placed on a performance test of 140 days and fed ad-lib until 12 or 13 months of age when final weights are taken. Heifers are often placed on a restricted feeding program or on pasture. On a lower nutritional level than bulls, final weights are then taken at 18 months to allow more time for full expression of postweaning differences (Frahm et al., 1985a).

The study of beef cattle populations and their genetic improvement relies at present upon the theory of quantitative genetics where phenotypic differences are of degree rather than being distinct qualitative differences (Seidel and Brackett, 1981). The study of quantitative traits, such as growth traits, requires the measurement of all individuals within a population, for the population is the unit of study, and a method of partitioning the phenotypic variation into genetic and environmental components (Falconer, 1981 p2).

Genetic

Genetic variation in quantitative traits results from the expression of many genes, each with a relatively small effect. Genetic effects which are transmissible from generation to generation form the additive genetic component of phenotypic variation.

The additive genetic effects on an individual's growth has two parts. The first is due to direct expression of the individual's genes. The other type of additive genetic effect on an individual's growth is provided by the dam of the individual and is known as the additive maternal effect. The maternal effect will be dealt with in a later section. Nonadditive genetic variation arises from the effects of combinations of genes that cause dominance and epistasis and these too can be passed from generation to generation via the mating system (eg. inbreeding and crossbreeding), but are generally not considered part of the selection response and consequently are not considered in this thesis. Additive direct genetic effects will be dealt with in the present section.

The study of the physiological and metabolic systems of beef cattle have identified some of the gene products that affect growth (see reviews by Sejrsen, 1986, and Beitz, 1985), but no technique is available to beef cattle breeders to use these gene products as part of the selection process (Mrode, 1988b). These gene products include growth hormone, somatomedin, thyroid hormones, and insulin, and are affected by environmental factors such as daylength, ambient temperature, nutritional quantity and quality. Genes which have a large effect upon growth (eg. dwarfism and double-muscling) are few. In mice, a major gene for rapid postweaning growth rate has been identified but the gene product is unknown (see review by Famula et al., 1986). This major gene causes postweaning growth rate and mature size to increase by as much as 50% through decreased energy maintenance requirements and increased energetic efficiency of growth, with little effect on body composition.

Sex is a genetic effect and is an important source of variation in beef cattle growth traits (Waugh and Marlowe, 1969; Leighton et al., 1982). Both Yodserance (1972) and Vesely and Robison (1973) reported that sex was the most important source of variation in weaning weight. Part of this variation was likely due to differences in degree of maturity between the sexes at the same chronological age (Brown et al., 1972b; Hanrahan and Eisen, 1973 with mice). Male calves are faster maturing and reach heavier mature weights, due primarily to extended growth during the linear phase and, after 24 months of age, partly to differences in postweaning nutrition between males and females (Brown et al., 1972b). Yodserance (1972) found that Shorthorn bull calves were 2.27 kg heavier at birth, grew 0.09 kg more per day, and were 15.92 kg heavier at weaning than heifer calves. From the records of the American Angus and American Hereford Associations, weaning weights of bulls were greater than heifers by 20kg and 19kg, respectively (Anderson and Wilham, 1978; Leighton et al., 1982). Bailey and Lawson (1986), from a 168d postweaning performance test, found that Angus and Hereford bulls, respectively, gained 49 kg and 38.6 kg more than heifers and grew 25% to 35% faster. In population studies, sex accounted for 9.8% and 96.5% of the variation in weaning weight and postweaning gain, respectively (Sharma et al., 1982; Chevraux and Bailey, 1977).

Environmental

Environmental variation includes all remaining variation not due to genetic (additive and nonadditive) sources of variation. Environmental variation includes effects due to nutritional and climatic factors, maternal effects when expressed as a trait of the

offspring (primarily milk production of the dam), errors associated with sampling and estimation, and "intangible" or unknown causes of variation (Falconer, 1981 p124). Climatic and nutritional factors can be partially accounted for by including year of birth and herd of origin in the genetic analysis model.

Some components of the environment are common to a group of individuals, for example, year of birth and herd of origin. Effects such as age and degree of development at which these conditions are encountered and the expression of the maternal effect are unique to each individual. The environmental conditions taken in total are unique for each individual because they will not be repeated exactly from one individual to the next.

Year of birth and herd of origin can be important effects on growth traits of beef cattle (eg. Vesely and Robison, 1973). Estimates of year of birth may be small when analysis involves a large number of herds over a wide geographical area because of large differences in nutrition and climate among herds but year effects within herd are important (Kennedy and Henderson, 1975). Kennedy and Henderson (1975) found that year effects accounted for less than 4% of the variation in any of the growth traits while year effects within herd accounted for 0-10% of the total variation in weaning weight, 7-14% in yearling weight, and 18-25% in postweaning gain. Chevraux and Bailey (1977) reported 6.7% of the variation in weaning weight and 2.8% of the variation in postweaning gain was attributable to year of birth. Mavrogenis et al. (1978) found that 11% of the variation in final weight and 39% of the variation in postweaning gain was due to year of birth.

Herd location and management differences were found to be the most important sources of variation (25% to 44%) affecting calf growth from birth to one year of age by Kennedy and Henderson (1975). Amal and Crow (1987) reported that herd of origin accounted for 22% to 30% and 15% to 16% of the total variation in final weight on test (390d) and test gain (140d), respectively, for Angus, Hereford, Charlais, and Simmental bulls on test at the Manitoba Bull Test Station, Canada. Herd of origin effects were found by Mavrogenis et al. (1978) to account for none of the variation in final weight and only 6% of postweaning gain variation. Nelsen and Kress (1981) found that herd accounted for 7.9% in Angus and 27% in Herefords of the variation in weaning weight.

The maternal effect, expressed by the dam only in the phenotype of her calf, is an environmental effect on the calf's growth. The maternal effect is primarily a function of the quantity of milk produced by the dam and is generally considered the most important environmental effect on preweaning growth (Koch, 1972). Maternal effects are discussed later.

Unaccounted sources of environmental variation can also be large. Kennedy and Henderson (1975) reported 40% to 58% of the total variation for growth traits was due to this source.

Associations among Traits

Weights and gains are part-whole relationships because they are a part of the same growth curve continuum and, as such, depend upon the growth obtained up to the point of measurement and the growth curve trajectory expected beyond that point.

Genetic changes achieved through selection are, for the most part, permanent. Environmental changes are temporary, although they can be permanent throughout the life of the animal.

Most studies report that genes active during different periods of development are the same (Mavrogenis et al., 1978; Swiger, 1961; Carter and Kincaid, 1959; Itulya et al., 1987) and that selection for weights and gains at any age will result in positive correlated responses in weights and gains at all other ages (Fitzhugh, 1976; Barlow, 1978; Buchanan et al., 1982).

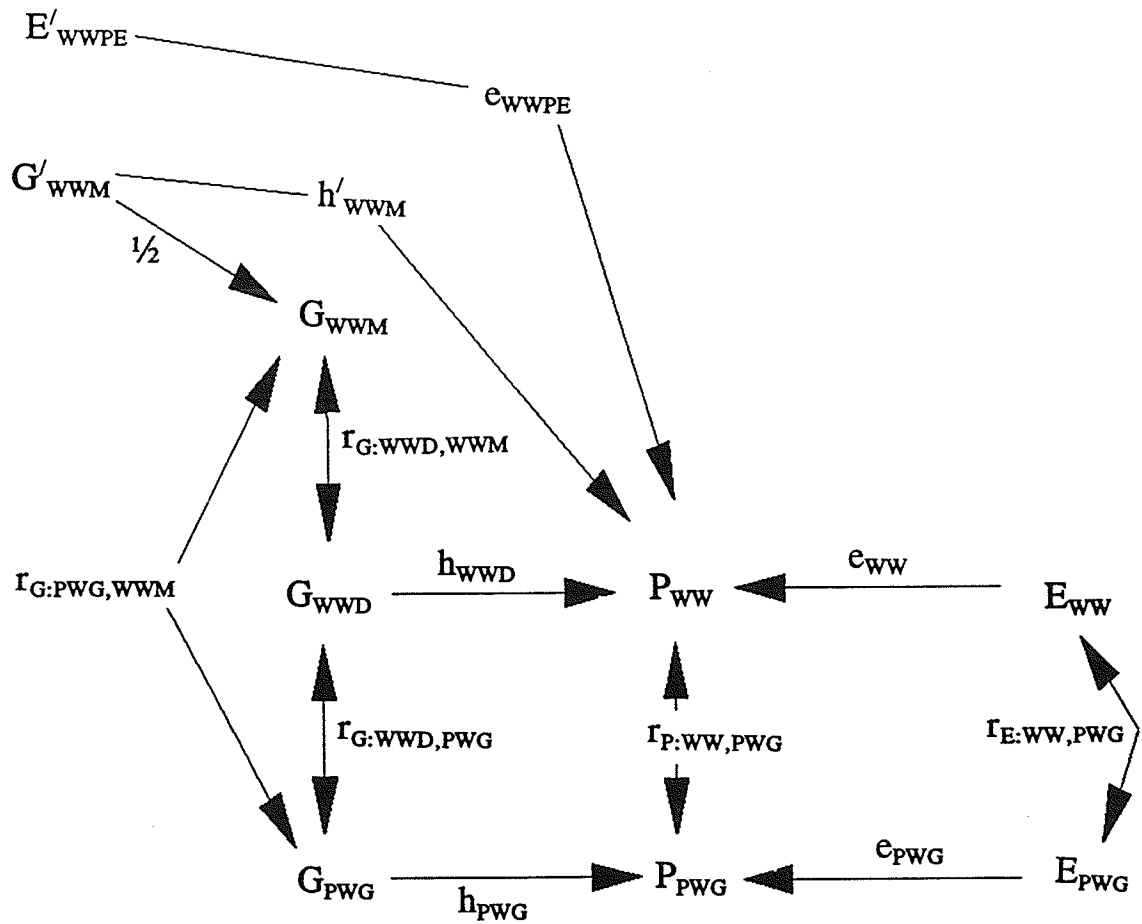
Studies which report that genes active during different periods of development are independent generally involve the periods preweaning and postweaning (Koch and Clark, 1955; Hanrahan and Eisen, 1973 in mice). This lack of genetic correlation between preweaning and postweaning growth may be due to the environment in which the cattle were raised, especially if the nutritional environment was poor (Carter and Kincaid, 1959; Bailey et al., 1971). Swiger (1961) reported that good preweaning environment reduced early postweaning gains but enhanced later gains. Anderson et al. (1974) found a low positive genetic correlation between preweaning and postweaning gain.

Brown et al. (1972a) presented genetic correlations between weights and gains at specific ages which suggested that weights and gains were not controlled by the same set of genes and that there was also a breed difference in the genetic control. Selection for increased weight at immature stages, for example, would increase mature

weight in Herefords but in Angus, would increase early growth rate with little effect on mature weight.

The relationship of weaning weight and postweaning gain, as applies to this thesis, is illustrated in Figure 1. The phenotypes for both weaning weight (P_{WW}) and postweaning gain (P_{PWG}) are influenced by genetic (G_{WWD} , G_{WWM} , G_{PWG}) and environmental components (E_{WW} , E_{WWPE} , E_{PWG}). These two measures of growth are not independent of each other - there are the genetic and environmental correlations between weaning weight and postweaning gain ($r_{G:WWD,PWG}$, $r_{E:WW,PWG}$), the direct-maternal genetic correlation of weaning weight ($r_{G:WWD,WWM}$), and the correlation between the direct genetic component of postweaning gain and the maternal genetic component of weaning weight ($r_{G:PWG,WWM}$). The maternal effect and its relationship to growth is discussed in a later section.

The nutritional environment of the calf is a major factor in the full expression of genetic potential and associations among traits. Genetic growth potential during any specified period will not be realized if the nutritional level is inadequate to meet both maintenance and growth requirements (Dickinson, 1960). In this context, because bull calves have a higher growth capacity, they require a higher nutritional level than heifer calves to reach their growth potential. Poor nutritional environments, due either to low milk production of the dam during preweaning growth and (or) a poor year (due to seasonal or climatic conditions affecting the nutritional intake of the dam, which is reflected in milk yield, and of the calf once it begins grazing) will therefore have a larger impact upon the growth of bulls (Ahunu and Makarechian, 1986; Sharma et al.,



$$P_{WW} = G_{WWD} + G'_{WWM} + E_{WWD} + E'_{WWPE}$$

$$P_{PWG} = G_{PWG} + E_{PWG}$$

where, prime (') denotes the dam of the individual expressing the phenotypic value for weaning weight, h_{WWM} , h_{WWD} , and h_{PWG} are the square roots of their respective heritabilities, and the other factors are explained in the List of Abbreviations.

Figure 1. Path coefficient diagram and linear model of the relationship between a maternally-influenced trait, weaning weight, and postweaning gain (after Hohenboken, 1973).

1982; Itulya et al., 1987; Anderson and Wilham, 1978; Waugh and Marlowe, 1969). Bull calves on young dams are especially affected (Elzo et al., 1987; Nelson and Kress, 1981). Selection of bulls in such an environment may not result in a choice of genetically superior bulls but instead a combination of genetics and (or) environmental adaptation (DeNise et al., 1988; Frisch, 1981). Compensation for a nutritionally poor preweaning environment can be provided through creep-feeding. Preston and Willis (1970), in a review of the literature, found almost unanimous agreement that creep-feeding increased weaning weight and was more effective when the nutritional environment was poor.

The nutritional environment pre- and post-weaning affects relationships between growth traits (Waugh and Marlowe, 1969). Waugh and Marlowe (1969), using Hereford heifer data, found that the type of feed fed during the preweaning and postweaning growth periods affected the heifers growth rate. Heifers creep-fed during the preweaning growth period, and fed mainly grain during the postweaning growth period, grew faster than noncreep-fed heifers. If the postweaning ration was mostly roughage, noncreep-fed heifers grew faster. Waugh and Marlowe (1969) also noted that inhibited growth during the preweaning period was not completely overcome by positive compensatory growth (i.e., accelerated growth following a period of inhibited growth, largely because of nutritional environments (Smith et al., 1976, 1989; Brown et al., 1972b)) during the postweaning growth period.

Selection for postweaning gain under different postweaning nutritional environments was found by Bailey and Lawson (1986) to affect the postweaning growth

traits as well as producing different responses in milk production. The calves fed concentrates, rather than roughage, had a 60 kg average advantage in postweaning gain and yearling weight. For the calves that became dams, milk yield was greater for the dams selected on the roughage diet. The authors speculated that perhaps selection "on the roughage diet was more efficient, or that the concentrate diet had a deleterious effect on the udder so that genetic potential could not be expressed".

In summary, the growth of an individual follows the pattern dictated by genetic differences acting within a unique set of environmental conditions. The growth traits, and of interest here are weaning weight and postweaning gain, are studied by the application of quantitative genetics to estimate the genetic change. Accounting for important sources of environmental variation (year of birth, herd of origin, maternal ability) and sex variation improves the accuracy of estimation. Selection for a particular growth trait, given an optimum environment, which may be different between bull and heifer calves, is expected to produce changes in the other growth traits because of the similarity of genes active from one developmental period to another.

Maternal Ability

The growth of the beef calf from birth to weaning is influenced in an important way by the maternal ability of the dam. The maternal effect is a phenotypic value of the dam that is expressed in the phenotype of her calf (Hohenboken, 1985a). It is genetic and environmental in origin and thus has genetic properties, such as heritability and genetic correlations with other traits. As an effect on the calf, it is entirely environmental.

Figure 1 illustrates the contribution of a maternal effect on the maternally-influenced trait, weaning weight (WW), and summarizes it in a linear model. The weaning weight of the calf (P_{WW}) reflects a genetic (G_{WWD}) and an environmental (E_{WW}) component. The dam's (') contribution to the calf's weaning weight is through two sources: the transmission of a sample half of her genes ($1/2 G'_{WWD}$) and the expression of her maternal genetic and permanent maternal environmental effects (G'_{WWM} and E'_{WWPE}). A direct-maternal genetic correlation ($r_{G:WWD,WWM}$) will also contribute to the direct genetic component of weaning weight (G_{WWD}). The sire's contribution is genetic only and is through transmission of a sample half of his genes. Illustrating the dam's importance to offspring weaning weight, Wright et al. (1987) found that the dam's contribution was almost seven times that of the sire's contribution.

The maternal effect of greatest importance is milk production. Other effects include the uterine environment and its effect on birth weight, the colostrum milk which confers passive immunity to the calf, the dam's behavior and protection towards her calf, the habitat in which the dam raises her calf, the lactation number of the dam,

and the suckling time and frequency of suckling by the calf (Hohenboken, 1985a; Drewry et al., 1959). The maternal effect, as defined by milk production, is affected by the nutritional level of the dam which influences the quantity and quality of the milk (Dickinson, 1960). Milk levels are likely related to reproductive traits (Willham, 1972a), such as age at puberty, age at first calving, first breeding date, pregnancy rate and calf crop percentage (Smith et al., 1989; Montano et al., 1986). The maternal effect primarily affects preweaning traits, but there may be a carry-over effect to postweaning growth traits (Hohenboken, 1985a).

Maternal ability cannot be estimated directly (Willham, 1980). Experimental methods for estimation of maternal ability in beef cattle have used primarily comparison of maternally-related individuals to paternally-related individuals (or half-sib analysis) and resemblances among other relatives (Koch, 1972; Willham, 1980). The problems involved in estimating maternal effects have been reviewed by Willham (1980). These problems include confounding of the maternal effect with the dam's direct genetic contribution to growth, the possibility of a genetic correlation between maternal ability and growth, and the expression of the maternal effect, by females only, a generation behind the direct genetic effect.

Milk Production

The effect of maternal ability on postnatal calf growth is the focus of beef cattle studies examining maternal effects. Evidence and importance of maternal effects in beef cattle come from studies and reviews which report a high correlation between milk production and preweaning growth and a greater similarity in performance of

maternal half-sibs than paternal half-sibs (Dickinson, 1960; Gleddie and Berg, 1968; Koch, 1972; Wilham, 1972a, 1980; Hohenboken, 1973; Barlow, 1978; Buchanan et al., 1982; Montano et al., 1986). Maternal effects have been found to be more important in determining the preweaning growth of the calf than the calf's own genetic potential for growth (Ray et al., 1970; Hohenboken and Brinks, 1971; Hohenboken, 1973; Fitzhugh, 1976).

Milk production of the dam peaks at about 60d postpartum (Drewry et al., 1959; Dawson et al., 1960; Robison et al., 1978). During the first month of milk production, overproducing dams will reduce milk production to meet the level of their calf's capacity and, consequently, the dam's potential may be underestimated (Gleddie and Berg, 1968; Drewry et al., 1959; Rutledge et al., 1971). By the second month, when both milk produced and calf appetite are equal and milk production is highest, the correlation between calf weight and dam milk yield is also highest (Gleddie and Berg, 1968). The correlation decreases as the calf begins to forage and milk is no longer the only source of nutrients. Creep-feeding and delayed weaning could also reduce the correlation between milk production and weights or gains (Gleddie and Berg, 1968). Robison et al. (1978) found that milk production was sufficient to meet growth and maintenance requirements during the first month only. By 4 months of age, the calf was obtaining only 65% of its energy requirements from milk.

Milk production has been shown to account for 16% to 66% of the variation in weaning weight (Preston and Willis, 1970; Neville, 1962; Jeffery et al., 1971; Robison et al., 1978). Montano et al. (1986) used three breeds of beef cattle with

different levels of milk production but of similar size and growth to investigate the relationship of calf growth to level of milk production. Progeny from high milk producing dams were heavier at weaning than moderate and low milk producing dams and maintained 63% and 54% of this advantage to final weight at about 16 months. Progeny from moderate milk producing dams maintained 90% of their weaning weight advantage to final weight compared to low milk producing dams. In general, dams producing more milk wean heavier calves (Morris and Wilton, 1976), and the quantity of milk is more important than the quality (Rutledge et al., 1971).

Age of Dam

Age-of-dam effects are largely a reflection of differential milk production associated with the growth patterns of dams (Drewry et al., 1959; Rutledge et al., 1971). Robison et al. (1978) found that milk yield of Hereford cows increased up to 5 years, plateaued from 5 to 8 years, then declined after 8 years. Rutledge et al. (1971) reported maximum milk yield from 8.4 year old Hereford dams. Preston and Willis (1970) summarized 17 studies which included the effect of age of dam and, in general, weaning weight was heaviest from 6 to 9 year old dams; the same age group which had the highest milk production levels. That the age-of-dam effect on weaning weight is really a milk yield effect was reinforced by a study by Neville (1962) who found that including milk yield as a variable in an analysis of weaning weight often removed the age-of-dam effect.

Age of dam often has a curvilinear effect on preweaning traits (Rutledge et al., 1971, Jeffery et al., 1971). Weaning weights generally increase with age of dam

until maturity (5-6 years), then level off (7-9 years), and decline (Leighton et al., 1982; Anderson and Wilham, 1978). Waugh and Marlowe (1969) reported that calves from young dams had the slowest growth rate to one year of age and that calves from mature dams (6-11 years) had the fastest growth rate. The age-of-dam effect has been found to explain from 2.4% to 12% of the total variation in weaning weight (Nelsen and Kress, 1981; Sharma et al., 1982).

Age-of-dam effects on postweaning traits have been found but they are indirect environmental effects (Elzo et al., 1987). If the preweaning genetic growth potential of the calf is met then postweaning traits would be independent of the age of dam effect. If genetic growth potential is not realized during preweaning growth then the calf may experience positive compensatory growth postweaning. On the other hand, if the calf is fed at a high nutritional level during the preweaning growth phase, it may not gain as much weight as expected during the postweaning growth phase (negative compensatory growth). Mavrogenis et al. (1978) found that Hereford bulls born to mature (5-8 years) dams tended to be heavier at all postweaning weights to one year of age.

Literature on beef cattle indicates that the age-of-dam effect on postweaning gain to a year of age is usually not of importance (Koch and Clark, 1955; Sharma et al., 1982; Mavrogenis et al., 1978). Inconsistent effects were observed by Itulya et al. (1987) where 12 and 20 month gain of bulls and 12 and 24 month gain of heifers had important age of dam effects but 24 month gain of bulls and 20 month gain

of heifers did not. Shelby et al. (1963) reported important age-of-dam effects on feedlot gain but only for 3 year old dams.

Postweaning weights are more often affected by age-of-dam effects than postweaning gains because weights are more dependent upon the part-whole relationship of growth than are gains, and postweaning weights are sometimes calculated as age-of-dam adjusted weaning weight plus postweaning gain. Important effects were found by Sharma et al. (1982) for yearling weight in males and 18-month weight in females and by Mavrogenis et al. (1978) for yearling weight of Hereford bulls. Mavrogenis et al. (1978) reported that age of dam effects accounted for 82% of the variation in yearling weight but only 24% of the variation in postweaning gain. Graser and Hammond (1985), studying the Australian Simmental sires in the National Beef Recording program, found that age-of-dam effects on yearling weight were similar to the 200-day effects. By 18 months, the age-of-dam effect was still apparent but much reduced.

Studies summarized by Woldehawariat et al. (1977) indicate that, on average, 8-year-old dams produced calves with the highest weaning weight, and 9-year-old dams produced calves with the highest postweaning gain and yearling weight.

Records affected by age-of-dam effects are often adjusted before analysis. Prior correction factors for age of dam, and inclusion of systematic effects (year, herd, sex) within the model, are used to eliminate variation due to these effects so that a more reliable estimate of genetic merit is used for selecting replacement stock (Leighton et al., 1982; Aaron et al., 1986a). Age-of-dam correction factors are specific to a population; are usually greatest for immature dams and can change with selection. Olthoff et al.

(1990a) reported that age-of-dam correction factors were smaller for calves from larger cows and for faster calf growth rates applied to birth, weaning, and yearling weights. Aaron et al. (1986a) suggested that the bias in age-of-dam effects introduced by selection for growth traits could be caused by correlated responses in milk yield and mature weight. However, increases in mature weight and milk yield could be partially offsetting effects because age-of-dam correction estimates would increase with milk yield but decrease with mature weight.

Permanent Maternal Environment

Important maternal effects also exist in the form of permanent maternal environment (Vesely and Robison, 1973). The permanent maternal environmental effect is that part of the phenotypic variation in weaning weight due to environmental factors which permanently affect a dam's performance throughout her lifetime. It is caused by an unique set of environmental conditions affecting the dam.

The permanent maternal environmental effect is of importance in a production system where each dam raises more than one offspring during her lifetime. Offspring from the same dam, though born in different years, will be similar not only because of common genes, but also because of shared permanent maternal environmental effects. This effect is a part of repeatability (Wright et al., 1987) and appears to be small, - 2% to 7.4% of phenotypic variation (Hohenboken, 1973; Deese and Koger, 1967; Wright et al., 1987).

Evidence exists of a negative relationship between the dam's permanent maternal environmental effect and the environmental effects that influenced the dam's

own weaning weight (primarily maternal but also a year effect in terms of climatic and nutritional conditions, and creep-feeding) (Koch, 1972; Reed et al., 1988; Riska et al. (in mice), 1985; Hohenboken, 1973; Robison, 1981). That is, high milk producing dams that wean heavy calves because of environmental rather than genetic causes, adversely affect the subsequent maternal ability of their female offspring (Hohenboken, 1973).

Associations with Growth

The size of the uterine cavity (a maternal effect) can influence the birth weight of the calf and the calf's subsequent growth curve. Depending upon uterine size, the calf may or may not be able to realize its genetic prenatal growth potential. High prenatal growth has been termed juvenile growth potential by Dickinson (1960). Without the expression of juvenile growth potential, the phenotypic ranking for birth weight largely reflects the genetic growth potential and is closely related to genetic ranking for mature weight. The growth of these calves is compensatory from one to four months with the birth weight correlation decreasing as the calf ages to four months. As maturity approaches, the correlation between birth weight and older age weights increases. Calves born to larger dams (and therefore larger uterine environments) are able to express the juvenile growth potential. The correlation between birth weight and later weights decreases from birth to weight at 9 months and then levels off. The birth weight correlations are higher for calves from larger dams until about 8 months of age when calves from smaller dams have greater birth weight correlations.

The relationship between growth and maternal ability is difficult to explain and probably relates to the different patterns of growth, as illustrated above and discussed

previously. Both negative and positive relationships have been reported, as well as a lack of correlation. Literature reviews by Robison (1981), Koch (1972), and Hohenboken (1973) indicate the relationship is negative. Robison (1981) presents evidence that the negative relationship can be carried through to postweaning traits such as final weight and gain. Explanations for a negative relationship include bias in the estimation of the maternal effect, an actual negative genetic correlation, a negative environmental correlation, or "compensatory evolutionary forces that tend to keep individual size relatively constant at weaning" (Koch, 1972; Willham, 1972a). Evidence points towards a positive, or weak negative, genetic correlation and a negative environmental correlation (Deese and Koger, 1967; Hohenboken and Brinks, 1971; Hohenboken, 1973; Robison, 1981; Mueller and James, 1985). This relationship is discussed further in the section headed "direct-maternal covariance".

In summary, the maternal effect is a phenotypic trait of the dam which is genetic and environmental in origin, but as a phenotypic trait of the calf, it is strictly environmental. The maternal effect is primarily expressed in the preweaning growth of the calf through the nutritional environment (milk production) provided by the dam. If the preweaning growth environment is unable to meet the calf's genetic growth potential then maternal effects may be carried over to postweaning traits. Because milk production varies with age, age of dam is often used to preadjust records that are maternally influenced. Unlike simply-inherited traits which can be measured directly, the maternal effect is estimated indirectly through various comparisons of relatives. The permanent maternal environmental variation is used in mixed model methodology to account for a

nongenetic cause of similarity between calves of the same dam. The literature indicates a negative relationship between maternal ability and growth, likely reflecting a weak negative, or positive, genetic correlation and a negative environmental correlation.

Selection Response

The evolutionary development of a species occurs through natural selection and gene mutation, effecting changes in morphology, physiology and behavior (Black, 1983). Changes can also occur within isolated populations (spatial or temporal differentiation) through genetic drift and migration, or gene flow. This evolutionary development through genetic change, or natural selection, operates within a framework provided by the environment. The extent to which an individual in a particular environment will be able to survive and reproduce, its 'fitness', is a function of its genes. Under artificial selection, man chooses which animals will become parents of the next generation, thereby causing differential reproduction among different genotypes which may or may not affect the fitness of the individual. Consequently, selection changes the population mean through a change in gene frequencies and this change is referred to as the selection response, or genetic response. The selection response of a particular trait may be of the selected trait (the direct response to selection) or a correlated trait (the correlated or indirect response to selection). Measurement of the selection response is, in theory, the difference in mean phenotypic value from one generation to the next of an infinite population. In practice, the population of study is finite and measurement requires some means of accounting for the environmental and genetic trends, such as comparison of an unselected control population to a selected population.

Selection experiments can provide information relating to the validation of theoretical predictions of direct and correlated responses, estimation of genetic

parameters, assessment of the importance of additive genetic and environmental factors in the phenotypic selection response, and efficient design of breeding programs (Irgang et al., 1985a).

Factors Affecting the Selection Response

Some of the factors affecting the direct and correlated selection responses are illustrated in Figure 2. The direct genetic response per year of selection for trait X (R_X) is affected by the heritability of the trait (h^2_X), the selection differential (D_X), and the generation interval (t) (Hohenboken, 1985a): $R_X = (h^2_X \cdot D_X) / t$. The correlated genetic response per year in trait Y (CR_Y) when selection is for trait X is affected by the heritabilities of both traits (h_X and h_Y), the genetic correlation between the two traits ($r_{G:XY}$), the selection differential of trait X (D_X), the phenotypic standard deviation of the correlated trait ($\sigma_{P:Y}$), and the generation interval (t) (Falconer, 1981 p286): $CR_Y = (h_X \cdot h_Y \cdot r_{G:XY} \cdot D_X \cdot \sigma_{P:Y}) / t$. Both the direct and correlated selection responses are affected by the environment, which is shown in Figure 2 as a large circle encompassing R_X and CR_Y . Other factors that can affect the selection response include genetic drift, inbreeding, the fitness of the individual, and the design of the experiment. The following discussion will define each factor and explain its significance to the selection response.

Selection Differential. The selection differential is a measure of the selection applied and is the phenotypic difference between the average of selected parents and the average of the population from which they were selected (Hohenboken, 1985a; Falconer, 1981 p171, 174-177). By dividing by the phenotypic standard deviation, the response to selection

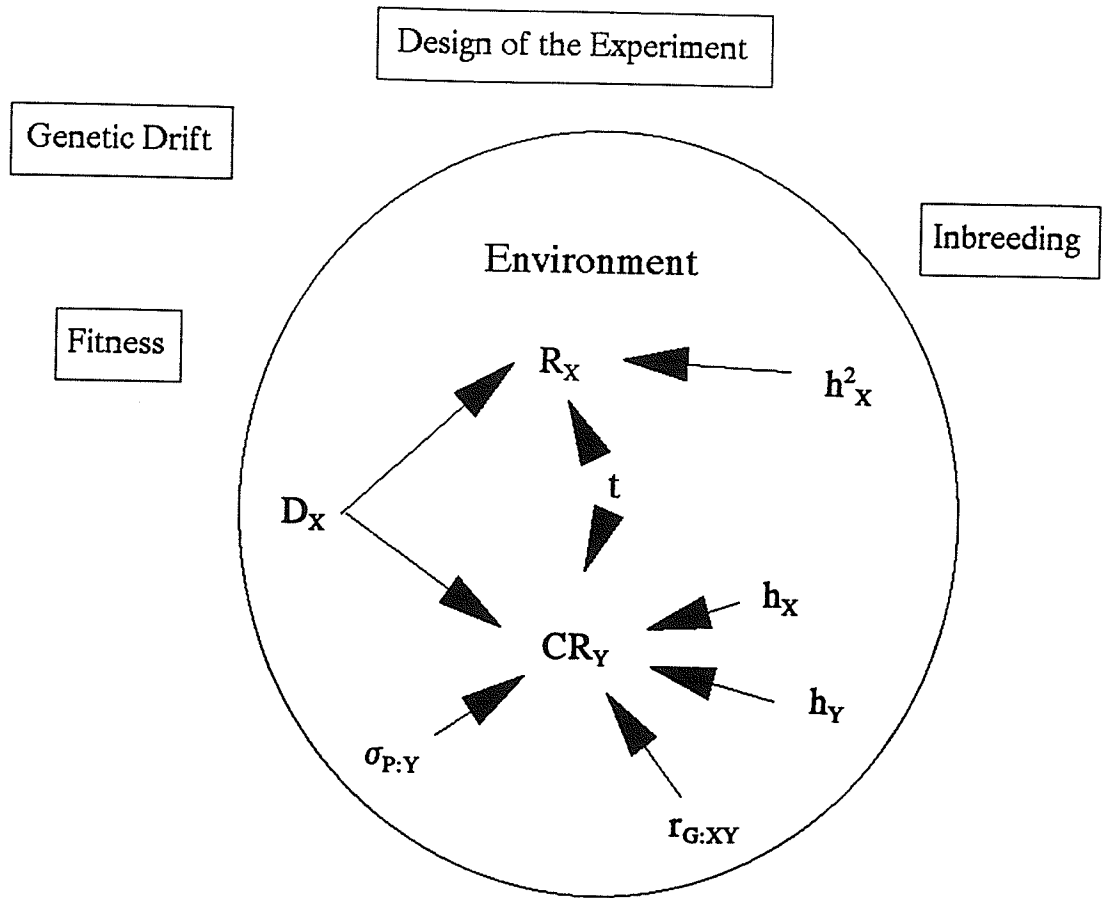


Figure 2. Diagrammatic representation of the factors affecting the selection response.

can be generalized and is called the intensity of selection (i), or standardized selection differential, and can be used to compare results from different selection experiments. This value expresses the number of phenotypic standard deviations by which parents exceed the average of the population from which they were selected. The smaller the proportion of selected parents, the greater will be the intensity of selection and the greater the genetic response expected. An estimate of the effectiveness of selection can be obtained from a comparison of the actual selection differentials of parents producing progeny to the maximum selection differentials of the highest ranking individuals had they produced progeny (i.e., actual vs. maximum) (Aaron et al., 1986a; Frahm et al., 1985a).

Selection differentials are usually low in beef cattle selection experiments (0.10 to 0.33 standard deviations per year), with most of the selection differential due to selection on sires (79% to 100%), because of the structure of beef cattle populations (Mrode, 1988b). Newman et al. (1973) reported that the pattern of cumulative selection differentials was slow in the early years but became more uniform in later years, with accumulation greater in the sires than in the dams. Actual selection differentials expressed as a percentage of maximum range from 77% to 100% for sires and 50% to 81% for dams from 7 studies reviewed by Mrode (1988b).

Generation Interval. In beef cattle, generations are not discrete but overlapping - at any one time most herds have cows drawn from at least two generations. The generation interval (t) is then the average age of the parents contributing progeny (Falconer, 1981 p177-179; Hohenboken, 1985a). The average generation interval of the studies

summarized by Mrode (1988b) was 4.4 years, with sires ranging from 2 to 4.3 years and dams ranging from 4 to 6.6 years. Minimizing the generation interval is expected to increase the genetic response. However, reducing the generation interval by increased culling of older cows increases the number of replacements required which reduces the selection intensity. With overlapping generations, the rate of genetic improvement is expected to be slow in the early years, and to be nonlinear, in fact, underestimating the linear response (Mueller and James, 1985). Nwakalor et al. (1976) reported that most of the genetic improvement in weaning weight occurred during the last two-thirds of the time period studied.

Heritability. Heritability (h^2) is a property of the trait, of the population, and of the environmental circumstances affecting the individuals of the population (Falconer, 1981 p148-151). Thus, it can vary from population to population and from generation to generation. Narrow-sense heritability (the definition used here unless otherwise specified) is defined as the ratio of additive genetic variance (V_A) to phenotypic variance (V_P) as follows: $h^2 = V_A/V_P$. Values are expected to be between zero and one and are estimated from the degree of resemblance between relatives. A heritability value of zero indicates that none of the phenotypic variation of the trait is due to additive genetic variation and a heritability value of one indicates that all of the phenotypic variation is due to additive genetic variation. A heritability value may be low (less than .25), moderate (.25 to .50), or high (greater than .50).

Heritability defined as the ratio of selection response to the amount of selection attempted is called realized heritability, or realized response to selection

(Hohenboken, 1985a; Falconer, 1981 p184). It can be calculated from the linear regression of the estimated genetic response per year on the selection intensity practiced (Newman et al., 1973; Irgang et al., 1985b; Blair and Pollak, 1984a): $h^2_r = b_{R/CSD}$, where b = regression (of the), R = selection response (on the), and CSD = cumulative selection differential, or selection intensity practiced. Average estimates from Mrode's (1988b) review of beef cattle selection experiments are .34 for weaning weight, .59 for postweaning gain, and .30 for yearling weight. Realized heritability is equivalent, in theory, to narrow-sense heritability but it is often different because of lack of knowledge of the true biological control of the selected trait. Antagonistic genetic correlations between the selected trait and fitness, for example, may limit realized selection response even when there is a lot of additive genetic variation in a trait.

The heritability of a maternally-influenced trait contains several terms, reflecting the partition of the additive genetic variance into direct (growth) and maternal components (Willham, 1972a). Heritability of weaning weight, for example, is:

$$h^2_{ww} = (V_{G:WWD} + 1.5COV_{G:WWD,WWM} + .5V_{G:WWM})/V_{P:WW}$$

or:
$$h^2_{ww} = h^2_{WWD} + 1.5r_{G:WWD,WWM} \cdot h_{WWD} \cdot h_{WWM} + .5h^2_{WWM},$$

where $V_{G:WWD}$ = direct additive genetic variance, $COV_{G:WWD,WWM}$ = direct-maternal additive genetic covariance, $V_{P:WW}$ = phenotypic variance, and $r_{G:WWD,WWM}$ = direct-maternal genetic correlation.

The heritability can be increased or decreased through changes in the additive genetic variation or phenotypic variation. The introduction of unrelated animals into a herd (or gene migration) may increase the additive genetic variation.

Consequently, Composite or Synthetic breeds, with a genetic makeup composed of several different breeds, contain greater additive genetic variation and typically have higher heritabilities than purebreds (Bertrand and Benyshek, 1987; Mrode, 1988b; Sharma et al., 1985). More commonly, heritability can be increased (as well as selection response) by reducing the environmental variation through the design of the experiment, management practices, and adjusting records for known, systematic sources. Field studies, for example, often have smaller heritability estimates than selection studies because of greater environmental variation due to variable management practices (e.g., creep-feeding, weaning age) and climatic and nutritional conditions (Itulya et al., 1987; Bertrand and Benyshek, 1987).

Genotype x Environment Interaction. When there is genotype x environment interaction (a change of degree, or ranking, of genotypes in different environments, Falconer, 1981 p290) then selection response depends upon the environment in which the trait is expressed. Frisch (1981) reported effective selection for high postweaning gain in Hereford-Shorthorn cross cattle under field conditions in a tropical environment. The response was achieved entirely through increased resistance to environmental stresses (disease organisms including cattle ticks, helminth species, and bovine infectious keratoconjunctivitis, high temperature, and poor nutrition) which affect growth rate and not to increases associated with genetic growth potential. Selection was against those genes causing environmental sensitivity. With improved nutritional conditions, the control line performed better than the select line, suggesting that high growth potential and high environmental resistance (drought tolerance) might be mutually exclusive.

Fowler and Ensminger (1960) investigated the effects of a high and low level of nutrition (full feeding versus restricted feeding) on postweaning gain selection in swine and found that different physiological mechanisms had been selected.

When genotype-environment interaction is important, selection of parents in the environment that their progeny will be expected to perform is suggested (Fowler and Ensminger, 1960; Falconer, 1980 p292). For the most part though, results indicate that this interaction is not of great importance for growth in temperate environments.

Genetic Drift, Fitness. In the absence of selection, migration and mutation, genetic drift (drift variance) will cause a change in gene frequencies resulting in a change in the population mean. Genetic drift (also sampling variation or chance variation) occurs when the individuals that become parents have gene frequencies different from the population at large (Falconer, 1981 p6; Hohenboken, 1985a). The smaller the number of parents chosen the higher the probability of genetic drift occurring. Drift variance can be reduced by choosing breeding individuals with performance close to the mean of all individuals in that generation, i.e., with a selection differential near zero (Hill, 1972). Nevertheless, genetic drift may still occur. Newman et al. (1973) found unintentional selection differentials in the control line of a beef cattle selection experiment.

The fitness of an individual refers to Darwinian fitness, a value associated with the survival and reproduction of a particular genotype, or individual. Differences in fitness between parents and offspring can alter gene frequencies and the response to selection will not be as expected (VanVleck, 1979 p7-8). Genetic correlation between the selected trait and fitness will determine whether natural selection is synergistic or

antagonistic (Hohenboken, 1985a). An example of an antagonistic genetic correlation is the condition of pale, soft, exudative meat in swine. The genes increase leanness and muscle mass but decrease the fitness (survival) of the individual (Webb et al., 1982).

Inbreeding. Inbreeding, the mating of related individuals, depends upon the population size (Falconer, 1981 p57). The smaller the population, the more likely that two individuals will be related through ancestry and therefore inbred. The inbreeding level, given as a percentage, represents the decrease in heterozygosity from the "original heterozygosity in the common ancestor" (Hutt and Rasmusen, 1982). Inbreeding can thus be viewed as the percent increase in homozygosity (Hutt and Rasmusen, 1982) which reduces the additive genetic variance and therefore the selection response. In some cases, selection may counteract the inbreeding effect. Selection for litter size in inbred lines of mice, for example, resulted in larger litter sizes in the surviving lines of inbred mice than in the original population (Falconer, 1981 p229-230). In general, reproductive traits are more adversely affected than growth traits (Falconer, 1981 p225).

Inbreeding effects on the phenotypic variation can vary from trait to trait and species to species, be age dependent, and (or) depend upon the environment (Hohenboken, 1985b; see Pirchner for examples, 1985 p243). In beef cattle, low levels of inbreeding in the dam (4.6% and 5%) and (or) calf (9.8% and 11%) do not usually have significant effects on growth traits, although weaning weight was adversely affected by inbreeding of the calf (-.50kg and -.45kg per 1% increase in inbreeding) (Chevraux and Bailey, 1977; Nelms and Stratton, 1967). Higher average levels of inbreeding in the calf (33.1%) and dam (21.8%) have been reported by Nwakalor et al. (1976). They

reported that the phenotypic and genetic trends of weaning weight were $-.35 \text{ kg yr}^{-1}$ and 1.17 kg yr^{-1} but adjusted for inbreeding of calf and dam, they were $.36 \text{ kg yr}^{-1}$ and 1.87 kg yr^{-1} . The linecross groups were $.58$ and 2.09 kg yr^{-1} , respectively, indicating that adjustment for inbreeding does not fully compensate for the detrimental effects of inbreeding.

Table 1 summarizes the effect of each factor discussed above on the expected change in the selection response if that factor was increased and all other factors held constant.

Design of the Experiment. The design of the experiment influences the type of information to be gained by analysis. For example, divergent selection is the most efficient design for estimation of genetic parameters (Hill, 1972). With designed experiments involving select and control populations, or divergently selected, populations, genetic trends can be obtained with relatively simple analyses (Hill, 1972). Where a control, or divergent, population is not a part of the design, mixed-model methodology (Henderson, 1973; Quaas and Pollak, 1980) can be used to estimate genetic trends. Mixed-model methodology can also be used to analyze populations with a control, or divergent, population. The experimental design of beef cattle selection studies to accurately measure genetic trend has been reviewed by Mrode (1988a). Improvements in designs such as increased population size, planned matings to minimize inbreeding and methods to adequately separate the genetic and environmental trends have been discussed by Mrode (1988b).

TABLE 1. Summary of the effect each factor would have on the selection response if that factor was increased and all other factors remained unchanged.

| Factor Increased | Change in the Selection Response |
|-------------------------|----------------------------------|
| selection differential | increase |
| generation interval | decrease |
| heritability | increase |
| environmental variation | decrease |
| genetic drift | cannot be predicted |
| fitness | increase |
| inbreeding | decrease |

Factors Affecting Heritability and Correlation

Some of the factors affecting heritability and correlation include selection, nutritional level, method of estimation, permanent maternal environment, and the direct-maternal covariance.

Selection. The effect of selection is to reduce the additive genetic variation. Consequently, heritability estimates are typically smaller in selected populations compared to unselected populations (Falconer, 1981 p179-181; Thrift et al., 1981). The selection of the top individuals in a population results in a reduced phenotypic distribution of the selected group compared to the phenotypic distribution of the population from which they were selected. The additive genetic variation is reduced equivalently. The resulting heritability estimate is reduced. The additive genetic variation lost through selection eventually becomes equalized to that restored through segregation and recombination of the gametes in the progeny. The reduction is greatest between the first and second generations of selection and, the higher the heritability, the greater the reduction.

Thrift et al. (1981) investigated the effects of selection on 2534 Hereford and Angus calf records. The paternal half-sib analysis of variance technique was used to obtain the genetic parameter estimates for each line (control and select) and sex (bulls and heifers) (Table 2). Heritability estimates from control-line data were larger than heritability estimates from select-line data by 1.3 (2.4), 7.0 (2.3), and 3.0 (3.5) times for weaning weight, postweaning gain, and yearling weight, respectively, of bulls (and heifers). The lower heritability estimates found in the select compared to control

TABLE 2. Heritabilities and correlations of weaning weight, postweaning gain, and yearling weight from Thrift et al. (1981) for select and control line calves by sex.

| Trait | Bulls | | Heifers | |
|------------------------------|--------|-------------------|---------|---------|
| | Select | Control | Select | Control |
| Heritabilities: | | | | |
| weaning weight (WW) | 0.27 | 0.39 | 0.16 | 0.39 |
| postweaning gain (PWG) | 0.13 | 0.92 ^a | 0.38 | 0.88 |
| yearling weight (YW) | 0.32 | 0.97 | 0.19 | 0.68 |
| Correlations: | | | | |
| Genetic: | | | | |
| WW, PWG | 1.04 | 0.51 | -0.08 | 0.13 |
| WW, YW | 1.01 | 0.85 | 0.68 | 0.77 |
| PWG, YW | 1.00 | 0.89 | 0.70 | 0.75 |
| Environmental ^b : | | | | |
| WW, PWG | 0.04 | -0.57 | 0.10 | -0.58 |
| WW, YW | 0.73 | 2.15 | 0.81 | 0.77 |
| PWG, YW | 0.70 | -2.65 | 0.62 | 0.00 |

^aHeritability estimates for selected and control line bulls differ ($P < .01$).

^bEnvironmental correlations calculated from the data.

line indicate a decline in additive genetic variance, as phenotypic variance was similar within both lines. Although the estimates of genetic correlations were not as consistent as those found for the heritabilities, the estimates from the control line were considered to be more realistic.

Nutritional Level. In the study by Thrift et al. (1981) above, bulls were fed ad-lib postweaning while heifers were maintained on pasture, heifers were thus on a lower nutritional level than bulls. The lower nutritional plane, if inadequate for expression of genetic growth potential, can increase the environmental variation and lower the heritability estimates. In general, heritabilities are lower when animals are on pasture compared to feedlot (Irgang et al., 1985b). Woldehawariat et al. (1971) reported average heritability values of .45 for feedlot gain and .34 for pasture gain. DeNise et al. (1988) estimated the genetic parameters for preweaning traits of Herefords in good, moderate and poor environments and found that the heritabilities and correlations were dependent upon the environment and were suggestive of an interaction of the environment with genotype and sex under the range conditions of southwestern United States.

Method of Estimation. The methodology used to estimate genetic parameters can affect their reported values. This is generally due to using simple analytical models which do not reflect the true biology of traits. Nearly all methods of estimating genetic parameters are based on observing the similarity of relatives. The observed similarity of relatives is assumed to be due to causal effects (genes or environment) which are in common. Willham (1972b) described a model for weaning weight (see Figure 1) and showed which

causal effects were responsible for the similarity of relatives. The observed similarity (i.e., covariance) of paternal half-sibs, for example, is assumed to be due only to genes which are in common between the sibs (one-quarter of genes), so that the covariance of paternal half-sibs provides an estimate of one-quarter of the additive genetic variance in weaning weight. The covariance in weaning weight for other types of relatives is less straight-forward. The offspring-sire covariance estimates one-half of the direct additive genetic variance plus one-quarter of the direct-maternal covariance. The offspring-dam covariance estimates one-half of the direct additive genetic variance, one and one-quarter of the direct-maternal covariance, and one-half of the maternal additive genetic variance. The maternal half-sib covariance estimates one-quarter of the direct additive genetic variance, the direct-maternal covariance, the maternal additive genetic variance, and the permanent maternal environmental variance. The above was based on Willham's (1972b) model, and is generally accepted.

Buchanan et al. (1982) compared predicted genetic response in weaning weight and yearling weight selection lines using parameters estimated from paternal half-sib analysis of variance (method I) and offspring-parent regression (method II). Differences in predictions were consistent with the exclusion of maternal effects with method I and inclusion of maternal effects with method II. For example, predicted genetic change per generation in yearling weight of the yearling and weaning weight selection lines were .28 and .23 genetic standard deviations for method I and .50 and .25 for method II. For weaning weight, method II predicted a greater genetic change occurring in the yearling weight selection line than the weaning weight selection line.

With method I, predicted genetic change in weaning weight was greatest in the weaning weight line. Anderson et al. (1974) examined the correlated growth responses in Shorthorn cattle selected on unadjusted yearling weight. Heritabilities for weaning weight ranged from .07 (paternal half-sib correlation) to .47 (paternal half-sib correlation adjusted for age of dam and dam birth year). Yearling weight heritabilities ranged from -.06 (paternal half-sib correlation) to .47 (son-sire regression adjusted for age of dam and dam birth year).

Direct-Maternal Covariance. If selection is on weaning weight and $COV_{G:WWD,WWM}$ is negative, heritability of weaning weight will be reduced, and selection progress will be slower than if it was zero or positive (Willham, 1972b).

Reports of the covariance and (or) correlation of the direct genetic effect and maternal ability (genetic origin) for growth traits, primarily weaning weight, have indicated a negative relationship (Bertrand and Benyshek, 1987; Vesely and Robison, 1973; Ray et al., 1970; Buchanan et al., 1982). Mavrogenis et al. (1978) reported that the covariance of maternal ability (WWM) with direct genetic growth for weaning weight (WWD), postweaning gain (PWG), and final weight were -432.0, -20.9, and -650.9, respectively, from sire-son regressions. For the $COV_{G:WWD,WWM}$ of weaning weight, Deese and Koger (1967) reported a value of -30%, expressing $COV_{G:WWD,WWM}$ as a percent of the phenotypic variance. Hohenboken (1973) indicated a strong negative correlation with the offspring-dam relationship included in the estimation ($r_{G:WWD,WWM} = -.79$ or -28% of the phenotypic variation), but a weak negative correlation when calculated with the offspring-sire relationship ($r_{G:WWD,WWM} = -.28$ or -8% of the

phenotypic variation). With the offspring-dam relationship excluded, $r_{G:WWD,WWM}$ estimates ranged from -.05 to -.28 (Mrode, 1988b). Koch (1972) reported an average $r_{G:WWD,WWM}$ of -.05 for the solutions without the offspring-dam relationship and -.23 when included.

Comparatively few studies have reported a positive relationship. Graser and Hammond (1985) found that the direct-maternal covariance for weaning weight was marginally positive. Skaar (1985) reported that the direct-maternal correlation was .16 and .25 for an Angus and Hereford population; Wright et al. (1987), .16 for Simmentals.

It has been suggested that the genetic correlation often reported as negative, is in fact a negative environmental correlation (between a heifer's preweaning environment and her subsequent maternal performance) while the true genetic correlation is positive. Koch (1972) stated that only a small part of the direct-maternal covariance is genetic and speculated that the negative environmental correlation is -.1 to -.2. Deese and Koger (1967) suggested that the direct-maternal genetic correlation is, at most, weakly negative under the usual environmental conditions because rapid growing breeds such as Holsteins and Charolais also have excellent milk production. Willham (1972a) postulated that natural selection may be operating on two levels: 1. increased milk production leading to reduced reproductive performance, and 2. excess fat deposition in the mammary gland leading to reduced milk production and causing the negative environmental correlation. Mendoza and Slanger (1985) indicated that yearling weight selection response was relatively unaffected by the $COV_{G:WWD,WWM}$ of weaning weight.

Research with other species tends to support the findings in beef cattle. Robison (1981) reviewed a swine cross-fostering study by Ahlschwede and Robison (1971). These authors found a positive direct-maternal correlation prior to 4 weeks which became negative after 4 weeks because of interactions with certain environmental factors. From 6 to 8 weeks (weaned at 8 weeks), the maternal effect became less important than the genetic effect. Robison's (1981) explanation was that young (swine or beef) consuming supplementary feed over-compensate for a low milk supply and this leads to the observed negative correlation between direct genetic effects and maternal ability for later weights, while the genetic correlation is positive. Robison (1981) also reviewed a study by Hill (1965) which showed $COV_{G:WWD,WWM}$ decreasing as age increased, from 195 at 90d to -334 at 210 days. Riska et al. (1985) observed an up and down trend in the maternal performance of mice from one generation to the next due to permanent maternal environmental effects.

A variety of environmental correlations probably play a role in the direct-maternal covariance of weaning weight. Mueller and James (1985) proposed that the effect of an environmental correlation on phenotypic response depends upon the length of the evaluation period. As the evaluation period lengthens, environmental correlations become less important because genetic contributions become relatively more important. Similarly, reducing the female generation interval and increasing the female selection intensity increases the importance of environmental covariances. Consequently, an environmental correlation could be important in short-term selection experiments (Riska et al., 1985), and most beef cattle selection experiments are short-term. Complete

knowledge of the genetic and environmental factors involved in weaning weight are lacking, leading to variable selection responses (see previous section "method of estimation" for that variability).

Selection: Same End-Point Phenotype, and Correlated Responses

Selection produces phenotypic changes through changes in the rate and (or) timing of the ontogenetic processes (biological development of the cells, tissues, and organs of the individual) (McKinney, 1988 p17). Selection, through the interconnectedness of the developmental processes, and pleiotropy, can produce the same end-point phenotype by operating on different developmental and physiological mechanisms (Atchley et al., 1990; Atchley, 1987).

Atchley et al. (1990) investigated the correlated response of 11 mandible traits in mice to divergent single-trait selection for percent fatness or leanness. They concluded that the significant correlated changes found in the mandible within and among lines were the result of selection altering the ontogenetic patterns and rates of growth of the mandible's contributing parts. Rutledge et al. (1974) found that selection for increased tail length in replicated lines of mice occurred either by an increase in the number of the caudal vertebrae or the length of them.

Variability of correlated responses, though direct responses are fairly consistent from one study to another, has been observed (Atchley et al., 1982). The variability is largely due to the fact that the genes which regulate a particular trait in a particular population vary and the genetic correlation structure varies likewise. If different developmental pathways are used to achieve the same end-point phenotype then

the underlying correlated genetic structure of these different mechanisms with the same skeletal, physiological, and reproductive traits is likely to be different (Atchley, 1987; Atchley et al., 1990). This feature may help explain the variability of correlated responses between growth traits and maternal ability reported in the literature, especially if the selection strategies differed or operated at different developmental stages of the same process to produce the same end-point phenotype.

Selection Experiment Results

The average rate of genetic change in weaning weight was 1.15 kg yr^{-1} from ten selection experiments reviewed by Mrode (1988b). That for postweaning gain averaged 2.21 kg yr^{-1} from three postweaning gain experiments, and that for yearling weight averaged 2.65 kg yr^{-1} from nine yearling weight experiments. These average genetic changes represented .63%, 2.03%, and .80%, respectively, of the mean performance.

Weaning weight selection produced average correlated responses of $2.58 \text{ g d}^{-1} \text{ yr}^{-1}$ in postweaning gain from four experiments and of 2.15 kg yr^{-1} in yearling weight from five experiments (Mrode, 1988b). Postweaning gain selection resulted in correlated increases in weaning and yearling weight of 3.47 and 1.97 kg yr^{-1} , both from one experiment each. Yearling weight selection gave correlated responses of $.67 \text{ kg yr}^{-1}$ in weaning weight from five experiments and $8.33 \text{ g d}^{-1} \text{ yr}^{-1}$ in postweaning gain from four experiments. In general, selection on yearling weight gave greater correlated responses in other growth traits than did weaning weight selection. From two experiments, the correlated response of weaning weight to yearling weight selection was

81% and 105% of the direct weaning weight selection response. Shelby et al. (1963) predicted 110% of the direct selection for weaning weight would be realized by selection on postweaning gain, and 140% by selection on yearling weight. Weaning weight selection would realize only 55% of direct selection for postweaning gain, and 53% for yearling weight. Direct selection on yearling weight would realize 112% of postweaning gain selection. Postweaning gain selection would realize 84% of yearling weight selection.

Luesakul-Reodecha et al. (1986) estimated correlated responses in reproductive, maternal, and longevity traits of 655 Angus cows, born over a 20-year period, to herd selection for increased 365d. weight. The genetic response in 365d. weight was 6.83 kg yr^{-1} and significantly different from zero. Responses in the correlated traits were not definitive, though trends were observed. Long-term selection for weight at one year of age suggested that mature body weight increases, sexual maturity becomes delayed, dystocia rate decreases, progeny weights are increased, and herd longevity is reduced. If these trends reflect real changes, then cow traits should be emphasized over selection for growth traits if a maternal line is required.

The following five experiments will illustrate selection responses achieved in weaning weight, postweaning gain, yearling weight, and maternal ability. These experiments use primarily the control-line method for analysis and Angus or Hereford breeds for study. Selection responses will be followed by an asterisk (*) if significantly different from the control line at the $P < .05$ level, or no asterisk if not significantly

different at the $P < .05$ level. The results are summarized in Table 3, along with a summary of the studies reviewed by Mrode (1988b).

Hough et al. (1985) investigated the selection response of sires selected on yearling weight expected progeny difference and used in an artificial insemination program. The method of analysis was the control-line method and 726 Hereford calf records were evaluated. Direct response in 365d. adjusted yearling weight was 5.5 kg yr^{-1} (*) with correlated responses of 4.6 kg yr^{-1} (*) in 205d. adjusted weaning weight, and $7 \text{ g d}^{-1} \text{ yr}^{-1}$ in postweaning gain. The high response in yearling weight was due to a high selection intensity in sires (top 1%) and a more accurate genetic evaluation of sires through expected progeny differences. Response in yearling weight was achieved largely through weaning weight improvement.

Frahm et al. (1985a,b) evaluated 1,949 calf records representing two Hereford selection lines, one for high adjusted weaning weight and the other for high adjusted yearling weight, and an Angus control line. Following weaning, bulls were placed on feedlot test and fed ad-lib while heifers were placed on pasture. Final weights were taken at 365d. and 425d, respectively. Environmental trend was negative because of a negative phenotypic trend in the control line. Responses in the weaning weight line for weaning weight, postweaning gain, and yearling weight were 1.12 kg yr^{-1} (*), $-1.61 \text{ g d}^{-1} \text{ yr}^{-1}$, and $.59 \text{ kg yr}^{-1}$. In the yearling weight line, responses were 1 kg yr^{-1} (*), $.85 \text{ g d}^{-1} \text{ yr}^{-1}$, and 1.07 kg yr^{-1} for the same three traits. A second method used to analyze the selection response (i.e., environmental estimate calculated from all herds using a multiple regression procedure) gave similar results, and yearling weight response was

TABLE 3. Summary of the direct and correlated responses to selection for weaning weight, postweaning gain, and yearling weight.

| Trait ^a | Mrode 1988b | Hough et al. 1985 | Aaron et al. 1986 | Frahm et al. 1985 | Irgang et al. 1985 |
|--|----------------|----------------------|----------------------|----------------------|-----------------------|
| WW direct response (kg yr ⁻¹) | 1.15 | | 1.53 | 1.12 | 1.07 |
| correlated response in PWG (g d ⁻¹ yr ⁻¹) | 2.58 | | 4.10 | -1.61 | -0.04 |
| correlated response in YW (kg yr ⁻¹) | 2.15 | | 2.11 | 0.59 | 1.50 |
| corr. response in milk yield (kg yr ⁻¹) | - | | 0.50 | 0.41 | 0.21 |
| PWG direct response | 2.21 | | | | 0.85 |
| correlated response in WW | 3.47 | | | | 1.36 |
| correlated response in YW | 1.97 | | | | 2.40 |
| corr. response in milk yield | - | | | | 0.27 |
| YW direct response | 2.65 | 5.50 | 3.51 | 1.07 | |
| correlated response in WW | 0.67 | 4.60 | 1.60 | 1.00 | |
| correlated response in PWG | 8.33 | 7.00 | 12.02 | 0.85 | |
| corr. response in milk yield | - | - | 0.46 | 0.39 | |

^aWW=weaning weight, PWG=postweaning gain, YW=yearling weight.

significant in the yearling weight line (.98 kg yr⁻¹). The small direct response in yearling weight, with most of the improvement due to a correlated response in weaning weight (93%), was attributable to the small response of postweaning gain in heifers (.78 g d⁻¹ yr⁻¹ compared to 1.36 g d⁻¹ yr⁻¹ in bulls) resulting from being placed on pasture. The heifers were on a lower nutritional level which varied greatly from year to year, and selected heifers were replaced by lower ranked heifers if they failed to conceive at their first breeding season. Respiratory infections plagued the postweaning feeding period of bulls and this may have contributed to the small direct response in yearling weight through the negative genetic trend in postweaning gain. The correlated response in milk yield was .41 kg yr⁻¹ and .39 kg kg⁻¹ in the weaning weight and yearling weight selection lines, respectively.

The experimental design and analysis of the Aaron et al. (1986a,b) study was similar to the study by Frahm et al. (1985a,b), with an additional selection line based on individual and progeny weaning weights. All lines were Angus cattle and the number of records evaluated was 2,749. Responses in the weaning weight line for weaning weight, postweaning gain, and yearling weight were 1.53 kg yr⁻¹ (*), 4.10 g d⁻¹ yr⁻¹, and 2.11 kg yr⁻¹ (*), respectively. Corresponding responses in the yearling weight line were 1.60 kg yr⁻¹ (*), 12.02 g d⁻¹ yr⁻¹ (*), and 3.51 kg yr⁻¹ (*). Direct yearling weight response was realized 45% through weaning weight and 55% through postweaning gain and was 105% as effective as weaning weight selection. In contrast, Frahm et al. (1985b) reported that selection on yearling weight as a means of increasing weaning weight was 89% as effective as selecting on direct weaning weight. Correlated

responses in milk yield (.50 kg yr⁻¹ in weaning weight line, .46 kg yr⁻¹ in yearling weight line, .45 kg yr⁻¹ in control line) and composition were similar for cows of both lines, with a trend for the weaning weight line cows to produce more milk than control line cows ($P < .10$).

Irgang et al. (1985a) selected only bulls for high adjusted 205d. weaning weight or postweaning gain from 205d. to 365d. from within sire families. Bulls were placed on feedlot test postweaning and heifers on pasture. Heifer weights were taken at 12 months to calculate postweaning gain. Bulls and heifers were analyzed separately. The control-line method and a multiple-regression procedure were used to analyze the data. Bull responses in the weaning weight line for weaning weight, postweaning gain, and yearling weight were 1.07 kg yr⁻¹, -.04 kg yr⁻¹, and 1.5 kg yr⁻¹, respectively (Irgang et al., 1985b). Heifer responses were less than bulls for weaning weight and yearling weight but larger for postweaning gain, though none were significantly different from zero. Bull responses in the postweaning gain line for weaning weight, postweaning gain, and yearling weight were 1.36 kg yr⁻¹ (*), .85 kg yr⁻¹, and 2.4 kg yr⁻¹ (*), respectively. Heifer values were 91%, 35%, and 63% of corresponding values for bulls. Selection for postweaning gain was more effective in improving weaning weight than weaning weight selection by 127% for bulls and 125% for heifers. Correlated response in milk yield was .21 kg yr⁻¹ for the weaning weight line and .27 kg yr⁻¹ (*) for the postweaning gain line (Irgang et al., 1985c). The positive response in milk yield was attributed to Sejrnsen's (1978 in Irgang et al., 1985c) explanation "that animals with high genetic

growth capacity would have higher growth hormone concentration in the blood and consequently better mammary tissue growth resulting in higher milk production".

Parnell et al. (1986) investigated the selection response of Angus cattle to divergent selection for yearling gain adjusted for age of dam. Their data were analysed by a multi-trait reduced animal model. Results are presented as a deviation from the control line. Bull responses for the high (and low) lines for 200d. adjusted weaning weight, yearling weight and adjusted yearling gain were 25 kg yr^{-1} (-20), 32 kg yr^{-1} (-41), and $7.4 \text{ g d}^{-1} \text{ yr}^{-1}$ (-10.7), respectively. Heifer responses were 76% (-85%), 77% (-68%), and 90% (-60%) of corresponding bull responses in the high (and low) lines.

In summary, selection is used by animal breeders to effect permanent changes in the genetic merit of a population. Selection for the same trait in different populations tends to produce similar responses in the selected trait, but variable responses in correlated traits. The underlying correlated genetic structure may be different and selection may be operating on different physiological and developmental systems to produce the same end-point phenotype. The selection response, nevertheless, depends fundamentally upon the heritability, selection differential, and generation interval. Inbreeding, genetic drift, fitness, design of the experiment, and the environment may also play a role in influencing the selection response. If the correlated selection response is of interest, genetic correlations may be an important factor. Factors which affect heritability and correlations include selection, nutritional level, method of estimation, permanent maternal environment, and direct-maternal covariance. The direct genetic-maternal ability covariance, or correlation, is difficult to interpret because it seems that

there is both a genetic and an environmental component due to maternal ability being a phenotypic trait with genetic and environmental components. Evidence suggests that the genetic correlation is positive, or weakly negative, while the environmental correlation is negative. Selection on weaning weight selects not only for the direct genetic component but also the maternal ability. Consequently, selection on weaning weight was least effective in improving yearling weight and postweaning gain and, in some cases, less effective than yearling weight or postweaning gain selection. Yearling weight direct selection response was achieved through changes in the correlated responses of weaning weight and postweaning gain. In some cases, most of the change in yearling weight was due to weaning weight response (93% from Frahm et al., 1985b) and, in others, to postweaning gain response (75% from experiments reviewed by Mrode, 1988b; 55% from Aaron et al., 1986b). The correlated genetic trend in milk yield to growth trait selection was positive and slightly greater for weaning weight selection lines than yearling weight selection lines, though responses were not significantly different from each other or the control lines.

Genetic Analysis of Selection Experiments

The genetic analysis of selection experiments relies upon the accurate separation of genetic and environmental trends. To illustrate, the control-line method results of Sharma et al. (1985) and Newman et al. (1973) are presented. Sharma et al. (1985) found that if the phenotypic trend had been taken as an estimate of genetic trend it would have underestimated genetic trend by 24% (.44kg) for weaning weight, 18% (2.42g d⁻¹) for postweaning gain, and 78% (4.54kg) for yearling weight because of a negative environmental trend. On the other hand, Newman et al. (1973) discovered that the phenotypic trend of yearling weight was greater than the genetic trend by an average of 60% and 63.5%, in the male and female datasets.

Genetic trend is a graphical representation of the selection response, and can be used to evaluate the effectiveness of selection applied, to "see" corresponding changes in other traits of interest, and to predict future performance based on changes in selection and (or) management practices (Wilson and Willham, 1986). The first two uses are present in this thesis. Average breeding values per year for each trait of interest are plotted against the year of birth to obtain the genetic trend. Breeding values cannot be measured but must be estimated, therefore breeding values are frequently termed estimated breeding values. The breeding value of an individual is an estimate of the genetic merit, or genetic worth, of that animal for the trait of interest. It is estimated from the records of the individual and its relatives and requires knowledge of genetic parameters (heritabilities and genetic correlations). Each record is weighted according to the types and numbers of relatives (Hohenboken, 1985a). Breeding value can thus be

estimated when the trait is sex-limited (maternal ability of bulls and heifers can be estimated even though only cows express the trait). From the dependence of the breeding value on the genetic parameters, it follows that breeding value is dependent upon the genes the individual transmits to its offspring, and the frequencies of those genes in the population (Falconer, 1981 p104-107; Hohenboken, 1985a). Consequently, additive genetic variation is also a measure of the breeding value variation in a population, and the regression of breeding value on phenotypic value is also a measure of heritability (Hohenboken, 1985a).

The genetic analysis of selection experiments is possible through a number of different methods, two of which are the control-line method (an unselected population is maintained) and the mixed-model methodology. These methods are considered to be more accurate in estimation of genetic trend and breeding values than methods used previously, such as repeat matings and intra-year regression of offspring on cumulative selection differential (Mrode, 1988a). Accuracy is important to the replication of experimental results and to the choice of the best combination of selection and mating system to meet producer goals. Hence, growth trait records are usually adjusted for age of dam and systematic (year of birth, sex, and herd) effects to obtain greater accuracy of progeny genetic values which are used in selection decisions.

Control-Line Method

In beef cattle, the effectiveness of using an unselected control population, or line, in conjunction with a selected line, to partition the phenotypic trend into genetic and environmental components was first shown by Newman, Rahnefeld, and Fredeen

(1973) in a population of Shorthorns selected for unadjusted yearling weight. The positive phenotypic response was shown to be a result of both positive environmental and genetic trends, with the genetic trend accounting for only 40% of the response. The authors remarked on the environmental masking of genetic change, the slowness of selection response in the early years, and the time required for visible genetic improvement, even in a highly successful program.

Briefly (see Newman et al., 1973 for details), the control-line method is as follows: At least two lines are required; an unselected control line, with breeding and management practices designed to minimize, or avoid, genetic change, and a selected line where genetic change is maximized. The yearly phenotypic change in the control line is equivalent to the yearly environmental change because the expected yearly genetic change is zero. Because the environmental change is assumed equal in both lines, genetic change in the select line is estimated by subtraction of the control-line phenotypic change from the select-line phenotypic change. The analysis involves the regression of contemporary group performance on year of birth for each line and then subtracting the control regression estimate from the select regression estimate to obtain the genetic trend in the select line. Hence, the analysis involves the comparison between mean yearly phenotypic performance of the control and select lines.

Recent beef cattle selection experiments designed with unselected controls to measure the selection applied and the direct and correlated responses to selection include those of Frahm et al. (1985a,b), Irgang et al. (1985a,b,c), and Aaron et al. (1986a,b).

The control-line method, though effective, has its limitations. Unintentional selection and genetic drift within the control line can reduce the genetic response estimated (Newman et al., 1973; Irgang et al., 1985a). Estimation of maternal effects uses the calf-suckling technique to measure milk production and estimate the maternal effect, but only a small number of cows are sampled because of the time involved (Irgang et al., 1985c; Aaron et al., 1986b).

Whereas the control-line method estimates genetic trend by subtraction, the mixed-model methodology estimates genetic values simultaneously with environmental values, bypassing the necessity of a control line. If a control line is available, selection response could be estimated by adjusting select line records with fixed effects estimated from the control line, or by analyzing each line separately and comparing fixed effects or checking for random genetic drift in average yearly breeding values (Blair and Pollak, 1984a). If fixed effects are similar, datasets could be combined for a more accurate fixed effects estimation.

Mixed-model Methodology

Mixed-model methodology, or the best linear unbiased prediction (BLUP) method with an animal model, has been shown to be effective in separating the genetic and environmental trends in populations without a control line (Sharma et al., 1985; Blair and Pollak, 1984a), and is applicable to the separation of direct and maternal genetic effects (Graser and Hammond, 1985; Quaas and Pollak, 1980). An accurate method of estimating breeding values in populations without a control, such as commercial herds, would be an invaluable tool. However, comparisons between mixed-model methodology

and other methods, such as the control-line method, have been few, particularly in the evaluation of the sensitivity of conclusions to variation in the assumed genetic parameters.

Mixed-model methodology involves solving for random, or fixed and random effects. It has been used to simultaneously estimate fixed effects, and predict breeding values and genetic trends (Henderson, 1973; Graser and Hammond, 1985). Introduced by Henderson (1973), routine application became possible with the easy method of inverting the relationship matrix (Henderson, 1975) and the advancement of computer technology which furthered the development of new models (Quaas and Pollak, 1980) and new computing strategies (Schaeffer and Kennedy, 1986; Misztal and Gianola, 1987).

The relationship matrix is a coefficient matrix of genetic relationships among all animals. A parent-offspring pair, for example, will have a relationship coefficient of one-half because the parent transmits one-half of its genes to its offspring, or 50% of their genes are in common. It is used in mixed-model methodology to estimate genetic trend and breeding values through genetic ties (Henderson, 1973). Accurate estimation depends upon the genetic ties that have been established across environments (eg. years, herds). These genetic ties are particularly useful when heritabilities are low or when predicted breeding values are desired for a trait not observed in an individual (Henderson and Quaas, 1976). The maternal breeding value of sires, for example, can be predicted from records on dams, daughters, and sisters. Genetic ties are also important when sires are replaced yearly (Blair and Pollak, 1984a). In selection experiments, base animals are included in the analysis because they establish

relationships among other animals even though they themselves are not related (VanVleck, 1979 p188). Analysis of select and control lines together will give more accurate estimates, or smaller sampling variance, of fixed and random effects, especially if the lines are genetically related (Sorensen and Kennedy, 1984).

The computing strategy implicit in the (reduced) animal model requires prior knowledge of the variances and covariances among the random effects of the model for all traits (Schaeffer and Wilton, 1981). Incorrect (co)variances can result in significant changes in animal rankings, a decrease in accuracy of estimates and changes in predicted genetic values (Schaeffer, 1984). If (co)variances used in computations are substantially different from true values, it is possible for prediction error to be larger than if correlated traits had not been used at all (Henderson and Quaas, 1976). The exact values of the (co)variances are not as important as the ratios, i.e., correlations and heritabilities (Schaeffer and Wilton, 1981). Small differences between the estimated and true correlations and heritabilities are probably not significant as the loss of accuracy is likely less than 5% (Schaeffer, 1984). The (co)variances can be estimated from the dataset or obtained from the literature. Literature values are presented in Table 4 for the trait weaning weight and in Table 5 for the additional trait postweaning gain or yearling weight.

The difference between an animal model and a reduced animal model is basically one of computing strategies (Quaas and Pollak, 1980). The reduced animal model is more computationally feasible because only parent solutions are solved directly. A number of data files are constructed from the original dataset and used in an iterative

TABLE 4. (Co)Variances, heritabilities, and correlations for the trait weaning weight^a.

| Source | N ^b | Breed ^c | V _{P:WW} | h ² _{WWD} | h ² _{WWM} | r _{G:WWD,WWM} | V _{E:WWPE} | V _{E:WW} |
|---|----------------|--------------------|-------------------|-------------------------------|-------------------------------|---------------------------------|---------------------|-------------------|
| Wright et al, 1987 | 114,899 | SM | 668 | 0.12 | 0.09 | +0.16 | 7.4 | 70 |
| Bertrand and Benyshek, 1987 | 53,494 | LM | 400 | 0.16 | 0.15 | -0.30 | 5.9 | 67 |
| Bertrand and Benyshek, 1987 | 46,661 | BN | 584 | 0.28 | 0.20 | -0.29 | 4.1 | 55 |
| Graser and Hammond, 1985 | 12,323 | SM | 523 | 0.10 | 0.13 | +0.04 | 0.0 | 76 |
| Mendoza and Slanger ^d , 1985 | - | - | 314 | 0.275 | 0.275 | +0.1, -0.1, -0.3, -0.5 | 0.0 | 42 to 59 |
| Vesely and Robison ^e , 1973 | 1,692 | HH | 493 | 0.52 | 0.34 | -0.58 | 8.5 | 30 |
| Hohenboken and Brinks, 1971 | 1,386 | HH | 507 | 0.23 | 0.54 ^f 0.34 | -.79 -0.28 | -2.0 | 53 ^g |
| Deese and Koger, 1967 | 725 | BR | 109 | 0.18 | 0.15 | .00 | 8.0 | 59 |
| Deese and Koger, 1967 | 466 | BRxSH | 99 | 0.40 | 0.46 | -0.73 | 7.0 | 38 |
| Hill et al., 1966 | 717 | HH | 312 | 0.32 | 0.29 | -0.31 | 7.7 | 41 |

^aV_{P:WW}=phenotypic variation (kg²), h²_{WWD}=direct genetic heritability, h²_{WWM}=maternal genetic heritability, r_{G:WWD,WWM}=direct-maternal genetic correlation, V_{E:WWPE}=permanent maternal environmental variance (%), V_{E:WW}=residual variance (%).

^bN=number of observations.

^cSM=Simmental, LM=Limousin, BN=Brangus, HH=Hereford, BR=Brahm, BRxSH=Brahm-Shorthorn cross.

^dValues used in the computer simulation but obtained from other authors.

^eThe values shown are for the 4:1 ratio of V^{G:WWM}:V^{E:WWPE} is 4:1.

^fThe 0.54 value includes the offspring-dam relationship, 0.34 includes the offspring-sire relationship.

^gIncludes the direct dominance effect.

TABLE 5. Heritability and correlations for the trait postweaning gain (and yearling weight).

| Source | Sex | N ^a | Breed ^b | h ² _{PWG} | r _{G:WWD,PWG} | r _{E:WW,PWG} | r _{G:WWD,WWM} |
|---|------|----------------|--------------------|-------------------------------|------------------------|-----------------------|------------------------|
| Smith et al., 1989 | F | 779 | HH | 0.33 | 0.49 | -0.14 | |
| DeNise and Ray, 1987 | M | 237 | HH | 0.47 | 0.95 | -0.12 | |
| Quaas et al., 1985 | F, M | 160,961 | SM | 0.20 | 0.52 | - | 0.25 |
| Mendoza and Slanger ^d , 1985 | - | - | - | (0.525) | (0.89) | (0.66) | (-0.30) |
| Graser and Hammond ^d , 1985 | - | 2,237 | SM | (0.26) | (0.60) | (0.60) | (0.00) |
| Buchanan et al., 1982 | M | 3,288 | HH | 0.35 | -0.02 | 0.27 | |
| Buchanan et al., 1982 | F | 3,077 | HH | 0.49 | 0.46 | -0.12 | |
| Thrift et al., 1981 | M | 383 | HH | 0.92 | 0.51 | -0.57 | |
| Thrift et al., 1981 | F | 345 | AN | 0.88 | 0.13 | -0.58 | |
| Preston and Willis ^e , 1970 | M | - | - | 0.50 ₅₆ | 0.49 ₁₀ | 0.04 ₃ | |

^aN=number of observations.

^bHH=Hereford, SM=Simmental, AN=Angus.

^cSee List of Abbreviations for definitions.

^dTrait is yearling weight.

^eValues are averages. The subscript values are the number of contributing studies.

process, rather than setting up the equations explicitly which often produces more than one equation per record. By iterating with data files, one relatively simple computer program can solve the mixed-model equations (Schaeffer and Kennedy, 1986). The structure of the relationship matrix is used to form parent equations, eliminating nonparents. Nonparent solutions are obtained by backsolving using the individual's record(s), the fixed solutions, and the solutions of its parents. The reduced animal model is illustrated by Schaeffer and Wilton (1987).

Blair and Pollak (1984b) compared the computing efficiency of the animal model to the reduced animal model in a three-trait evaluation. Both models, especially the reduced animal model, achieved sufficiently accurate ranking of animals long before an accurate representation of genetic trend. The reduced animal model fixed effect solutions converged faster than random effects because of the greater density of the fixed effects coefficient matrix. Both models converged faster as the amount of genetic trend in a particular population declined.

The multiple-trait, reduced animal model improves the accuracy of ranking of individuals for each trait, removes bias caused by selection, and predicts breeding values for all traits, regardless of whether there is an actual observation or not, because of the utilization of genetic and environmental correlations among traits and the genetic relationships among individuals (Schaeffer, 1984; Pollak et al., 1984).

Selection Experiments

Application of mixed-model methodology with a reduced animal model has become more widespread in recent years in the estimation of breeding values and genetic

trend, but comparison of results obtained from the mixed-model methodology and control-line method have been few.

Winder et al. (1988) used a single-trait reduced animal model to evaluate genetic trends of sires and dams from 76,560 field records of the Red Angus Association of America. Estimated breeding values (EBV's) were calculated for birth weight, direct and maternal components of weaning weight, and postweaning gain. Yearling weight EBV's were the sum of direct weaning weight and postweaning gain EBV's. The maternal component of weaning weight showed a positive trend initially but became negative for both sires and dams, with dams lagging two years behind that of sires. The postweaning gain trend was initially constant but became positive at the time sire trend for the maternal effect became negative and by a similar amount. The EBV's of the direct component of weaning weight increased during the period of evaluation for dams but declined during the last few years for sires. Three explanations for the observed trends, especially the reduction in milk production potential concurrent with increased postweaning gain potential, were put forth. First, selection pressure within this population was actually reducing milk production potential. If selection pressure were on postweaning gain, individuals with high genetic growth potential nursing low milk producing dams would experience compensatory growth postweaning and thus excel under these conditions. Second, if selection pressure is favoring larger mature weights, increased nutrients for self growth and maintenance and of reduced nutrient availability for milk production would confound the lack of expression of milk production potential with genetic merit. Third, if weaning weight age-of-dam adjustment factors were too

small for young dams, a bias in EBV's could be introduced. Years with higher concentrations of young cows, i.e., recent years, would depress average EBV's for maternal ability and increase average EBV's for postweaning gain through compensatory growth.

Blair and Pollak (1984a) evaluated selection response to heavy 14-month greasy fleece weight in sheep using a single-trait animal model with and without the use of a control population. Three estimates of genetic response were obtained and compared: 1) deviation of select line from control line of predicted yearly phenotypes, 2) deviation of select line predicted yearly phenotype from control-line year estimate, and 3) analysis of select line only for mean yearly breeding value. Results obtained with approach three are most applicable to the work reported in this thesis. The realized heritability estimates (.20, .23 and .23 for approach 1, 2 and 3, respectively) were less than the assumed parameter value of .30 because selection was on unadjusted records, but the estimates were not statistically different from zero. Approach 1 estimate was lowest because it did not account for the slight genetic drift which occurred in the control line. A much smoother graphical representation of the genetic response was obtained by approach 3. The year to year variation from approaches 1 and 2 was "due largely to the differences between the year effects estimated from the two flocks".

Varying the heritability value from .10 to .20 to .30 increased the average yearly breeding value and correspondingly decreased the year solution so that predicted yearly phenotypic trend remained unchanged. Fixed effects, other than year, were relatively unchanged. Heritability realized from approach 1 was constant at .20 for all

parameter values because phenotypic trend remained unchanged. Heritabilities realized from approach 2 were .21, .22 and .23 reflecting increased estimated genetic drift in the control group as heritability increased. The genetic response estimated by approach 3 was the most modified (.10, .16 and .23). As the heritability increased, the mean breeding value increased and year effect decreased. The heritability value thus assumed may influence the results and conclusions.

This study indicated that 1) at an assumed heritability of .30, the mixed-model methodology (approach 3) was as effective as the least-squares techniques (approximated by approach 1 and 2) in separating the genetic and environmental trends, 2) "approach 3 could be used to estimate the genetic trend from the selected group only" or "to estimate genetic trends in commercial data, where no control information is available".

Sharma et al. (1985) estimated the genetic trend in both a Hereford and a multi-breed (Synthetic) population selected for high adjusted yearling weight in bulls. Two methods were compared: 1) deviation from a control population and 2) sire evaluation using the best linear unbiased prediction (BLUP) procedure. Traits analyzed included weaning weight, postweaning gain and yearling weight of bulls. BLUP estimates yielded lower genetic values for all traits in the Synthetic population (by 48% for weaning weight, 35% postweaning gain, and 40% yearling weight) and for weaning weight (39%) in the Hereford population than comparable control line estimates. For postweaning gain and yearling weight genetic values in the Hereford population, BLUP estimates were higher (31% and 41%, respectively).

Parnell et al. (1986) analyzed eleven years of data (1974-1984) for divergent selection of yearling gain adjusted for age of dam. A multiple-trait reduced animal model was used to estimate breeding values for 200d. weaning weight (direct and maternal components) and yearling weight in three lines: 1. a control line, 2. a line selected for high yearling gain, and 3. a line selected for low yearling gain. The yearling weight trend in the control line was graphically smooth with few peaks. The high line was relatively smooth from 1976 to 1984. The low line was characterized by peaks and valleys which were large during the first half of the experiment and smaller in the latter half. Response in yearling weight estimated breeding values was slightly greater in the low line than the high line. The direct weaning weight trend was graphically similar to that for the yearling weight but values were about three times smaller. The response in both lines was similar when compared to the control, though in opposite directions. The maternal weaning weight trend of the control line was essentially straight. The high line was represented by peaks and valleys, with a slight positive slope. The response was less than that of the low line. The low line decreased gradually until 1980 and was smooth until 1984. The maternal response compared to the direct response was about one-half for the high line and about the same for the low line.

In summary, two methods of separating the phenotypic response into genetic and environmental components were presented. The control-line method uses an unselected line to measure the environmental change and, by subtraction from the select line, estimates the genetic change. The mixed-model methodology used with the reduced animal model estimates the genetic trend in a population, regardless of whether selection

is occurring or not, and depends upon the (co)variances used and the genetic connectedness provided by the relationship matrix. Breeding values are estimated for all traits in the model, whether there is an actual observation or not. Selection experiment results indicate that mixed-model methodology with a reduced animal model is effective in the estimation of the genetic trend.

MATERIALS AND METHODS

Materials

The data, collected over a 12-year period (1958-1969), were obtained from a beef cattle selection experiment conducted at the Brandon Agriculture Canada Research Station, Manitoba, by G.W. Rahnefeld (Newman et al., 1973). The experiment explored the rate and duration of response to 10 years of single-trait selection for unadjusted yearling weight of beef Shorthorn cattle.

The beef herds at Melita, Manitoba and Indian Head, Saskatchewan were amalgamated with the Brandon, Manitoba herd in the fall of 1960 and 1964, respectively. The herd was fed hay and (or) silage in winter and had access to board fence windbreaks. In summer, from May to September, the herd was pastured. Breeding season began June 15 for 42 days. The bulls used had passed a semen test and physical soundness check. Calving occurred from the third week of March to the first week of May. Calves had access to supplemental (creep) feed from 8 weeks of age to weaning at 182 ± 4 days. The postweaning ration consisted of barley, oats and chopped hay in about equal amounts and fed as: 1) a pelleted feed twice a day at Indian Head and Melita, 2) a non-pelleted feed twice a day at Brandon from 1958 to 1963 for the male calves and from 1958 to 1961 for the female calves, 3) a nonpelleted feed ad-lib at Brandon from 1962 to 1964 for the female calves and in 1964 for the male calves, and

4) a pelleted feed ad-lib from 1965 to 1969. Yearling weights were calculated as an average of three weekly weights bracketing the weigh day on which the calf reached 364 ± 4 days of age.

The first two calving years of the project (1958 and 1959) established a base population from which an unselected control line and a select line were initiated. Progeny born in the base population were sired by 12 bulls from unrelated outside herds. The bulls were used to introduce new genetic material to maximize the response to selection, a practice which increases the genetic variation and reduces any accumulated inbreeding. Bulls were exchanged annually until amalgamation at Brandon, Manitoba in order to reduce genetic drift between the herd locations.

The base population was divided into two lines for the 1959 breeding season, with the first group of select and control line progeny born in 1960. Cows were randomly assigned to the lines; with two-thirds assigned to the select line and one-third to the control line. Between 1960 and 1962, 15 dams and heifers were reassigned from one line to the other, primarily from control to select. An average of 250 cows were present each year, with an average of 90 cows in the control line and 160 cows in the select line, of which an average of 77% in the control line and 79% in the select line had weaned calves.

Bulls were assigned to the lines based on unadjusted yearling weight; highest for the select line and randomly for the control line. The method resulted in one bull common to both lines; the select line for the 1959 breeding season and the control

line for the 1960 to 1968 breeding seasons. Bulls were assigned 12 to 18 cows by random sampling within cow age for each line.

The 1960 calf crop of each line was sired by an unique set of 1958 born bulls, and by a common set composed of two of the unrelated bulls. A different set of bulls sired the 1961 to 1969 calf crops in the control line. This set remained constant except in 1963 when one bull was substituted for another. In the select line, the set of 1958 and 1959 born bulls that sired the 1961 and 1962 calf crops differed by one bull. Bulls born in 1960 were not used. Bulls born in 1961 and later were used for only one year.

Genetic change in the control line can be minimized in a number of ways to more accurately measure the environmental trend. In the present work, repeat matings were used as much as possible. Parents were culled only for health reasons and, for dams, failure to calve in two successive years. Culled bulls were replaced by sons, or frozen semen of the culled bulls was used. Replacements were randomly chosen from those calves which deviated by less than one standard deviation from the mean unadjusted yearling weight.

In the select line, genetic change can be maximized in a number of ways to increase the selection response. In the present work, cow breeding groups were rerandomized every year and bulls were replaced annually. Culling of dams was based on failure to calve in any one year, poor health, older age, or poor progeny performance. Replacements of both sexes were selected for high unadjusted yearling weight. To minimize inbreeding, half-sib matings and matings with more than one

common grandparent (also applied to the control line), were avoided. Additionally, a replacement limit of three sons from any one sire was imposed.

The data for the final calf crop year (1969) contains matings between control-line sires of the 1959 breeding season and select-line dams, and between control-line dams and select-line sires. The authors (Newman et al., 1973) used these matings to calculate another estimate of realized heritability to compare it against the estimate obtained from the selection study data. The matings are used in this thesis because the genetic relationships between the parents and offspring offer further connections in the estimation of breeding values.

Twins were included in the dataset, with no adjustment made to their records other than the age-of-dam adjustment. There were 22 twins born in the twelve-year period, with only 12 pairs surviving to one-year-of-age. The other 10 twins had one of the pair die before either weaning or yearling weights were taken.

In the final year, 84% of the dams with weaned calves were selected females born in 1963 and later. The average parent age in the final year was 8.71 years for the control line and 3.25 years for the select line. The average number of progeny born to select-line sires was 12.4 calves. The average annual replacement rate of select-line cows was 22%, and 13% for control-line cows.

Methods

The traits of interest in the present study were weaning weight and postweaning gain. The analytical method was designed to determine how the change in yearling weight was achieved, by study of: a) the direct genetic component of weaning

weight, b) the maternal genetic component of weaning weight and, c) the direct genetic component of postweaning gain. The information required from each calf record was weaning weight, yearling weight, age of dam at the time the trait was expressed, line of calf (base, control, select), year of record or birth year, sex of calf, herd of origin (Brandon, Indian Head, Melita) dam, and sire. The data were edited to correct a small number of discrepancies regarding unique identifications, and to delete all records not containing weaning weight information. The Complete dataset yielded 2357 weaning weight records for analysis (Table 6). Two subsets of the Complete dataset, the Select dataset and the Control dataset, were also created and are shown in Table 6.

A multiple-trait reduced animal model (RAM) (modified by G.H. Crow after Schaeffer and Wilton (1987), using the computing strategy of Schaeffer and Kennedy (1986) and the model of Quaas and Pollak (1980)) was used to analyze the data. The mixed-model methodology is used by performance and breed organizations to evaluate commercial herds because a control population, which is rarely a part of the design of these herds, is not required for the estimation of genetic trend. There are few available papers on the effectiveness and accuracy of this method compared to methods which use some form of control, such as an unselected control population.

The fixed effects to be included in the RAM were determined using general analysis of variance procedures. The software system for data analysis was the SAS (1985) system for mainframes. The Control dataset was used to examine the effects of year of record, sex, and herd of origin because select line data would confound the year of birth effect with the annual selection changes. Similarly, the age-of-dam a prior

TABLE 6. Number of records evaluated by the animal model method, by dataset.

| Dataset | Calf Weaning Weight Records | | | | Parents - no WW records | Total |
|----------|-----------------------------|-----------------|----------------|--------------------|----------------------------|-------|
| | Base Line | Control Line | Select Line | Total | | |
| Complete | 316 | 688 | 1,275 | 2,357 ^a | 239 | 2,596 |
| Select | 316 | - | 1,275 | 1,591 | 233 | 1,824 |
| Control | 316 | 688 | - | 1,004 | 232 | 1,236 |

^aThe total includes 78 line-cross calves from the final year of the experiment. Without these calves, the total is 2,279 records.

Note1: The control and select datasets have 464 animals in common.

Note2: Parents without weaning weight records differ between datasets because dams were included in the subsets Select and Control only if they produced a calf with a weaning weight record.

adjustment calculated from the Control dataset avoids confounding progeny genetic superiority of young, selected dams (in contrast to mature, less selected dams) and the progeny's environmental disadvantage of being born to a young dam (Blair and Pollak, 1984a).

The initial models for weaning weight and postweaning gain included the main effects sex, year, herd, and the two-way interactions, and, in the weaning weight model, the age-of-dam covariate. Some of the interactions were significant, but the models containing only main effects were simpler, thus easier to interpret, and the coefficient of determination decreased by only 0.04 units. Henderson (1973) has stated that the simplest model that accounts for known and important sources of variation is desired and, when unimportant elements are removed from the model, computational costs and sampling variances become smaller. Thus, the only fixed effects in the RAM were sex of calf, year of birth, and herd of origin. Weaning or yearling age was not included in the model because the experiment was designed to eliminate these age variables.

The age-of-dam adjustments (Table 7) were calculated from the Control dataset. In a model containing sex of calf, year of birth, herd of origin, age of dam, and age of dam squared, all of which were significant effects ($P < .05$), the linear and quadratic terms were used for the age-of-dam adjustment. This adjustment was applied to the weaning weight records of all calves (control and select line) before the mixed-model analysis.

TABLE 7. Weaning weight age-of-dam adjustment factors.

| Age of Dam | Adjustment (kg) |
|------------|-----------------|
| 2 | 23.9 |
| 3 | 16.5 |
| 4 | 10.5 |
| 5 | 5.9 |
| 6 | 2.6 |
| 7 | 0.6 |
| 8 | 0 |
| 9 | 0.7 |
| 10 | 2.8 |
| 11 | 6.3 |
| 12 | 11.1 |
| 13 | 17.2 |
| 14 | 24.7 |

The genetic trend of calf estimated breeding values (EBV's) for the maternal and growth components of weaning weight and for the growth component of postweaning gain were obtained by regressing the genetic solutions from the RAM on the year of birth of the calf. The results of Newman et al. (1973) and Olthoff et al. (1990b), both of whom used the Brandon-station data and the control-line method of analysis to estimate genetic trends, were compared to the genetic solutions obtained by the RAM. Solutions obtained from the Complete dataset, the Control dataset, and the Select dataset were compared to determine the effect of less available information in terms of the number of records and the effect of analyzing a selected herd without comparison to an unselected herd.

The model for the traits weaning weight or postweaning gain was:

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + D_l + M_m + PE_m + e_{ijklmn}$$

where,

Y_{ijklmn} = an individual weaning weight (or postweaning gain) observation,

μ = population mean,

a_i = fixed sex effect (male, female),

b_j = fixed year of birth effect (1958 to 1969, inclusive),

c_k = fixed herd of origin effect (Brandon, Melita, Indian Head),

D_l = random direct additive genetic effect with mean zero and variance $V_{G:WWD}$
or $V_{G:FWG}$,

M_m = random maternal additive genetic effect of the calf's dam for weaning weight observations only, with mean zero and variance $V_{G:WWM}$,

PE_m = random permanent maternal effect of the calf's dam for weaning weight observations only, with mean zero and variance $V_{E:WWPE}$, and

e_{ijklmn} = random residual effect for each observation with mean zero and variance $V_{E:WW}$ OR $V_{E:PWG}$.

The use of mixed-model methodology implies that the mixed-model solutions will have a dependency on the (co)variances. In this present study, the sensitivity of the results to variation in the genetic and environmental correlations (covariances) between weaning weight and postweaning gain, and the direct-maternal genetic correlation (covariance) of weaning weight were investigated. The parameters used in the base run are shown in Table 8 as parameter set one. Parameter set one uses +0.5 for the genetic correlation between weaning weight and postweaning gain, -0.2 for the environmental correlation between weaning weight and postweaning gain, and zero for the direct-maternal genetic correlation of weaning weight. The base run uses the Complete dataset and parameter set one, and it is this run against which all other parameter combinations and analyses are compared. The detailed (co)variance matrix for the base run is given in Appendix A.

The assumed parameter values used in the RAM (Table 9) were based on literature values (Tables 4 and 5, in part). Literature values were assumed because the required parameters could not be calculated accurately from the dataset because of its relatively small size. As well, one of the objectives was to determine the sensitivity of the results and conclusions to variation in the correlations. The values are representative of those found in the literature for beef cattle, primarily British breeds (Shorthorn,

TABLE 8. The parameter set numbers assigned to each unique parameter combination and their corresponding (co)variances^a.

| Set # | Parameter | | | (Co)Variance | | | | | |
|----------------|-----------------|----------------|-----------------|--------------|----------------|------------|------------------|-------------------|-----------------|
| | Combination | | | Parent | | Nonparent | | | |
| | $r_{G:WWD,PWG}$ | $r_{E:WW,PWG}$ | $r_{G:WWD,WWM}$ | $V_{E:WW}$ | $COV_{WW,PWG}$ | $V_{E:WW}$ | $COV_{E:WW,PWG}$ | $COV_{G:WWD,PWG}$ | $COV_{WWD,WWM}$ |
| 1 ^b | + .5 | - .2 | .0 | 144 | -40 | 400 | 3 | 83 | 0 |
| 2 | + .5 | + .2 | .0 | 144 | 40 | 400 | 163 | 83 | 0 |
| 3 | + .5 | - .2 | + .5 | 102 | -34 | 316 | 15 | 83 | 42 |
| 4 | + .5 | + .2 | + .5 | 102 | 34 | 316 | 151 | 83 | 42 |
| 5 | + .5 | - .2 | - .5 | 186 | -45 | 484 | -7 | 83 | -42 |
| 6 | + .5 | + .2 | - .5 | 186 | 45 | 484 | 173 | 83 | -42 |
| 7 | - .1 | - .2 | .0 | 144 | -40 | 400 | -97 | -17 | 0 |
| 8 | - .1 | + .2 | .0 | 144 | 40 | 400 | 63 | -17 | 0 |
| 9 | - .1 | - .2 | + .5 | 102 | -34 | 316 | -85 | -17 | 42 |
| 10 | - .1 | + .2 | + .5 | 102 | 34 | 316 | 51 | -17 | 42 |
| 11 | - .1 | - .2 | - .5 | 186 | -45 | 484 | -107 | -17 | -42 |
| 12 | - .1 | + .2 | - .5 | 186 | 45 | 484 | 73 | -17 | -42 |

^aSee List of Abbreviations for definitions.

^bParameter set one is the base run against which all other parameter combinations are compared.

TABLE 9. Assumed values of heritabilities, genetic and environmental correlations, and phenotypic variances used to calculate the genetic trend.^a

| Trait | PWG | WWD | WWM | $V_{P:PWG}$ |
|--|----------|----------|-------------|------------------|
| Direct effects on postweaning gain (PWG) | .47 | +.2, -.2 | -.06 | 521 |
| Direct effects on weaning weight (WWD) | +.5, -.1 | .32 | +.5, 0, -.5 | $V_{P:WW}$ |
| Maternal effects on weaning weight (WWM) | 0 | 0 | .18 | 350 ^b |

^aHeritability estimates are on the diagonal; genetic correlations above, and environmental correlations below. $V_{P:PWG}$ or $V_{P:WW}$ is the phenotypic variation in kg².

^bPhenotypic variation in weaning weight contains variation due to direct and maternal genetic effects, as well as other components.

Hereford, and Angus). The genetic correlation between weaning weight and postweaning gain was assumed to be +0.5 or -0.1, where -0.1 represents those cases where a small, negative value has occasionally been reported. The environmental correlation between weaning weight and postweaning gain was assumed to be +0.2 or -0.2, and the direct-maternal genetic correlation of weaning weight was assumed to be +0.5, 0.0, or -0.5. The (co)variance values that change with the changing parameters are the residual variance of weaning weight, the residual covariances of weaning weight and postweaning gain, the direct genetic covariance of weaning weight and postweaning gain, and the direct and maternal genetic covariance of weaning weight. Each parameter combination is assigned a number from 1 to 12 (Table 8) to facilitate presentation in the results and discussion section.

Conducting the sensitivity analysis at an individual level, 10 select line bulls with progeny and 10 select line yearling bulls born in 1969 were randomly chosen and were ranked by EBV's for weaning weight and postweaning gain for each of the parameter set solutions obtained. The yearling EBV's simulate the breeder situation in which bulls are chosen within year. The sire EBV's simulate the artificial insemination industry where bulls are available across years.

The number of animals evaluated by the RAM, including parents without weaning weight records, was 2596 animals (Table 6). An example of the RAM method of analysis is given in Appendix B for a dataset with two fixed effects and eleven calf records. The number of calf records per year used to calculate the genetic trends in the Select and the Control datasets are shown in Table 10.

TABLE 10. Number of weaning weight records upon which the genetic trends and fixed effects estimates are based.

| Fixed Effect | Dataset | |
|-----------------|---------|---------|
| | Select | Control |
| Year: | | |
| 1958 | 137 | |
| 1959 | 179 | |
| 1960 | 87 | 59 |
| 1961 | 108 | 60 |
| 1962 | 124 | 71 |
| 1963 | 134 | 69 |
| 1964 | 133 | 71 |
| 1965 | 138 | 72 |
| 1966 | 140 | 75 |
| 1967 | 126 | 84 |
| 1968 | 142 | 83 |
| 1969 | 143 | 44 |
| Sex: | | |
| male | 844 | 479 |
| female | 747 | 525 |
| Herd of origin: | | |
| Brandon | 1,221 | 687 |
| Melita | 81 | 81 |
| Indian Head | 289 | 236 |

Basic statistics are given in Tables 11 and 12. Table 11 gives the number of observations, means, and standard deviations for the base, select, and control line calves. Table 12 presents the EBV's across all years and lines. The EBV correlation values are more positive than the genetic correlations assumed in the RAM. The correlation of direct weaning weight and postweaning gain EBV's was 0.60 and the direct-maternal correlation for weaning weight EBV's was 0.30. The corresponding genetic correlations were assumed to be 0.50 and 0.00, respectively. The correlation of postweaning gain and maternal ability EBV's was 0.35, whereas the genetic correlation was -0.06. The above results show how the EBV's, and the correlations among them, are dependent both on the data and the assumed genetic parameters.

The fixed effects estimates are presented in Table 13. Standard errors of these solutions could not be calculated because of the nature of the analysis method.

The sex effects are presented as means while herd-of-origin effects are presented as differences from the Indian Head herd of origin and, year effects, from the 1969 birth year. Bull calves were heavier at weaning and grew faster postweaning than heifer calves. Calves from Brandon and Melita weighed less at weaning than calves from Indian Head but gained more postweaning.

Selection differentials and intensities of selection were used to explore the genetic progress in yearling weight and the correlation of yearling weight with postweaning gain and weaning weight. Selection differentials for the traits yearling weight, postweaning gain, and weaning weight were calculated as the differences between the phenotypic means of the chosen group and the phenotypic means of the group from

TABLE 11. Number of observations, means, and standard deviations for base, select, and control line calves.

| Calf Line | Mean \pm Standard Deviation (kg \pm kg ²) | | | | | |
|-----------|---|------------------|------------------|-------|------------------|------------------|
| | N ^a | adj. WW | Weaning Wt. | N | PWG | Yearling Wt. |
| Base | 316 | 192.6 \pm 20.0 | 181.8 \pm 20.5 | 309 | 147.7 \pm 27.4 | 329.5 \pm 38.9 |
| Select | 1,275 | 199.5 \pm 22.2 | 188.7 \pm 24.9 | 1,201 | 191.7 \pm 38.7 | 380.4 \pm 53.5 |
| Control | 688 | 193.8 \pm 21.7 | 185.6 \pm 23.6 | 660 | 172.4 \pm 35.1 | 358.0 \pm 48.4 |

^aN=number of observations, adj. WW=weaning weight adjusted for age of dam, PWG=postweaning gain.

TABLE 12. Estimated breeding value (EBV) statistics of the base run - the means, standard deviations, minimum and maximum values, and correlations - for postweaning gain, direct weaning weight, and maternal ability.

| Trait | Mean ^a | Std. Dev. | Min. | Max. |
|------------------------|-------------------|-----------|--------|-------|
| postweaning gain (PWG) | 5.38 | 13.72 | -39.63 | 48.48 |
| weaning weight (WWD) | 1.02 | 8.59 | -44.74 | 34.75 |
| maternal ability (WWM) | 0.92 | 4.40 | -12.55 | 16.49 |

| | Correlation of EBV's | Genetic correlation ^b |
|----------|----------------------|----------------------------------|
| WWD, PWG | .60 | .50 |
| WWD, WWM | .30 | 0 |
| PWG, WWM | .35 | -.06 |

^aMean is based on 2,279 records (see Table 6).

^bGenetic correlations are those assumed in the RAM.

TABLE 13. Fixed effects estimates for weaning weight (WW) and postweaning gain (PWG) obtained from the base run.

| Fixed Effect | Weaning Weight | | Postweaning Gain | |
|-----------------|----------------|--------|------------------|--------|
| | N ^a | (kg) | N ^a | (kg) |
| Sex: | | | | |
| bulls | 1,162 | 210.20 | 1,144 | 185.36 |
| heifers | 1,117 | 190.84 | 1,100 | 141.76 |
| Herd of origin: | | | | |
| Brandon | 1,842 | -17.80 | 1,752 | 20.82 |
| Melita | 81 | -9.24 | 78 | 25.62 |
| Indian Head | 434 | 0.00 | 414 | 0.00 |
| Year: | | | | |
| 1958 | 137 | 4.82 | 137 | -29.01 |
| 1959 | 179 | 5.36 | 172 | -33.31 |
| 1960 | 147 | 0.39 | 139 | -29.36 |
| 1961 | 168 | -2.31 | 148 | -26.17 |
| 1962 | 195 | 9.71 | 189 | -10.64 |
| 1963 | 202 | 1.33 | 197 | -15.88 |
| 1964 | 204 | 9.37 | 193 | 17.14 |
| 1965 | 210 | 10.46 | 194 | 17.29 |
| 1966 | 215 | 22.94 | 208 | -1.56 |
| 1967 | 210 | 10.19 | 197 | 18.75 |
| 1968 | 225 | 13.92 | 219 | -8.94 |
| 1969 | 265 | 0.00 | 251 | 0.00 |

^aN=number of observations.

which they were chosen. The later group was based on contemporaries born in the same line, year, and of the same sex. The herd-of-origin, though used in the analysis, was not used in the calculation of selection differentials. Olthoff et al. (1990b), who studied the component traits of yearling weight and cow reproductive performance characteristics using the Brandon-station data as well, did not account for herd of origin in the control-line method of analysis, as preliminary analysis indicated that this effect was not significantly different from zero. Using the Brandon and Lacombe station data, Newman et al. (1973) considered herd-of-origin because, although top-ranked bulls for unadjusted yearling weight were chosen for the select line when possible, a minimum number were chosen from the locations within each station.

Selection intensities were calculated by dividing the selection differentials by the contemporary group standard deviations. The selection differentials and intensities of selection for the select line sires and replacement heifers are given in Tables 14 and 15, respectively. Observation of the selection intensities for the traits postweaning gain and weaning weight gives an indication of the correlation of these traits to yearling weight. If a correlation did not exist, these selection intensities would be expected to be zero. For example, 1967 born sires had a selection intensity of 1.22 for postweaning gain and 1.18 for weaning weight. These values, expressed as a percent of the selection intensities for top ranked bulls, were 78% for postweaning gain and 74% for weaning weight. A strong, positive correlation is indicated. Similarly, the heifer selection intensity data also supports a strong, positive correlation between postweaning gain and weaning weight.

TABLE 14. Selection differentials and intensities of selection for the select line sires^a.

| Year | N(%) | Yearling Weight | | | | Postweaning Gain | | | | Adj. Weaning Weight ^b | | | |
|------|----------------|-----------------|------|--------|------|------------------|------|--------|------|----------------------------------|------|--------|------|
| | | Selected | | Ranked | | Selected | | Ranked | | Selected | | Ranked | |
| | | D | i | D | i | D | i | D | i | D | i | D | i |
| 1958 | 9° | 14.1 | .48 | 43.5 | 1.47 | -2.7 | -.16 | 30.1 | 1.79 | 13.4 | .69 | 29.8 | 1.54 |
| 1959 | 7° | 35.5 | 1.51 | 42.1 | 1.79 | 13.2 | .76 | 31.0 | 1.78 | 17.4 | 1.02 | 23.3 | 1.37 |
| 1960 | None selected. | | | | | | | | | | | | |
| 1961 | 19.6 | 39.7 | 1.36 | 39.7 | 1.36 | 19.2 | 1.04 | 26.4 | 1.43 | 13.8 | .68 | 28.6 | 1.40 |
| 1962 | 16.2 | 39.5 | 1.19 | 40.7 | 1.22 | 20.0 | .85 | 34.2 | 1.46 | 17.1 | .74 | 34.5 | 1.50 |
| 1963 | 16.4 | 34.1 | 1.40 | 34.9 | 1.43 | 7.8 | .38 | 26.2 | 1.26 | 26.5 | 1.10 | 37.8 | 1.56 |
| 1964 | 20.4 | 40.6 | 1.18 | 43.8 | 1.27 | 17.4 | .60 | 36.4 | 1.26 | 17.3 | .83 | 31.4 | 1.50 |
| 1965 | 16.4 | 55.7 | 1.36 | 55.8 | 1.36 | 34.1 | 1.11 | 40.4 | 1.32 | 19.3 | 1.04 | 26.0 | 1.41 |
| 1966 | 15.7 | 49.4 | 1.30 | 50.8 | 1.34 | 32.6 | 1.19 | 39.2 | 1.43 | 14.3 | .75 | 26.8 | 1.40 |
| 1967 | 15.3 | 50.8 | 1.53 | 53.5 | 1.61 | 26.3 | 1.22 | 34.0 | 1.57 | 22.6 | 1.18 | 30.6 | 1.59 |

^aSelection differentials (D) are expressed as differences from the contemporary group, in kg. Intensities of selection (i) are the selection differentials expressed in standard deviation units.

^bAge-of-dam adjusted weaning weight.

^cThe number of bulls chosen are expressed as a percentage of those available because the actual number remains constant at 11 bulls, after 1960. The 1958 and 1959 numbers are the actual numbers chosen from that year, and the bulls may have been used in more than one year.

TABLE 15. Selection differentials and intensities of selection for the select line replacement heifers.^a

| Year | N(%) ^b | Yearling Weight | | | | Postweaning Gain | | | | Adj. Weaning Weight | | | |
|------|-------------------|-----------------|-----|--------|-----|------------------|------|--------|------|---------------------|-----|--------|-----|
| | | Chosen | | Ranked | | Chosen | | Ranked | | Chosen | | Ranked | |
| | | D | i | D | i | D | i | D | i | D | i | D | i |
| 1958 | 39.7 | 7.3 | .27 | 25.1 | .94 | -.7 | -.04 | 16.3 | 1.03 | 5.8 | .29 | 17.5 | .88 |
| 1959 | 51.1 | 8.1 | .35 | 18.0 | .79 | 2.7 | .14 | 14.8 | .78 | 4.6 | .30 | 11.8 | .77 |
| 1960 | 78.9 | 3.0 | .12 | 9.2 | .35 | 1.2 | .08 | 4.9 | .33 | 2.0 | .09 | 6.1 | .27 |
| 1961 | 78.9 | 5.1 | .27 | 6.6 | .35 | 3.1 | .25 | 4.3 | .35 | 2.3 | .12 | 6.9 | .35 |
| 1962 | 50.9 | 17.7 | .66 | 22.8 | .80 | 6.6 | .27 | 18.4 | .75 | 6.4 | .39 | 13.1 | .80 |
| 1963 | 63.5 | 12.9 | .48 | 15.6 | .58 | 5.0 | .19 | 17.2 | .65 | 7.8 | .38 | 10.8 | .53 |
| 1964 | 51.4 | 16.5 | .75 | 16.5 | .75 | 9.2 | .49 | 14.0 | .74 | 5.1 | .31 | 12.1 | .74 |
| 1965 | 57.9 | 19.3 | .63 | 19.5 | .64 | 13.8 | .62 | 15.0 | .68 | 5.6 | .32 | 11.2 | .64 |
| 1966 | 72.3 | 16.1 | .44 | 16.1 | .44 | 10.7 | .39 | 12.8 | .47 | 5.6 | .31 | 8.1 | .45 |
| 1967 | 75.0 | 13.5 | .45 | 13.5 | .45 | 6.6 | .33 | 9.1 | .46 | 6.9 | .39 | 8.6 | .49 |

^aSelection differentials (D) expressed in kg, selection intensities (i) expressed in standard deviations.

^bN is the percentage of heifers chosen from those available.

RESULTS AND DISCUSSION

Genetic and Environmental Trends Estimated from the Base Run

Phenotypic response over time in a selection experiment is composed of a change in the additive genetic mean of the population for the trait being selected as well as a change in the environmental effects on the trait. In the present study, yearling weight was the selected trait; genetic and environmental changes in the component traits - weaning weight and postweaning gain - will be presented. Two other factors were part of the model, sex of calf and station of origin, and these will be briefly presented.

Genetic Change

Genetic changes in postweaning gain (PWG), direct weaning weight (WWD), and maternal weaning weight (WWM) for the control and select line calves are shown in Figure 3 as yearly averages of estimated breeding values (EBV's). The genetic trends are shown in Table 16. These results are from the base run (the analysis of the Complete dataset (Table 6) using parameter set one (Table 8)), and they will form the basis for subsequent comparisons. The parameter values used in this analysis were +0.5 and -0.2, respectively, for the genetic and environmental correlations between weaning weight and postweaning gain, and zero for the direct-maternal correlation of weaning weight.

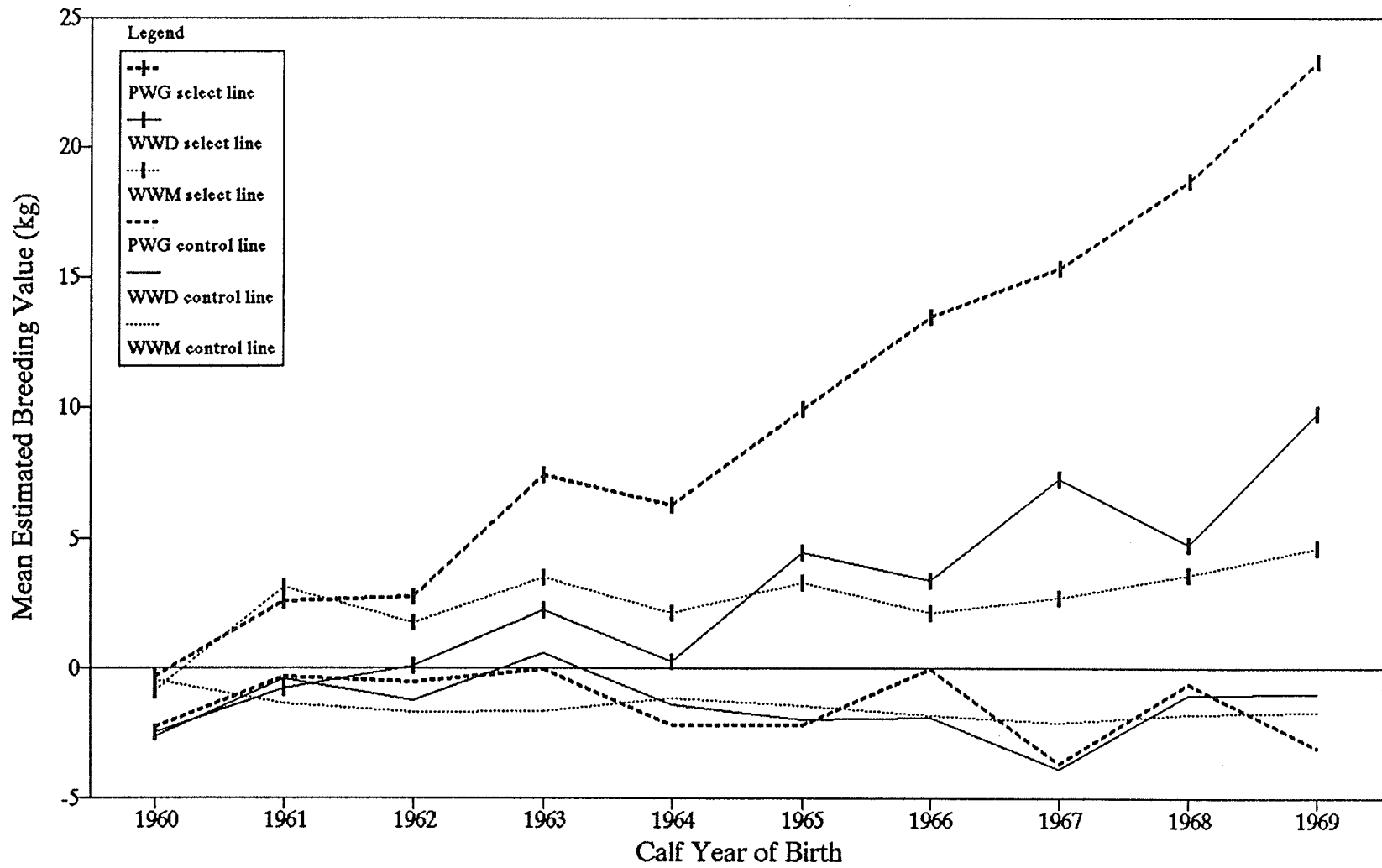


Figure 3. Annual genetic trend in postweaning gain (PWG), direct weaning weight (WWD), and maternal weaning weight (WWM) of the select and control line calves in the base run.

TABLE 16. Annual genetic trend (in kg yr⁻¹ ± standard error) of each calf trait by line and dataset^a.

| Line | Complete Dataset | | Separate Analyses | | Range ^d |
|-----------------|--------------------------|-------------------------|-------------------------|-------------------------|--------------------|
| | 1960 to 1969 | 1963 to 1969 | 1960 to 1969 | 1963 to 1969 | 1960 to 1969 |
| Select Line: | | | | | |
| YW ^b | 4.25 ^c ± .36 | - | 3.70 ^c ± .30 | - | Complete Dataset |
| PWG | 2.52 ^c ± .11 | 2.78 ^c ± .29 | 2.07 ^c ± .26 | 2.43 ^c ± .53 | 2.01 to 2.59 |
| WWD | 1.16 ^c ± .08 | 1.22 ^c ± .35 | 1.17 ^c ± .09 | 1.23 ^c ± .16 | 0.50 to 1.30 |
| WWM | 0.30 ^c ± .04 | 0.21 ± .16 | 0.30 ± .13 | 0.18 ± .19 | 0.04 to 0.73 |
| Control Line: | | | | | |
| YW ^b | -0.28 ± .28 | - | 0.00 ± .12 | - | Select Dataset |
| PWG | -0.14 ± .15 | -0.27 ± .28 | 0.03 ± .09 | -0.13 ± .10 | 1.43 to 2.19 |
| WWD | -0.10 ± .10 | -0.20 ± .26 | -0.09 ± .05 | -0.08 ± .13 | 0.50 to 1.26 |
| WWM | -0.11 ^c ± .04 | -0.07 ± .05 | 0.05 ± .03 | 0.01 ± .04 | 0.00 to 0.72 |

^aYW=yearling weight, PWG=postweaning gain, WWD=direct weaning weight, WWM=maternal component of weaning weight

^bYearling weight was calculated as discussed in the text.

^cSignificantly different from zero at P < .05.

^dRange refers to the range in genetic trends over the 12 parameter sets per dataset.

The genetic trend in postweaning gain for the select line was 2.52 kg yr^{-1} ($P < .05$). The response by the select line was characterized by fluctuation in the early years (1960-1964) and a relatively smooth slope in the later years (1965-1969). The response line was similar to the postweaning gain response lines of the bull and heifer calves shown by Olthoff et al. (1990b) in their Figure 2. The genetic trend for the period 1963 to 1969 was 2.78 kg yr^{-1} ($P < .05$), indicating that selection progressed more rapidly after the first three years of the experiment. These results are within the top range of values reported in the literature. Olthoff et al. (1990b), using this Brandon-station data with the control-line method of analysis, reported a genetic trend of 2.75 kg yr^{-1} (or $15 \text{ g d}^{-1} \text{ yr}^{-1}$) ($P < .05$), which represented 40% of the phenotypic trend. The experimental results presented by Mrode (1988b) ranged from 0.80 to 14.00 $\text{g d}^{-1} \text{ yr}^{-1}$ for the correlated response of postweaning gain to yearling weight selection.

For the control line, genetic trend in postweaning gain was not significantly different from zero (-0.14 kg yr^{-1} , $P > .05$). The trend line was relatively stable in the early years (1960-1963), but fluctuated in the later years (1964-1969). The 1963 to 1969 regression was slightly more negative but still not significantly different from zero (-0.27 kg yr^{-1} , $P > .05$).

The genetic trend in direct weaning weight for the select line was 1.16 kg yr^{-1} ($P < .05$). The response line was characterized by a smooth slope in the early years (1960-1963), but fluctuated in the later years (1964-1969). The response line was similar to the weaning weight response line of the heifer calves shown by Olthoff et al. (1990b) in their Figure 1. The 1963 to 1969 regression was 1.22 kg yr^{-1} ($P < .05$), indicating a

greater genetic response during the period when postweaning gain response was more rapid. Literature values range from 0.71 to 4.6 kg yr⁻¹ for the correlated response of weaning weight to yearling weight selection (Mrode, 1988b; Hough et al., 1985). Olthoff et al. (1990b) reported a genetic trend of 1.85 kg yr⁻¹ ($P < .05$), which represented 92% of the phenotypic trend.

For the control line, genetic trend in direct weaning weight was not significantly different from zero (-0.10 kg yr⁻¹, $P > .05$). The trend line was characterized by mild fluctuation throughout the selection experiment. The 1963 to 1969 regression was slightly more negative but still not significantly different from zero (-0.20 kg yr⁻¹, $P > .05$).

The genetic trend in maternal ability for the select line was 0.30 kg yr⁻¹ ($P < .05$). The trend line was characterized by decreasing fluctuation as the selection experiment progressed. The maternal response was about 25% of the direct response in weaning weight, compared to about 50% in the yearling gain selection experiment of Parnell et al. (1986). The 1963 to 1969 regression was not significantly different from zero (0.21 kg yr⁻¹, $P > .05$). In the literature, Frahm et al. (1985b) and Aaron et al. (1986b) found that milk yield, as a maternal characteristic, was positively affected by yearling weight selection, 0.39 and 0.46 kg of milk yr⁻¹, respectively, though not significantly different from the control line ($P > .05$) in both cases. In the postweaning-gain selection experiment reported by Irgang et al. (1985c), milk yield response was 0.27 kg yr⁻¹ ($P < .05$).

For the control line, genetic trend in maternal ability was -0.11 kg yr^{-1} ($P < .05$), and relatively smooth. The 1963 to 1969 regression was not significantly different from zero (-0.07 kg yr^{-1} , $P > .05$).

The maternal trend in both the select and control lines was significantly different from zero ($P < .05$) over the 10 year period but not ($P > .05$) when regressed over the last 7 years. A similar situation was presented by Winder et al. (1988) in the analysis of Red Angus field records. They found that an increase in postweaning gain EBV's was occurring concurrently with a positive to negative change in the maternal EBV's. Three explanations were offered. First, selection pressure within this population actually reduced milk production potential. This reduction could occur if the selection pressure was on postweaning gain, and if individuals with high genetic growth potential nursed low milk producing dams, and then experienced compensatory growth postweaning. Second, if selection pressure favored larger mature weights, increased nutrients for self growth and maintenance and of reduced nutrient availability for milk production would confound the lack of expression of milk production potential with genetic merit. Third, if weaning weight age-of-dam adjustment factors were too small for young dams, a bias in EBV's could be introduced. Years with higher concentrations of young cows, i.e., recent years, would depress average EBV's for maternal ability and increase average EBV's for postweaning gain through compensatory growth.

The genetic trend in yearling weight for the select line was not calculated directly in this study, but was constructed using the sum of its parts. This was done for both the control and select lines, then the control-line regression estimate was subtracted

from the select-line estimate, making it comparable to the control-line method. The parts that were summed to obtain the yearling weight annual response were the yearly means of postweaning-gain calf EBV's, direct weaning weight calf EBV's, maternal weaning weight dam EBV's, and permanent maternal environmental dam EBV's. The select line yearling weight trend was then 4.25 kg yr⁻¹ ($P < .05$), and the control-line trend was -0.28 kg yr⁻¹ ($P > .05$). By subtraction, the yearling weight response was 4.53 kg yr⁻¹. This value is within the ranges reported by Newman et al. (1973) and Olthoff et al. (1990b) using the control-line method of analysis. Newman et al. (1973) reported a yearling weight genetic response of 4.05 kg yr⁻¹ for the Brandon-station data, and, Olthoff et al. (1990b), 4.70 kg yr⁻¹ ($P < .05$). Differences between the Newman et al. (1973) and Olthoff et al. (1990b) studies are likely due to the statistical model applied to the data. The Lacombe, Alberta Agriculture Canada Research Station data yielded 3.20 kg yr⁻¹ (Newman et al., 1973). Andersen et al. (1974) reported 4.20 kg yr⁻¹ ($P < .05$) for the Brandon-station data and 3.77 kg yr⁻¹ ($P < .05$) for the Lacombe-station data, based on a small subset of the 1969 data. The genetic trend in yearling weight was 42% of the phenotypic response at the Brandon station and 35% at the Lacombe station for the Newman et al. (1973) study. Olthoff et al. (1990) reported 53%. Yearling weight selection results presented in the "Literature Review" section ranged from 1.07 to 5.50 kg yr⁻¹.

The above results show that ten-year selection for high yearling weight produced a correlated response in postweaning gain, a correlated response in direct weaning weight which was slightly less than half of that for postweaning gain, and a

correlated response in maternal weaning weight which was about one-quarter of the direct weaning weight response. Positive genetic changes were expected in postweaning gain and direct weaning weight given the selection intensities (Tables 14 and 15) and the findings reported in the literature to high yearling weight selection. For example (Table 14), the sire group born in 1967 differed from their contemporaries by 26.3 kg for postweaning gain, or 1.22 standard deviation units, and by 22.6 kg for adjusted weaning weight, or 1.18 standard deviation units. Expressing the selection intensities as a percent of the top-ranked values, they were 78% for postweaning gain and 74% for weaning weight. If no relationship existed, these selection intensities, and their ratios of selected group to top-ranked group, would be expected to be near zero. Yearling weight change was achieved primarily through postweaning gain change. Of five experiments which reported correlated responses to yearling weight selection (discussed in the Literature Review, in addition to those reviewed by Mrode (1988b)), three found that the greatest contribution to yearling weight change was change in postweaning gain. The other two experiments found that weaning weight change accounted for most of the change in yearling weight. Yearling weight selection had little effect on the maternal component of weaning weight, and this result is supported by circumstantial evidence found by Olthoff et al. (1990b).

For all traits, the mixed-model methodology yielded lower estimates of genetic change than the control-line method over the 10-year selection period. These estimates, expressed as a percent of the control-line method estimates (using the results of Olthoff et al. (1990b)), were 96% for yearling weight, 92% for postweaning gain, and

63% for direct weaning weight. Similarly, Sharma et al. (1985) compared the genetic estimates of the control-line method to the best linear unbiased prediction (BLUP) method used in a sire evaluation. The BLUP estimates were lower for all traits (weaning weight, postweaning gain, yearling weight) in the Synthetic population and for weaning weight in the Hereford population. These estimates, expressed as a percent of the control line estimates, were 52% and 61% for weaning weight in the Synthetic and Hereford populations, respectively, and 65% for postweaning gain. For postweaning gain in the Hereford population, the corresponding value was 131%.

The genetic trends in postweaning gain and direct weaning weight were found to be greater for the last 7 years of selection than the 10 year selection period. This result supports Newman et al.'s (1973) observation that selection differentials accumulate slowly in the early years of selection. This initially slow genetic progress could be due to the method of choosing replacement bulls and heifers in the early years of the selection study for both the control and select lines, or to the management practices. The following discussion looks at some possibilities for the slow initial genetic progress.

Males were replaced annually at relatively high selection intensities, and females were replaced, on average, every 4.5 years at relatively low selection intensities. The 1960-born bulls were not used and the same set of bulls, except for one, sired the 1961 and 1962 progeny, which in turn sired the 1963 and 1964 progeny, and so on. The resulting step-wise pattern of accumulated selection differentials may explain the early fluctuation in postweaning-gain trend, the continuing fluctuation in direct weaning

weight, and the decreasing fluctuation in maternal ability. As selected heifers entered the herd, and represented a greater proportion of the female herd, this pattern would be reduced or eliminated, as is the case for postweaning gain and maternal weaning weight genetic trends. The increasing contribution of the dams, and the greater contribution of the sires to their progeny, can be seen in Figure 4. Initially, the calf EBV response line followed one-half of the weighted sire EBV response line (only one-half of sire EBV's are transmitted to the progeny), but, as the selection program proceeded, the response lines diverged. This divergence was due to the increasing contribution of the dam because, when one-half of the dam EBV response line was added to that of the sire, the progeny and parent response lines became nearly identical. The pattern was similar for weaning weight, both direct and maternal, though less dramatic (not shown).

The random assignment of the replacement heifers, born in 1958 and 1959, to the control and select lines resulted in positive yearling weight selection differentials (Table 15). These selection differentials were greater in the control line than in the select line for heifers born in 1958, 1959, and 1960. The differences were, respectively, +3.3 kg, +1.4 kg, and +9.7 kg.

The bulls chosen for the select line were not always the individuals with the highest yearling weights, and, for the control line, not always the average. The 1958-born bulls chosen for the select line, for example, differed from the nine, top-ranked bulls by 29.4 kg (Table 14), with the top-ranked bull chosen for the control line. For the select-line bulls, this could be due to: 1. The failure of a top-ranked bull to pass a physical soundness check for breeding. 2. The limitation of choosing a maximum of

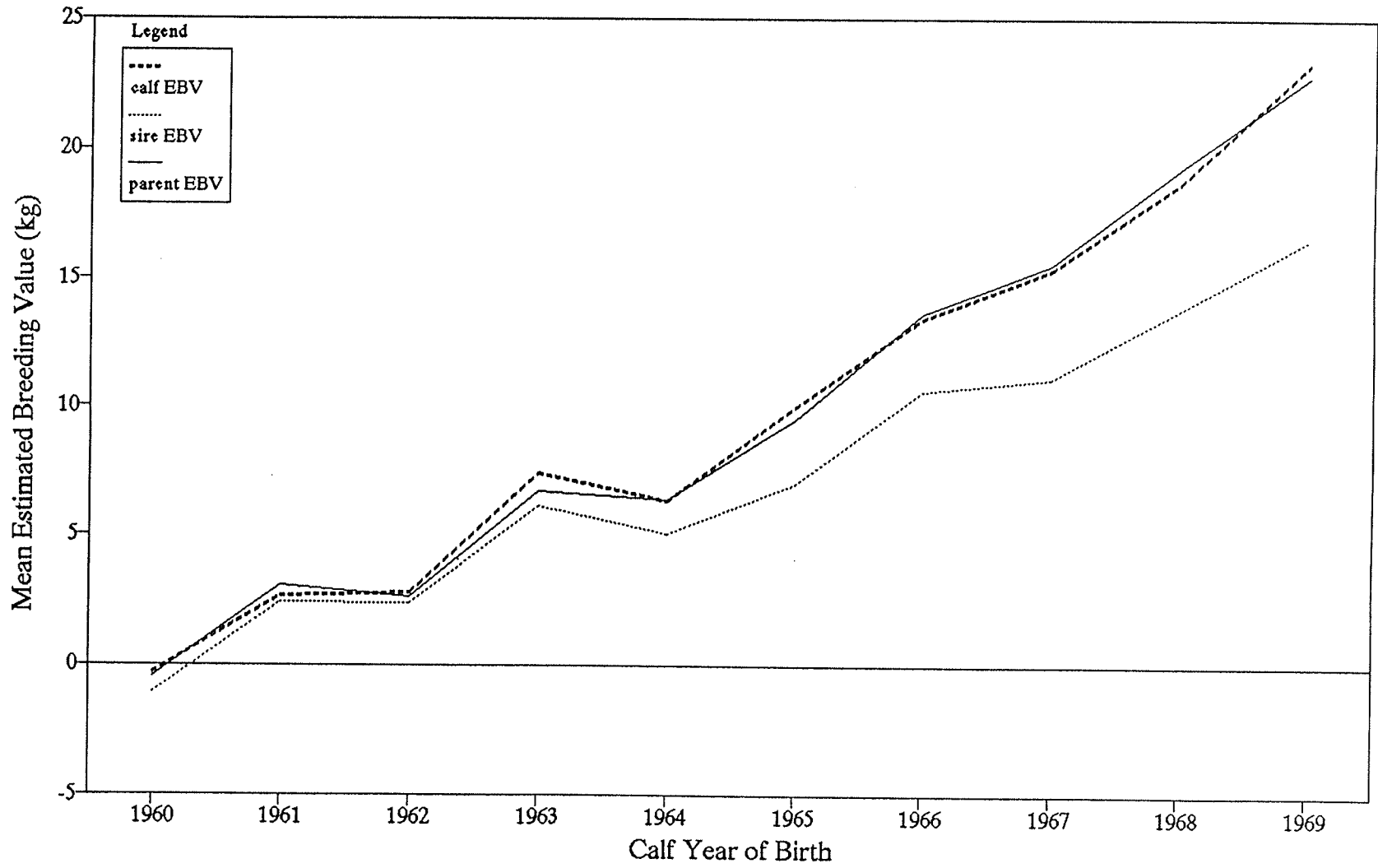


Figure 4. Comparison of the estimated breeding value trends of calves, of one-half the weighted sire means, and of one-half the parent means.

three paternal half-sib yearling bulls. Nevertheless, in 1967, four paternal half-sibs were chosen. 3. In 1962 and 1964, the herd of origin. In 1964, the 26th top-ranked bull was chosen because three bulls from the Indian Head location were not yet represented.

The random sampling within cow age by which cows were assigned to bulls was not always observed by the time the progeny were weaned. In the base years (1958-1959), one sire produced 16 weaned progeny but only from two-year-old dams. In the select line years (1960-1969), the percentage of weaned progeny from different sires from two-year-old dams ranged from 0 to 50%. This could affect the sire EBV's.

The frequency of feeding the postweaning-gain ration may have contributed to the initially slow genetic progress. Female calves were changed from twice-a-day feeding to ad-lib feeding in 1962, and male calves, in 1964. The phenotypic correlation between weaning weight and postweaning gain was calculated across line and sex, but within year, and is shown in Table 17. An anomaly appeared in 1963 where the correlation was negative (rather than positive). The 1962 value was the smallest positive correlation. These values indicate an effect due to feeding frequency. The twice-a-day feeding of bulls, especially select-line bull calves, may have restricted the expression of their genetic postweaning growth potential, whereas heifers may have been less affected by the change from twice-a-day feeding to ad-lib feeding. The implication is that if the phenotypic correlations are significantly different from each other, then the genetic and environmental correlations assumed constant in all years in the mixed model may introduce bias into the EBV's.

TABLE 17. Phenotypic correlation of postweaning gain and weaning weight across line and sex, within year.

| Year | Correlation |
|------|-------------|
| 1958 | .42 |
| 1959 | .19 |
| 1960 | .22 |
| 1961 | .25 |
| 1962 | .15 |
| 1963 | -.12 |
| 1964 | .27 |
| 1965 | .59 |
| 1966 | .54 |
| 1967 | .57 |
| 1968 | .28 |
| 1969 | .34 |

The foregoing anomalies in choosing replacement stock could have contributed to the slight genetic drift observed in the control line by Newman et al. (1973). These anomalies may also be responsible for the change in maternal ability from a positive, significant trend ($P < .05$) for the 10-year selection period to a nonsignificant ($P > .05$) trend over the last 7 years of the selection period.

Finally, selection at 12 months of age for both bulls and heifers may not be operating on the same developmental mechanisms. If the 13-month weight of bulls and 18-month weight of heifers represents the same developmental stage (Nwakalor et al., 1986), then yearling weight selection may be less effective for females than males, and realized genetic change less than expected genetic change. This may account, in part, for the unexplained finding of Newman et al. (1973) that "selection pressure was accumulating more rapidly in the sires than in the dams of the selected line".

Environmental Effect

An environmental change is a nongenetic effect on the trait of interest. One of the most important environmental effects may be that due to yearly climate affecting the nutritional quantity and quality of feed and the animal's ability to cope with environmental stresses, such as high and low ambient temperatures. In this study, the year of birth effect is used to estimate the yearly environmental effect on the growth traits, postweaning gain and weaning weight.

The estimates of the year effects for postweaning gain and weaning weight are presented in Table 13 and shown as differences from the 1969 year of birth. Year effects were a very significant source of variation in weaning weight and postweaning

gain. Year estimates for weaning weight (-2.31 to 22.94) were less variable than postweaning gain year estimates (-33.31 to 18.75).

A positive trend was observed in both the weaning weight and postweaning gain year estimates as the selection experiment progressed. A trend can exist because of yearly improvements in management practices, but also because of random fluctuations in climatic conditions. Part of the positive environmental trend in postweaning gain could be due to management change of the feeding program. The large, positive increase in year effect estimates from 1963 to 1964 (or -15.88 to 17.14) occurred concurrently with a change in feeding frequency from twice a day in 1963 to ad-lib in 1964 for bull calves. The twice-a-day feeding schedule may have been insufficient to meet the genetic growth potential of select line bull calves, but sufficient for heifers. As a result, ad-lib feeding would have relatively little effect on females (feeding frequency changed in 1962) compared to males.

Regressions of the year of birth environmental effect estimates on year for the 10-year selection period were calculated. The weaning weight regression was not significantly different from zero (1.08 kg yr^{-1} , $P > .05$). The postweaning gain regression was 3.48 kg yr^{-1} ($P < .05$). These should correspond to the regressions reported by Olthoff et al. (1990b) for the control line: 0.15 kg yr^{-1} for weaning weight and 4.25 kg yr^{-1} for postweaning gain, values which represented, respectively, 8% and 60% of the phenotypic trend.

In summary, selection for high yearling weight, analyzed with mixed-model methodology, gave an estimate of yearling weight response of 4.53 kg yr^{-1} ,

correlated genetic responses of 2.52 kg yr⁻¹ for postweaning gain, 1.16 kg yr⁻¹ for direct weaning weight, and 0.30 kg yr⁻¹ for maternal weaning weight. Compared to the control-line method of Olthoff et al. (1990b), the estimated trends were lower. Yearling weight response estimated in the present study was 96% of that estimated with the control-line method, postweaning gain was 92%, and direct weaning weight was 63%. Olthoff et al. (1990b) found that the phenotypic response in postweaning gain was due equally to genetic and environmental effects, but, in weaning weight, the phenotypic response largely reflected the genetic response. From this, the genetic trend in the correlated trait with the greatest response (postweaning gain) came closest to the corresponding control-line method estimate.

Genetic and Environmental Trends Estimated from Separate Line Analyses

In this section, the results and conclusions from the base run are compared with the separate line analyses to provide information on the effectiveness of mixed-model methodology to estimate genetic trend without the use of an unselected control population. The separate line analyses were two subsets of the Complete dataset - a Select dataset and a Control dataset (Table 6) - using the base run parameters (Table 8). The Select dataset could be considered to represent the situation where a producer maintains and selects one herd. The Control dataset represents the situation where an unselected herd is maintained through management practices designed to minimize genetic change.

Genetic Change

The genetic trends for postweaning gain and direct weaning weight, of the select and control lines analyzed separately, are presented in Table 16. The response lines for postweaning gain are shown in Figure 5. Corresponding graphs for weaning weight, direct and maternal, are not shown.

The genetic trend in postweaning gain for the select line was 2.07 kg yr^{-1} ($P < .05$) for the 10-year yearling weight selection period, and 82% of the corresponding trend in the base run analysis. The response line was relatively smooth in the early years (1960-1963), flat in the middle years (1964-1965), and fluctuated in the later years (1966-1968). This representation was almost opposite to that observed in the base run analysis. Stated another way, the response line for the Select dataset became more variable as selection progress accumulated more rapidly, whereas, in the Complete dataset, it became less variable. The 7-year (1963-1969) regression line was 87% of the corresponding base run trend.

For the Control dataset line, the postweaning gain genetic trend was not significantly different from zero (0.03 kg yr^{-1} , $P > .05$). The response line was similar to the corresponding base run response line, though slightly less variable than the Complete dataset line.

The genetic trend in direct weaning weight for the Select dataset line was 1.17 kg yr^{-1} ($P < .05$), over the 10-year selection period, and 101% of the corresponding trend in the base run analysis. The response line was less variable in the Select dataset than in the Complete dataset (not shown), and the lines varied in their orientation to one

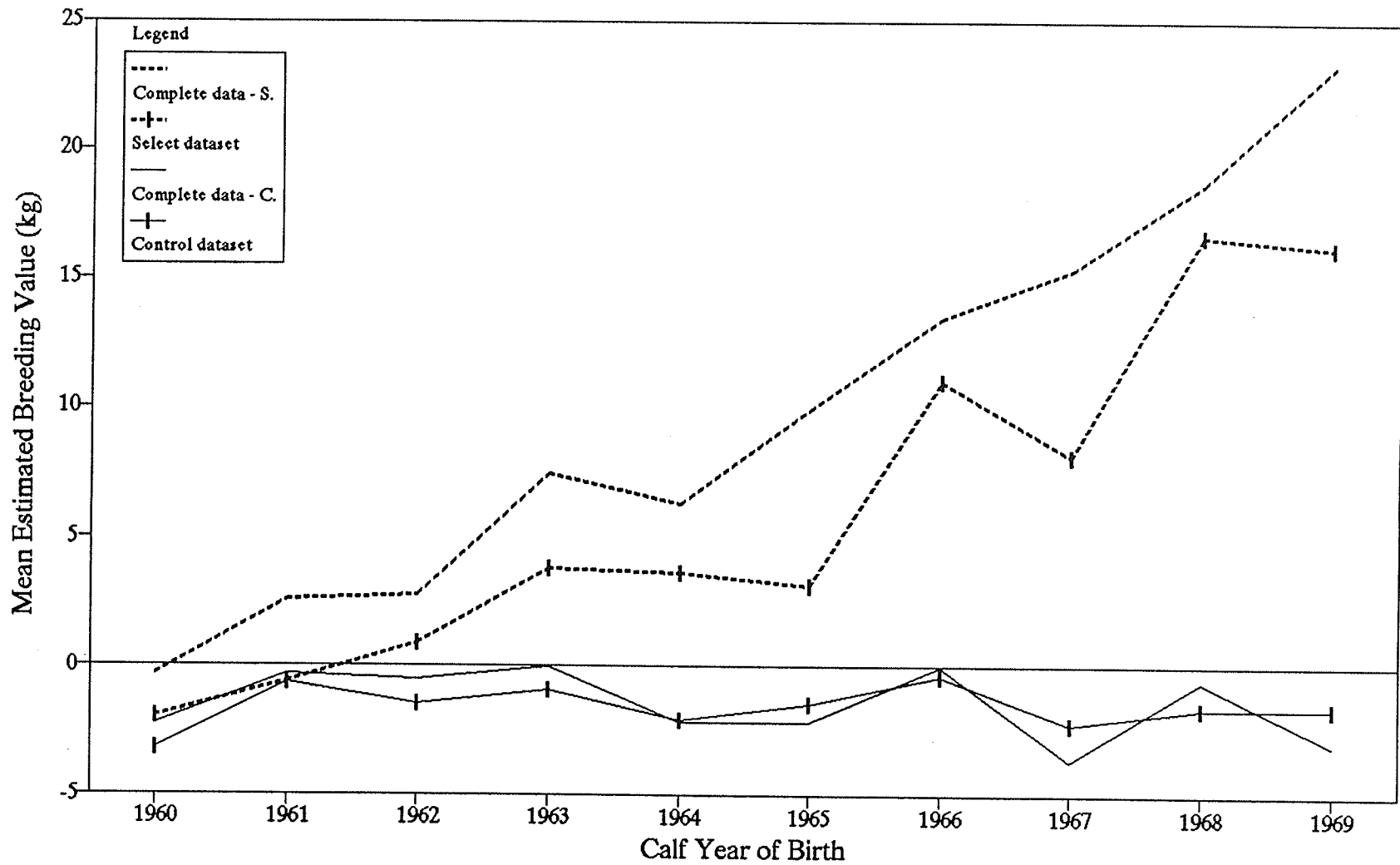


Figure 5. Comparison of the genetic trend for postweaning gain of the select and control line calves from the Complete dataset and the Select and Control datasets.

another. The 7-year regression line was also 101% of the corresponding trend in the base run trend.

For the Control dataset line, the direct weaning weight trend was not significantly different from zero (-0.09 kg yr^{-1} , $P > .05$). The trend line was similar to that of the base run analysis; though slightly divergent from 1965 to 1967 (not shown).

The genetic trend in maternal ability for the Select dataset line was 0.30 kg yr^{-1} , over the 10-year selection period, and 100% of the corresponding base run analysis. This value was not statistically different from zero ($P < .05$), even though the estimates from the Select and Complete datasets were equal and the Complete dataset value was significantly different from zero ($P < .05$). The Select dataset regression had a higher standard error. The response line was essentially the same as that for the base run analysis. For the Control dataset line, the weaning weight maternal trend was not significantly different from zero (0.05 kg yr^{-1} , $P > .05$), but the corresponding base run trend line was statistically different from zero at -0.11 kg yr^{-1} ($P < .05$).

Yearling weight was not directly calculated, but it was constructed from its parts as discussed previously (p94). The Select dataset yielded a response of 3.70 kg yr^{-1} ($P < .05$), and the Control dataset, 0.00 kg yr^{-1} . The select response represents 82% of the base run response.

The correlated trait most affected by analysis without the control-line data was postweaning gain, which had the greatest response to yearling weight selection. From Olthoff et al. (1990b), the phenotypic response was 40% genetic and 60% environmental. The traits less responsive to yearling weight selection, direct weaning

weight and maternal ability, were not affected by analysis without the control-line data. From Olthoff et al. (1990b), direct weaning weight phenotypic response was 92% genetic. If the maternal component of weaning weight phenotypic response was largely genetic, then perhaps the following statement may have validity: Traits whose phenotypic responses are primarily genetic in origin are least affected by the mixed-model methodology with a reduced animal model, and those traits whose phenotypic responses have a large environmental component are most affected.

Environmental Effect

The environmental effect is estimated from the year of birth effect. Year effect estimates were obtained from the Control and Select dataset analyses and compared to the corresponding control and select lines in the Complete dataset analysis.

The postweaning gain and weaning weight year effect estimates in the Select and Control dataset analyses indicate a positive trend, similar to that observed in the Complete dataset analysis. For the postweaning gain year effect estimates, the largest year difference in the Control dataset was still that from 1963 to 1964, but, in the Select dataset, it was the 1967 to 1968 difference, the 1963 to 1964 difference was the second largest. Similar to the Complete dataset, the 1963 to 1964 difference probably reflects the change in feeding frequency of the male calves. The 1967 to 1968 difference may be a reflection of the method and model, or something peculiar to 1967, such as an interaction.

The results, presented as deviations from the Complete dataset estimates, are shown in Figure 6. For example, the 1963 year effect in postweaning gain from the

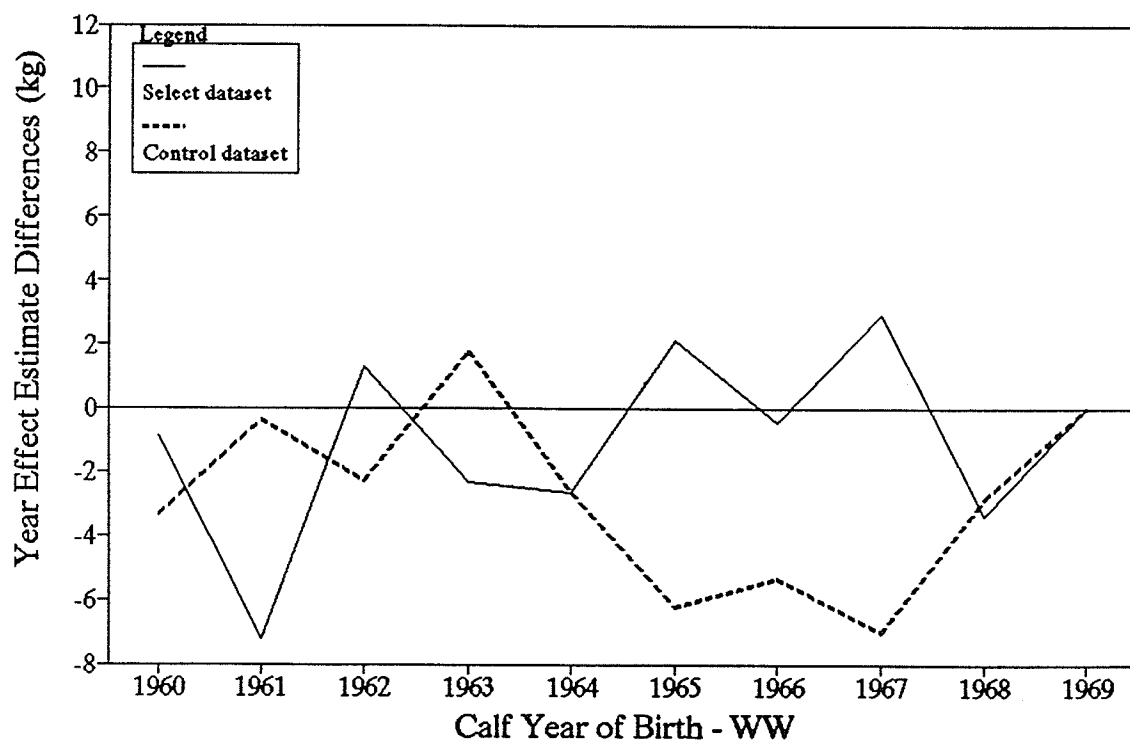
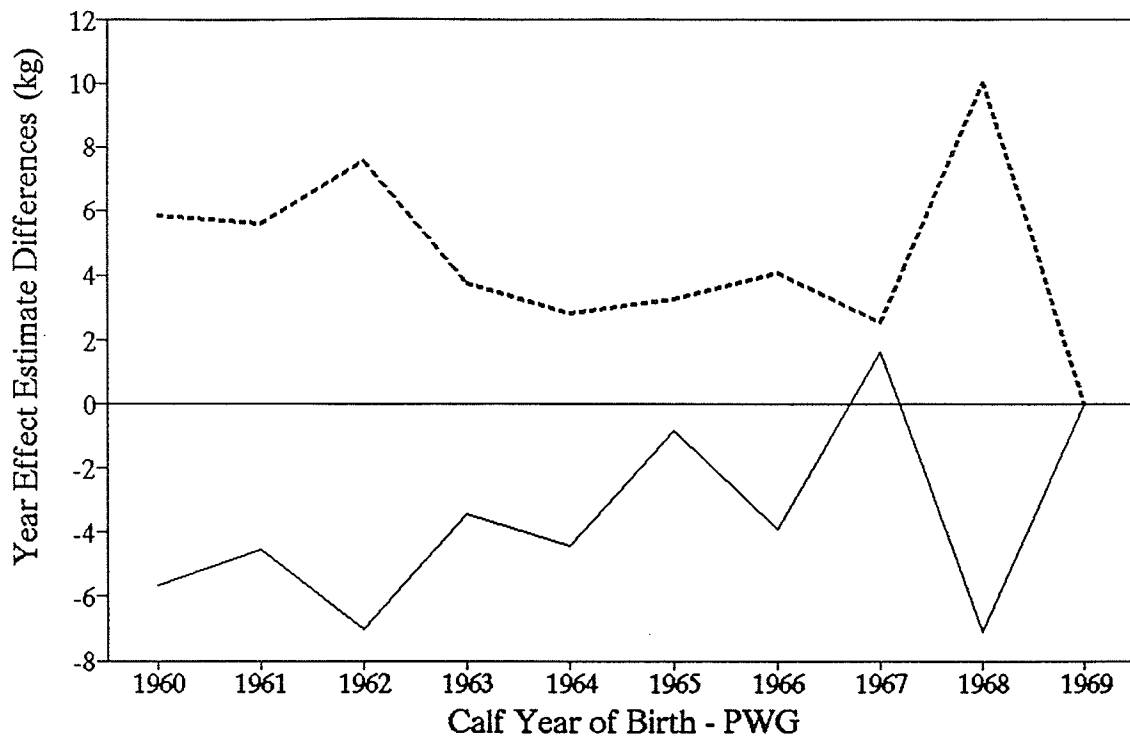


Figure 6. Postweaning gain (PWG) and weaning weight (WW) year effect estimates of the Select and Control datasets expressed relative to the Complete dataset estimates (shown in Table 13).

Select dataset was -3.43 kg (Figure 6), i.e., the deviation of the Complete dataset analysis estimate (-15.88 from Table 13) from the Select dataset analysis estimate (-19.31 and not shown). The year effect estimates on postweaning gain were underestimated by the Select dataset, except for the 1967 year effect estimate. If the phenotypic response is consistent between datasets, the high environmental effect should be paired with a low genetic effect. As can be observed in Figure 5, the 1967 postweaning gain EBV mean is low in comparison with the 1966 and 1968 means. When the lines are analyzed together in the Complete dataset analysis, the same sort of genetic trend observed in the Select dataset is transferred to the control line trend, thus allowing the select line trend to be relatively smooth, i.e., in the Complete dataset, the 1967 EBV mean is between the 1966 and 1968 means, but, in the Select dataset, it is less. The year effect estimates on postweaning gain were overestimated by the Control dataset, when compared to the Complete dataset. Estimates of year effects on weaning weight, from both datasets, were, on average, less than those found in the Complete dataset.

In summary, both yearling weight response and the correlated genetic response of postweaning gain were underestimated when the control population was not used in the analysis. The genetic trends in direct weaning weight and maternal weaning weight were unaffected. The environmental effect on postweaning gain was overestimated by the Control dataset and underestimated by the Select dataset when compared to the Complete dataset estimates. Weaning weight year effects were less variable and tended, on average, to be similar and less than the Complete dataset estimates. Perhaps selection, a change in additive genetic means of a population for the

selected trait, is not being effectively accounted for by the model and method, or the reduced number of records is insufficient to provide an accurate analysis, particularly when a trait has a large environmental component in its phenotypic response (postweaning gain was 60% whereas weaning weight was 8%).

Sensitivity of Estimates of the Genetic and Environmental Trends to Assumed Parameters

Mixed model solutions tend to have a dependency on the (co)variances used. In this study, the genetic and environmental correlations between direct weaning weight and postweaning gain were assigned a positive and a negative value, as was the direct-maternal correlation of weaning weight. This was done to investigate the sensitivity of the results and conclusions obtained from the base run analysis to possibly incorrect parameter values. To investigate the sensitivity of results and conclusions at an individual level, the EBV rankings of 10 select line bulls with progeny, and 10 select line yearling bulls born in 1969, were obtained. The rankings were made within each parameter set, for each trait - postweaning gain and weaning weight (direct and maternal) - and compared to the base run analysis. The environmental effect, year of birth, was also investigated for its role in the results and conclusions reached.

For this section, read genetic correlation as the genetic correlation between weaning weight and postweaning gain, environmental correlation as the environmental correlation between weaning weight and postweaning gain, and direct-maternal correlation as the direct-maternal genetic correlation of weaning weight.

Genetic Change

Estimates of genetic change using mixed-model methods appear to be parameter-driven, i.e., are a reflection of assumed heritabilities, etc., though modified by the data. This can be seen to some extent in the correlations between EBV's. For example, from Table 18, the genetic correlation of -0.1 forces the EBV correlation between direct weaning weight and postweaning gain downwards, but the data prevents it from becoming negative (ranges from 0.01 to 0.31). The genetic trend is likewise reduced (Table 19).

Genetic Trend. The four postweaning gain response lines (two from the Complete dataset, one from the Select dataset, and one from the Control dataset), and their orientation to one another, were very similar across all twelve parameter sets (Figure 7). Expressing all response lines as a percent of the base run trend (calculated from Table 19 as the response estimated assuming parameter set "x" divided by the response estimated using parameter set 1 with the Complete dataset), the range is 80% to 103% for the Complete dataset and 57% to 87% for the Select dataset. The response in postweaning gain estimated using parameter set three and the Select dataset (2.19 kg yr^{-1}) divided by the response estimated using parameter set one and the Complete dataset (2.52 kg yr^{-1}) is 87%. Postweaning gain genetic trend of each parameter combination used with the select dataset, expressed as a percent of the corresponding parameter combination used with the Complete dataset, ranged from 71% to 85% (calculated from Table 19; for example, parameter set 2 Select (1.79) to Complete (2.30) is 78%).

TABLE 18. Correlations of the estimated breeding values for the Complete dataset analyses, across lines.^a

| Parameter Set # | $r_{G:WWD,PWG}$ | $r_{E:WWD,PWG}$ | $r_{G:WWD,WWM}$ | $r_{EBV:WWD,PWG}$ | $r_{EBV:WWD,WWM}$ |
|--------------------|-----------------|-----------------|-----------------|-------------------|-------------------|
| 3 | +0.5 | -0.2 | +0.5 | .77 | .70 |
| 1 | +0.5 | -0.2 | 0 | .60 | .30 |
| 5 | +0.5 | -0.2 | -0.5 | .47 | -.39 |
| 4 | +0.5 | +0.2 | +0.5 | .66 | .70 |
| 2 | +0.5 | +0.2 | 0 | .52 | .31 |
| 6 | +0.5 | +0.2 | -0.5 | .42 | -.32 |
| 9 | -0.1 | -0.2 | +0.5 | .31 | .66 |
| 7 | -0.1 | -0.2 | 0 | .27 | .25 |
| 11 | -0.1 | -0.2 | -0.5 | .19 | -.28 |
| 10 | -0.1 | +0.2 | +0.5 | .11 | .65 |
| 8 | -0.1 | +0.2 | 0 | .09 | .24 |
| 12 | -0.1 | +0.2 | -0.5 | .01 | -.29 |

^aSee List of Abbreviations for definitions.

TABLE 19. Annual genetic trend (in kg yr⁻¹ for the period 1960-1969) of each trait as affected by the correlations used in calculating the estimated breeding values of select line calves.^a

| Parameter Set # | | | | PWG | | WWD | | WWM | |
|--------------------|------------------------|-----------------------|------------------------|------|------|------|------|-----|-----|
| | r _{G:WWD,PWG} | r _{E:WW,PWG} | r _{G:WWD,WWM} | C | S | C | S | C | S |
| 1 ^b | .5 | -.2 | .0 | 2.52 | 2.07 | 1.16 | 1.17 | .30 | .30 |
| 3 | .5 | -.2 | .5 | 2.59 | 2.19 | 1.30 | 1.26 | .47 | .53 |
| 5 | .5 | -.2 | -.5 | 2.54 | 2.03 | 1.07 | 1.13 | .10 | .00 |
| 2 | .5 | .2 | .0 | 2.30 | 1.79 | 1.01 | .95 | .30 | .29 |
| 4 | .5 | .2 | .5 | 2.36 | 1.88 | 1.16 | 1.05 | .45 | .48 |
| 6 | .5 | .2 | -.5 | 2.30 | 1.76 | .90 | .90 | .13 | .04 |
| 7 | -.1 | -.2 | .0 | 2.26 | 1.71 | .73 | .76 | .39 | .37 |
| 9 | -.1 | -.2 | .5 | 2.26 | 1.72 | .85 | .83 | .73 | .72 |
| 11 | -.1 | -.2 | -.5 | 2.27 | 1.71 | .61 | .61 | .04 | .01 |
| 8 | -.1 | .2 | .0 | 2.03 | 1.46 | .61 | .62 | .37 | .34 |
| 10 | -.1 | .2 | .5 | 2.02 | 1.43 | .73 | .68 | .67 | .63 |
| 12 | -.1 | .2 | -.5 | 2.01 | 1.44 | .50 | .50 | .07 | .03 |

^aSee List of Abbreviations for definitions. C=Complete dataset analysis, S=Select dataset analysis.

^bThe base run.

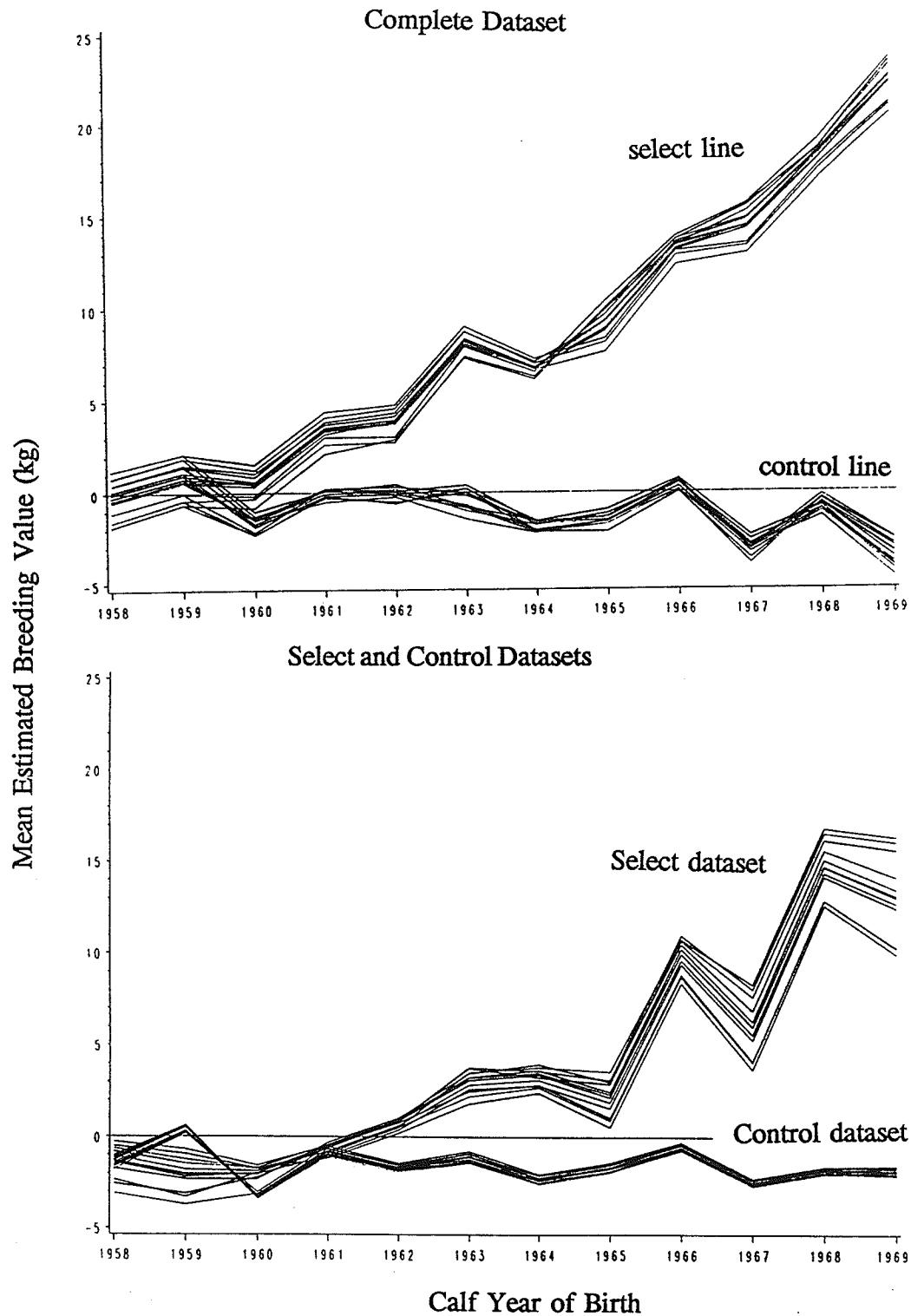


Figure 7. Postweaning gain response lines from the Complete dataset for the select and control lines and from the Select and Control datasets of all parameter sets.

The four weaning weight direct response lines were very similar across all parameter sets (Figure 8). The lines, however, did not maintain the same orientation among each other from one set to another. Expressing all of the response lines as a percent of the base run gave values ranging from 43% to 112% for the Complete dataset and from 43% to 109% from the Select dataset. Expressing the trends obtained with the Select dataset for all parameter sets as a percent of the corresponding Complete dataset trends gave values ranging from 91% to 106%.

The four weaning weight maternal response lines were very similar across all parameter sets (Figure 9). The orientation between the pair of control lines and the pair of select lines was similar, but the distance between lines, within pairs, varied. There is a large range in the expression of the genetic trend as a percent of the base run. This is due to the relatively small genetic trends. For example, 0.03 (parameter set 12 of the Select dataset) divided by 0.30 (parameter set 1 of the Complete dataset) is 10%, the same difference ($.30 - .03 = .27$) in postweaning gain genetic trend is 90% (2.26 from parameter set 7 of the Complete dataset divided by 2.52 from the base run).

Observation of the genetic trends in Table 19 can be used to make some general conclusions regarding the sensitivity of the results to the assumed parameters. First, the postweaning gain genetic trend is sensitive to the genetic correlation and somewhat sensitive to the environmental correlation. Increasing the assumed genetic correlation increases the genetic trend, and increasing the assumed environmental correlation decreases the genetic trend. There is little influence of the direct-maternal

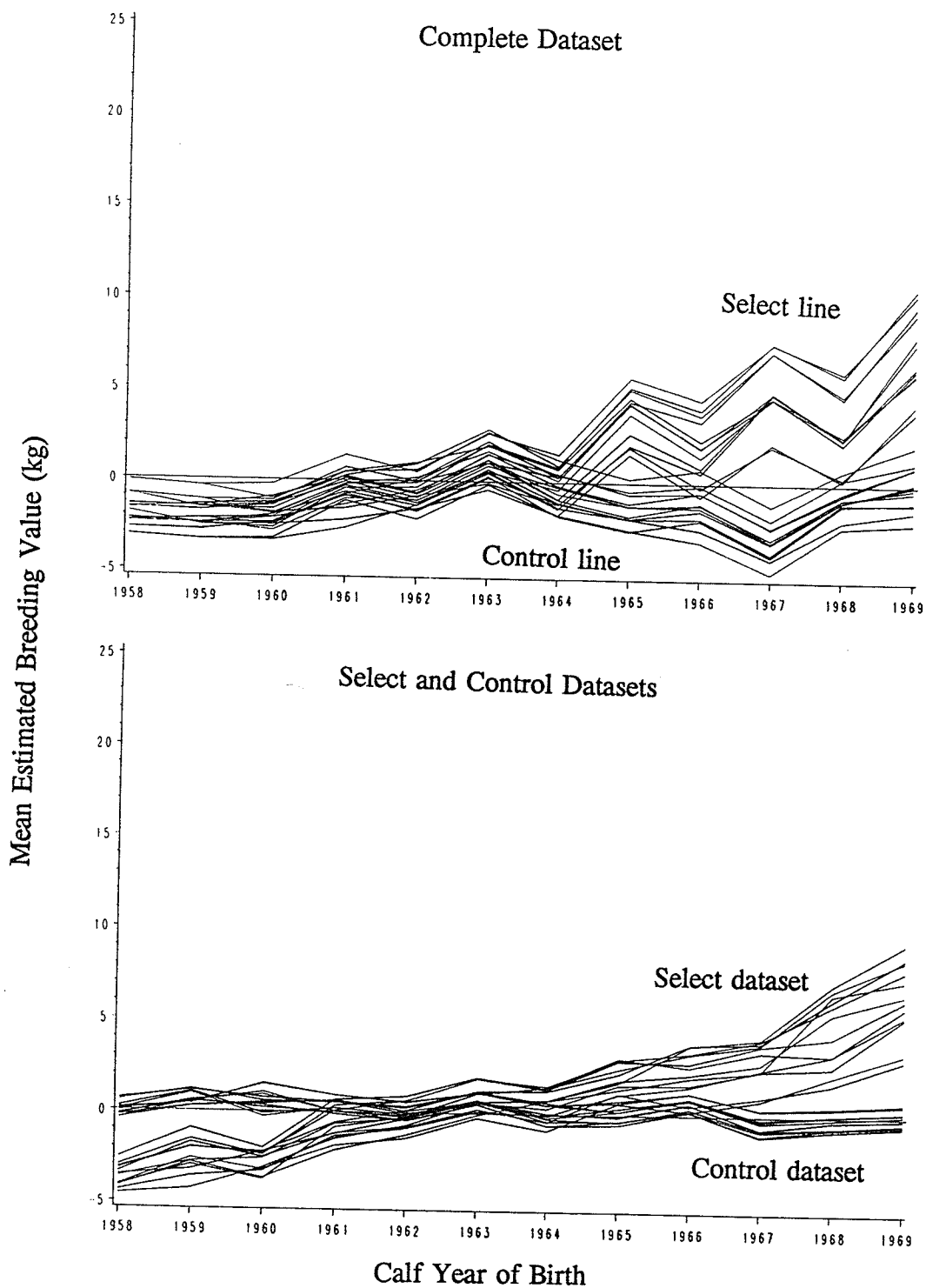


Figure 8. Direct weaning weight response lines from the Complete dataset for the select and control lines and from the Select and Control datasets of all parameter sets.

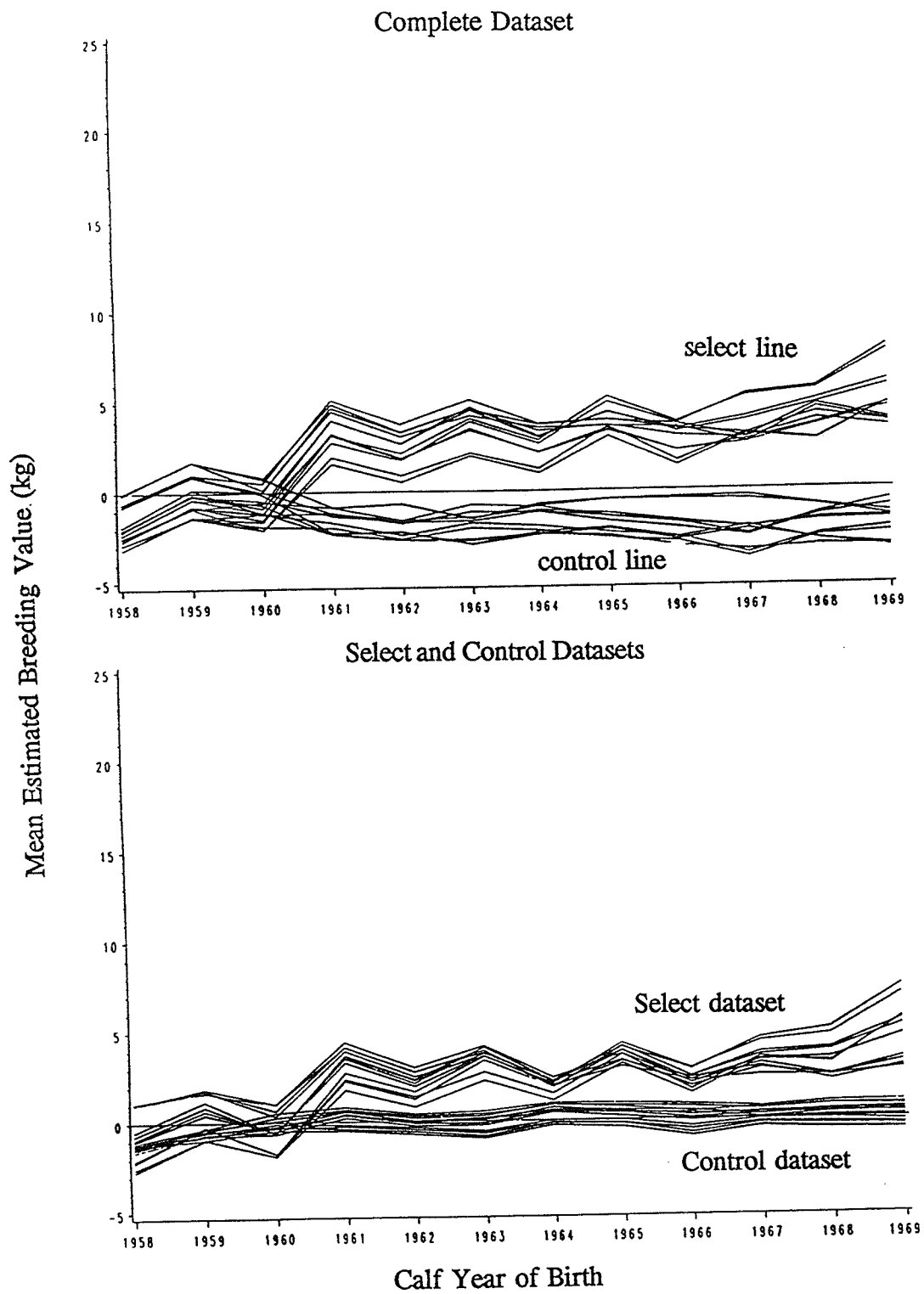


Figure 9. Maternal weaning weight response lines from the Complete dataset for the select and control lines and from the Select and Control datasets of all parameter sets.

correlation, probably because it is an indirect effect, whereas the other two correlations seem to have more direct effects.

Second, the genetic trend of direct weaning weight is sensitive to the genetic correlation and somewhat sensitive to the direct-maternal correlation. Increasing the assumed genetic and/or direct-maternal correlations increases the genetic trend. There is little influence of the environmental correlation.

Third, the maternal weaning weight genetic trend is most sensitive to the direct-maternal correlation and somewhat sensitive to the genetic correlation. Increasing the assumed direct-maternal and/or genetic correlations increases the genetic trend. There is little effect of the environmental correlation.

The postweaning gain genetic trends, obtained from the Complete dataset, can be grouped into four clusters based on the genetic and environmental correlations. The highest genetic trends (2.52 to 2.59 kg yr⁻¹) were obtained with a parameter combination of +0.5 for the genetic correlation and -0.2 for the environmental correlation (parameter sets 1, 3, and 5). The next highest (2.30 to 2.36 kg yr⁻¹), with +0.5 and +0.2 (sets 2, 4, and 6). Then (2.26 to 2.27 kg yr⁻¹), -0.1 and -0.2 (parameter sets 8, 10, and 12). The lowest genetic trends (2.10 to 2.03 kg yr⁻¹) are from the combination of -0.1 for the genetic correlation and +0.2 for the environmental correlation of weaning weight and postweaning gain (parameter sets 7, 9, and 11).

The direct weaning weight genetic trends, obtained from the Complete dataset, can be roughly grouped as for postweaning gain genetic trend. Higher genetic trends occur with the assumed positive genetic correlation (0.9 to 1.30 kg yr⁻¹), compared

to the negative (0.50 to 0.85 kg yr⁻¹), but are not exclusive for a given assumed value of the environmental correlation. Within each genetic and environmental correlation combination, though, the assumed value of the direct-maternal correlation increases genetic trend as it goes from -0.5 to 0.0 to +0.5.

The maternal weaning weight genetic trends, obtained from the Complete dataset, can be roughly clustered into three groups based on the direct-maternal correlation. Genetic trend increases as the assumed direct-maternal correlation increases from -0.5 (0.04 to 0.10 kg yr⁻¹), to 0.0 (0.30 to 0.39 kg yr⁻¹) to +0.5 (0.45 to 0.73 kg yr⁻¹). Within the first two groups, increasing the assumed genetic correlation decreases the genetic trend. When the direct-maternal correlation is negative, increasing the assumed genetic correlation increases the genetic trend.

The genetic trends obtained from the Select dataset analyses show similar clustering to that of the Complete dataset for each of the calf traits - postweaning gain, direct and maternal weaning weight.

The genetic trends in the Control dataset analyses were not statistically different from zero ($P > .05$) for postweaning gain and direct weaning weight. For maternal weaning weight, except for parameter sets #6 and #10, the trends were statistically different from zero ($P < .05$).

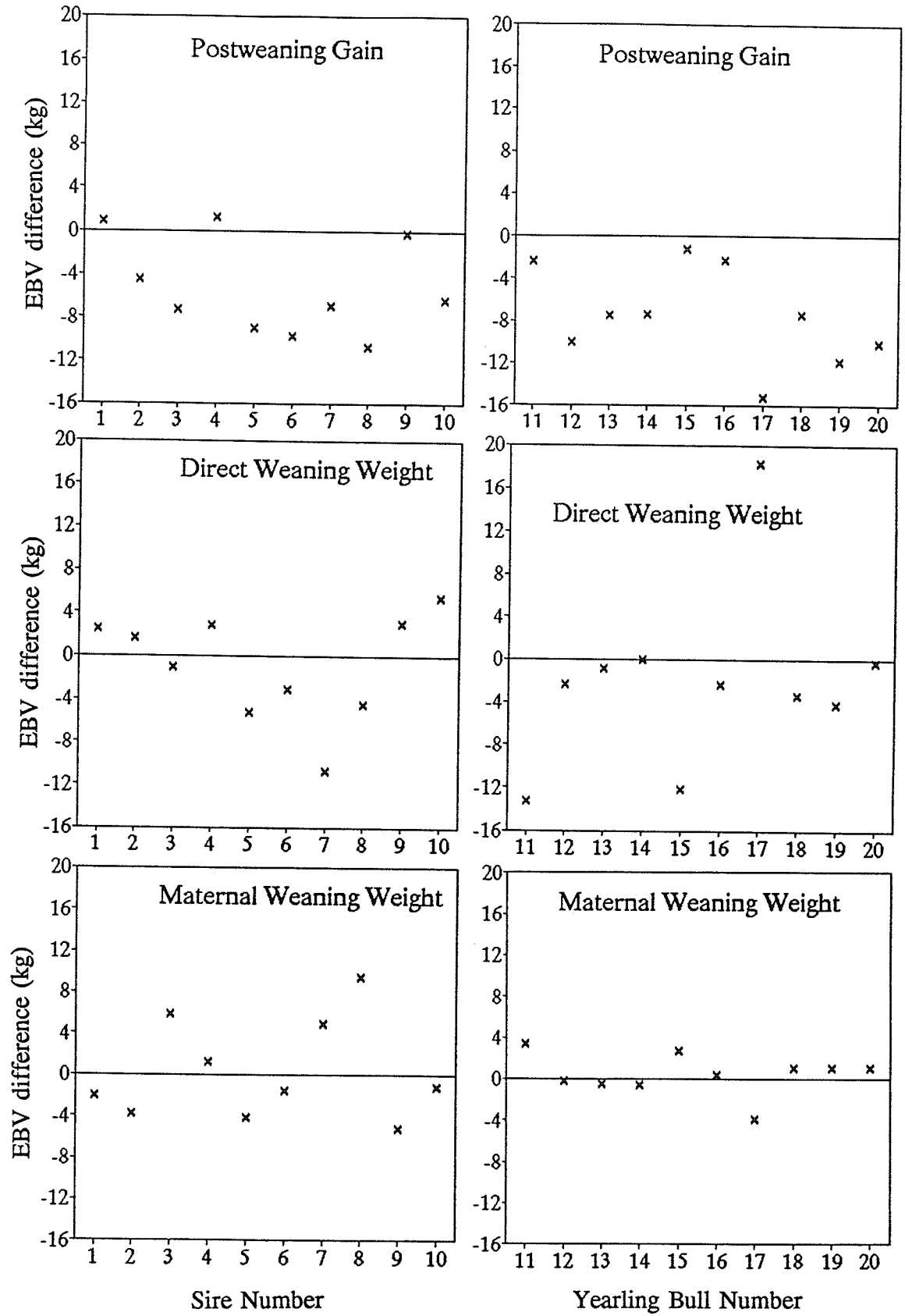
Individual Genetic Ranking. The EBV's of ten select line sires and ten select line yearling bulls born in 1969, as affected by dataset analysis with the base run parameters, are given in Table 20. The difference of the base run analysis subtracted from the Select dataset analysis is shown in Figure 10. For example, EBV's of sire #10 in the Select

TABLE 20. Estimated breeding values (kg) of ten select line sires and ten select line yearling bulls as affected by dataset analysis with the base run parameters.

| Bull # | WWD | | WWM | | PWG | |
|------------|--------|--------|-------|-------|-------|--------|
| | C* | S | C | S | C | S |
| Sires: | | | | | | |
| 1 | 11.40 | 13.82 | 12.25 | 10.12 | 17.98 | 18.87 |
| 2 | 1.19 | 2.87 | 6.53 | 2.68 | 12.34 | 7.87 |
| 3 | 8.91 | 7.84 | -2.51 | 3.30 | 4.89 | -2.40 |
| 4 | 2.76 | 5.58 | 2.32 | 3.56 | 22.20 | 23.50 |
| 5 | 10.75 | 5.48 | 3.93 | -0.26 | 16.18 | 7.17 |
| 6 | 14.33 | 11.22 | 3.89 | 2.29 | 21.46 | 11.74 |
| 7 | 6.62 | -4.16 | 0.40 | 5.28 | 8.17 | 1.25 |
| 8 | 7.75 | 3.27 | -3.25 | 6.19 | 13.11 | 2.31 |
| 9 | 12.33 | 15.38 | 2.14 | -3.15 | 30.52 | 30.31 |
| 10 | 3.68 | 9.13 | 5.68 | 4.44 | 28.68 | 22.30 |
| Yearlings: | | | | | | |
| 11 | 24.10 | -10.88 | 7.08 | 10.42 | 11.64 | 9.31 |
| 12 | 6.80 | 4.44 | 5.86 | 5.61 | 4.05 | -6.01 |
| 13 | 7.81 | 6.96 | 7.00 | 6.46 | 36.63 | 29.12 |
| 14 | 5.87 | 5.85 | 3.62 | 3.02 | 22.60 | 15.23 |
| 15 | 13.81 | 1.66 | -3.42 | -0.81 | 36.55 | 35.31 |
| 16 | 19.28 | 16.93 | 7.67 | 7.97 | 31.87 | 29.60 |
| 17 | -20.95 | -2.65 | 6.84 | 2.99 | -2.99 | -18.25 |
| 18 | 22.92 | 19.51 | 5.40 | 6.41 | 38.28 | 30.95 |
| 19 | 9.00 | 4.82 | 3.36 | 4.41 | 20.26 | 8.43 |
| 20 | -2.73 | -3.05 | 1.46 | 2.53 | 23.52 | 13.32 |

*C=Complete dataset analysis, S=Select dataset analysis. See List of Abbreviations for definitions.

Figure 10. Sire and yearling bull estimates of the Select dataset, expressed relative to the Complete dataset for the traits postweaning gain, direct weaning weight, and maternal weaning weight (estimates shown in Table 20).



dataset analysis differ from the corresponding EBV's in the base run by -6.38 kg for postweaning gain, 5.45 kg for direct weaning weight, and -1.24 kg for maternal weaning weight. The ranking of sires and yearlings was done for each of the twelve parameter sets for both the Complete and Select datasets. For graphing purposes, the sires (and yearling bulls) are arranged in rank order on the X-axis based on their average rank across all parameter set analyses but within dataset.

The ranking of sires and yearlings for postweaning gain EBV's is fairly consistent across parameter set numbers and datasets (Figure 11). In the Complete dataset analyses, if the top 5 sires were chosen based on postweaning gain, they were the same regardless of the parameter set used. In the Select dataset analyses, four of the same sires chosen in the Complete dataset analyses were the same regardless of parameter set used, but the fifth bull was either #6 or #2. If the parameter set was 7, 8, 10, 11, or 12 (which have in common a genetic correlation of -0.1), the sire was #2.

If the top 5 yearling bulls for postweaning gain were chosen, four of them were the same regardless of parameter set used and dataset analyzed. In the Complete dataset analyses, yearling bull #20 was chosen unless parameter set 3 was used, in which case yearling bull #14 was chosen. In the Select dataset analyses, yearling bull #20 was chosen unless parameter set number 1, 3, or 5 was used. Parameter sets 1, 3, and 5 have in common the positive genetic correlation and negative environmental correlation.

The ranking of sires and yearlings on direct weaning weight EBV's was variable both within and across datasets and from one parameter set to another (Figure 12). The top 5 sires of the base run analysis, from highest to lowest rank, were #6, #9,

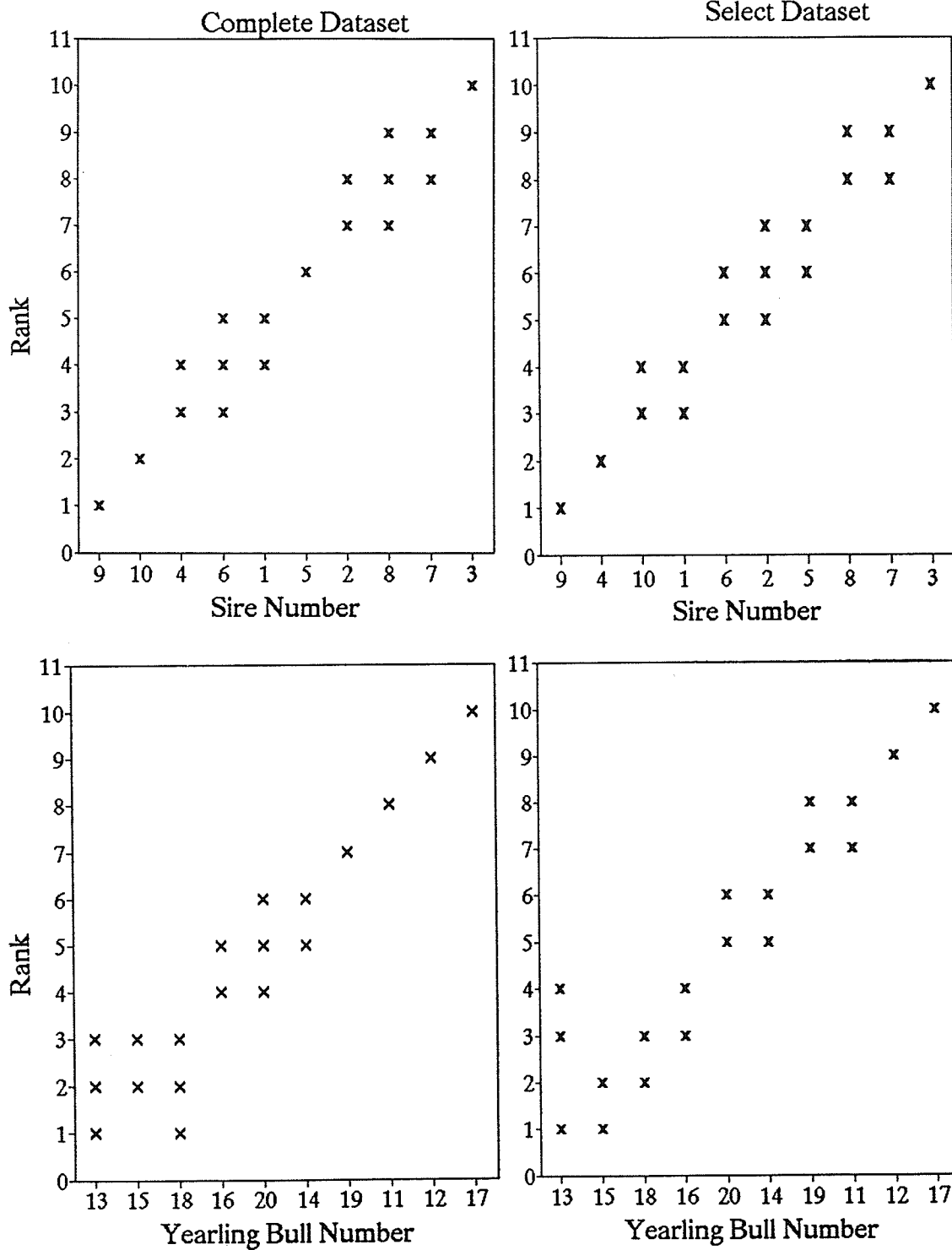


Figure 11. Rank of ten sires and ten yearling bulls across parameter sets, and by datasets, for the trait postweaning gain.

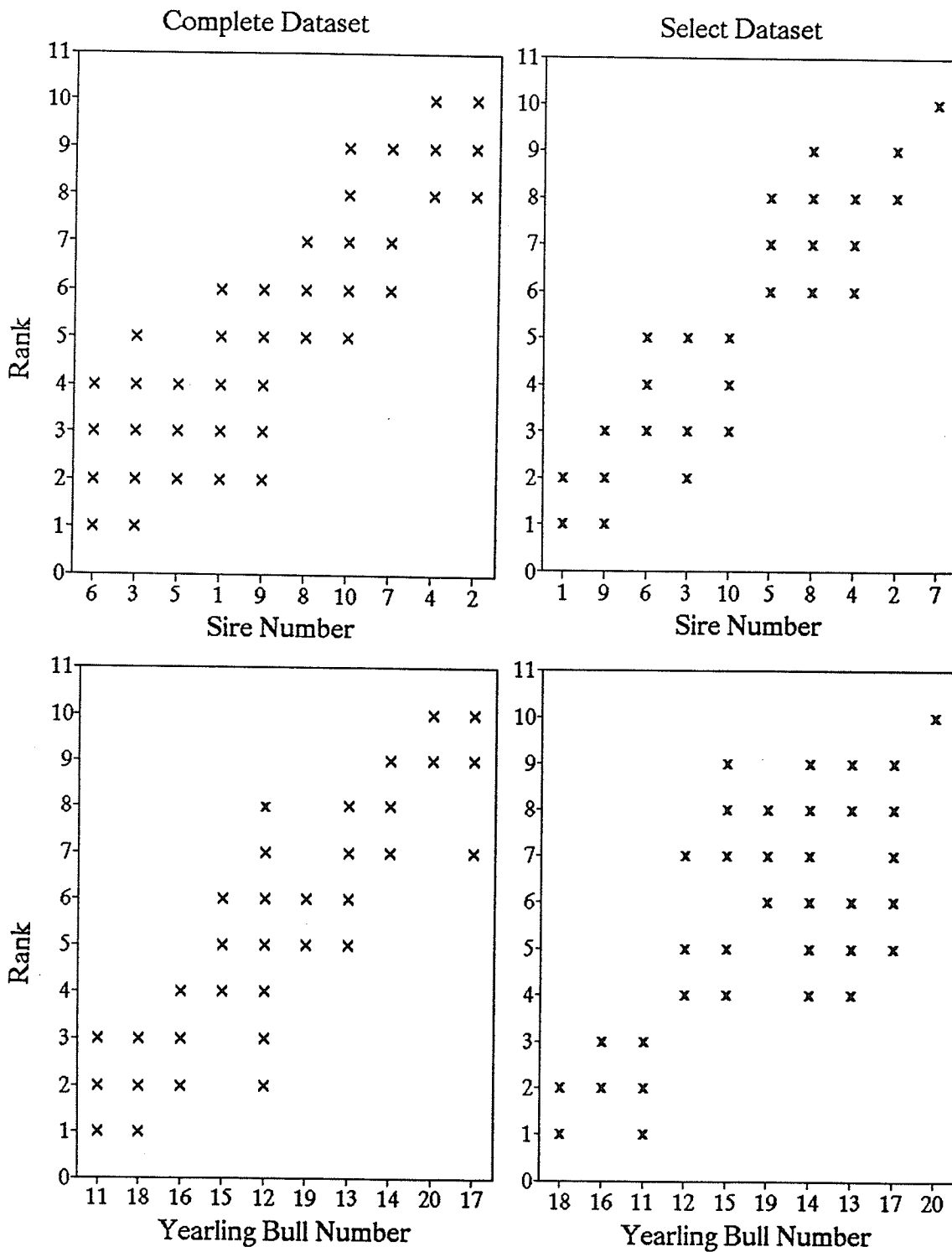


Figure 12. Rank of ten sires and ten yearling bulls across parameter sets, and by datasets, for the trait direct weaning weight.

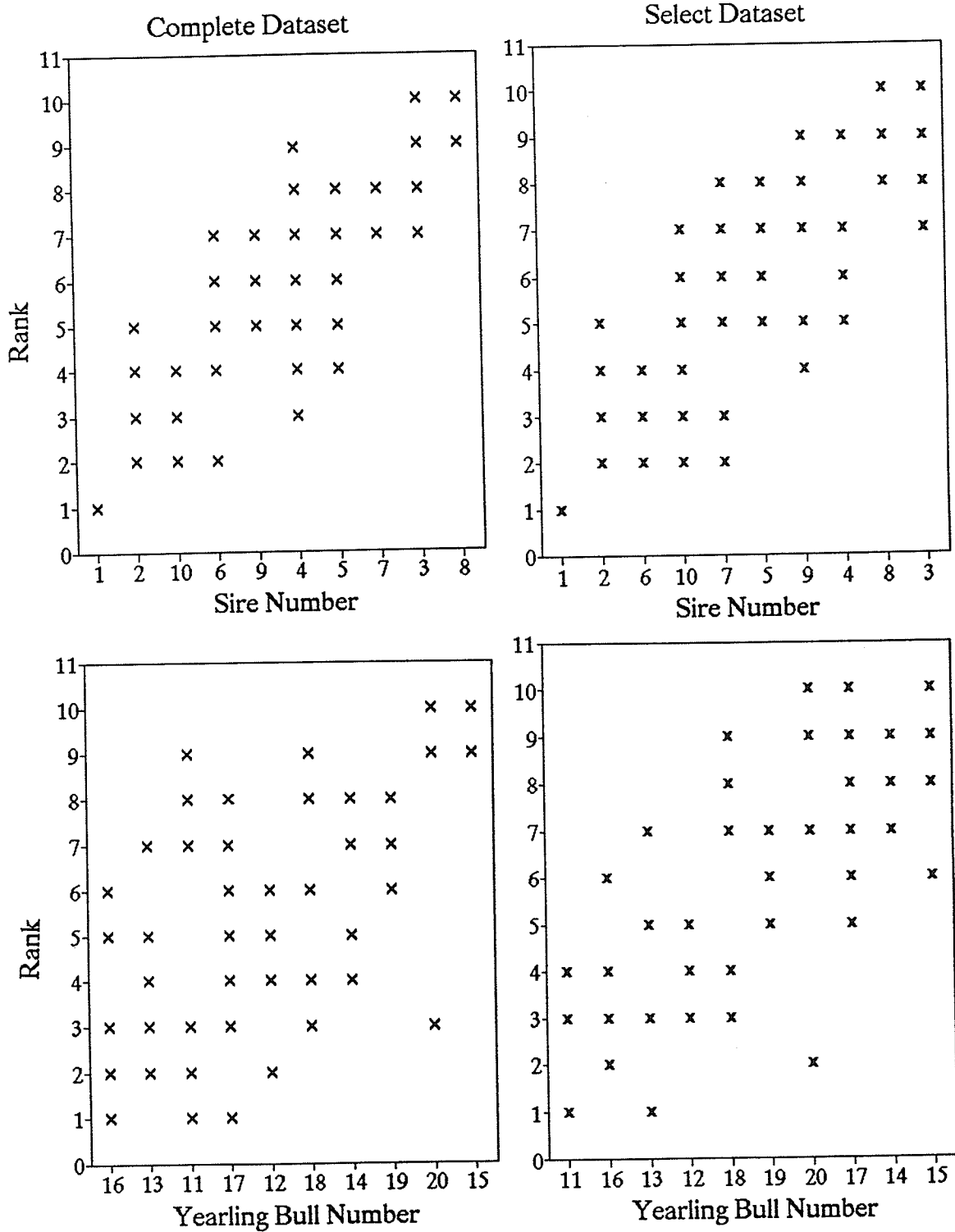


Figure 13. Rank of ten sires and ten yearling bulls across parameter sets, and by datasets, for the trait maternal weaning weight.

#1, #5, and #3. Two sires were common to both datasets. In the Complete dataset, three sires were the same regardless of parameter set used. In the Select dataset, all top 5 sires were the same. The top five yearling bulls of the base run, from highest to lowest rank, were #11, #18, #16, #15, #19. Three bulls were common to both datasets, and they were the same regardless of parameter set used.

The EBV rankings of maternal weaning weight for sires and yearlings are shown in Figure 13. The top 5 sires of the base run, from highest to lowest rank, were #1, #2, #10, #5, and #6. Two sires were common to both datasets. Within datasets, three were the same regardless of parameter set. The top 5 yearling bulls in the Complete dataset depended entirely upon the parameter set used in the analysis. In the base run they were, from highest to lowest, #16, #11, #13, #17, and #12. Only yearling bull #19 was not in the top 5 with at least one of the parameter sets. In the Select dataset, two yearling bulls were in the top 5 regardless of parameter set used, and only yearlings #14 and #15 were not in the top 5 with at least one of the parameter sets.

Environmental Effect

Year effect estimates were obtained from the Select and Complete dataset analyses to compare select line estimates between datasets and parameter sets. The year effects for the traits postweaning gain and weaning weight are shown in Figures 14, 15, and 16 as affected by dataset and parameter set, and expressed relative to the base run. For example, the 1960 year effect of postweaning gain for the Complete dataset with parameter set three was -31.99 kg and the Complete dataset with parameter set one (the base run) was -29.36 kg, giving a difference of -2.63 kg, which is the Complete dataset

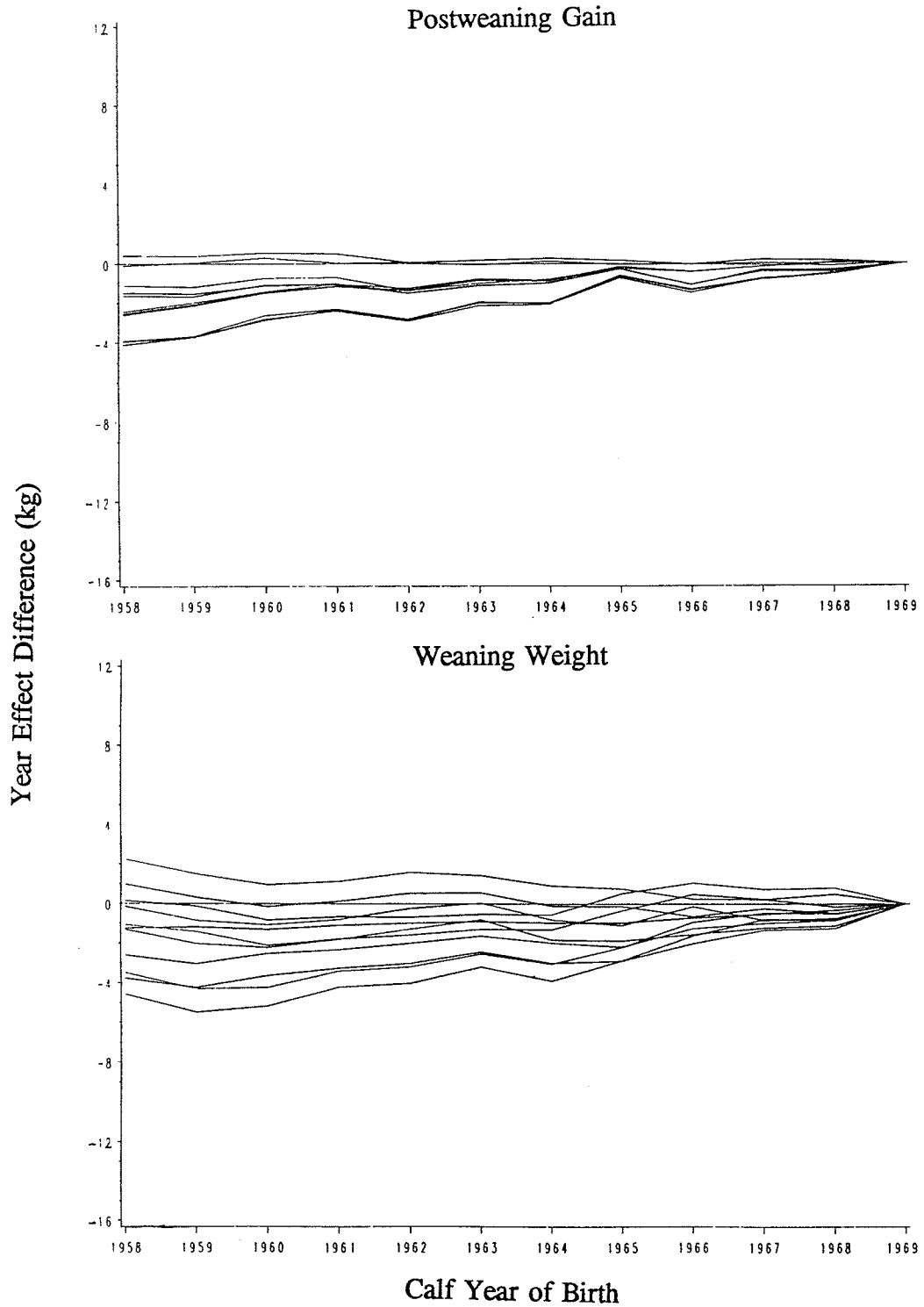


Figure 14. Year effect estimates of postweaning gain and weaning weight as affected by parameter set using the Complete dataset, and expressed relative to the base run.

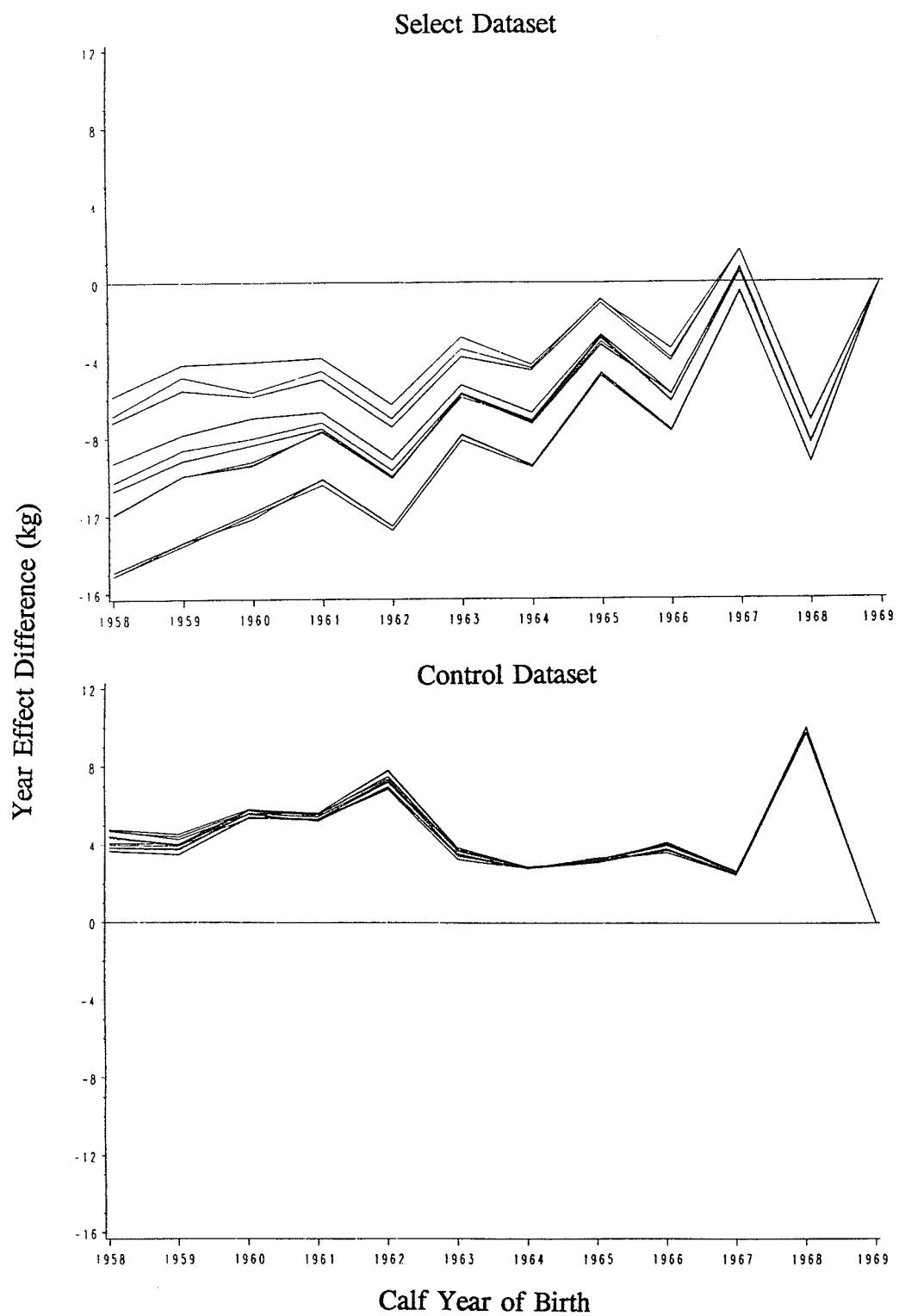


Figure 15. Postweaning gain year effect estimates from the Select and Control datasets as affected by parameter set, and expressed relative to the base run.

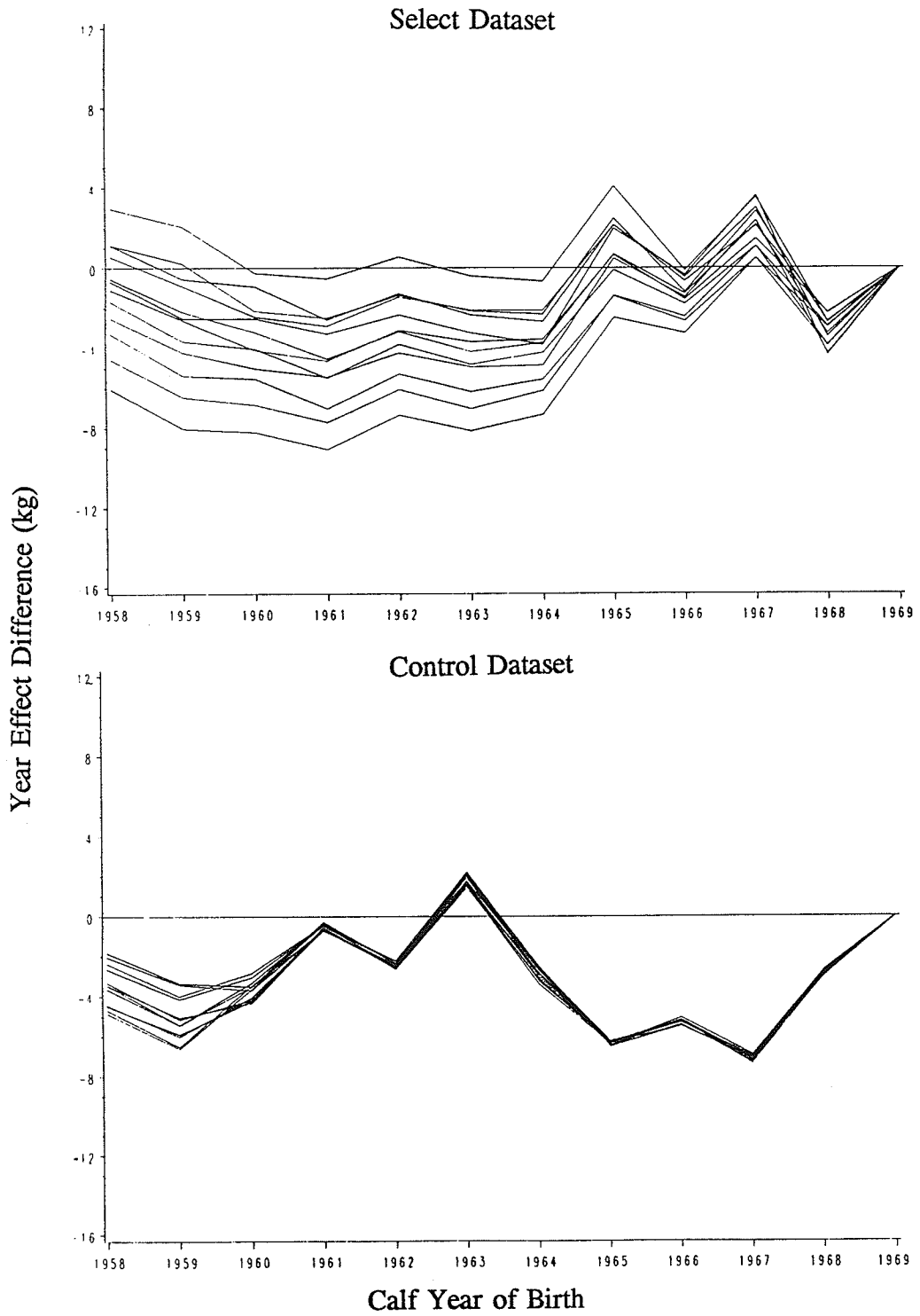


Figure 16. Weaning weight year effect estimates from the Select and Control datasets as affected by parameter set, and expressed relative to the base run.

value graphed in Figure 14. Similarly, the 1960 year effect in the Select dataset was -41.20 kg, giving the Select dataset value graphed in Figure 15 ($-41.20 - -29.36 = -11.84$ kg).

The trends over all parameter sets were similar to the positive trend discussed previously under "genetic and environmental trends estimated from separate line analyses". The largest difference in weaning weight year effects was between 1963 and 1964, and, in postweaning gain, between 1967 and 1968.

The postweaning gain year effects, relative to the base run, can be roughly clustered into 4 groups based on the genetic and environmental correlations, regardless of dataset (Figures 14 and 15). The group that most closely approximates the base run trend has in common a positive genetic correlation and a negative environmental correlation (parameter sets 1, 3, and 5). Then the group with positive genetic and environmental correlations (parameter sets 2, 4, and 6). Next is the group with negative genetic and environmental correlations (parameter sets 7, 9, and 11). The least similar year effects are associated with a negative genetic correlation and a positive environmental correlation (parameter sets 8, 10, and 12). This clustering is the same as that observed for the postweaning gain genetic trends across parameter sets, within datasets. In fact, as the estimates of the genetic trends increase, the estimates of the year trends decrease.

The range in postweaning gain year effects for the Select dataset analyses, across parameter sets, is 3.6 times that of the Complete dataset analyses. Estimates of year effects did not seem to be affected by the assumed direct-maternal correlation.

The weaning weight year effects for the Complete dataset analyses are shown in Figure 14. From 1960 to 1964, the lines remained separate from each other. From 1965 to 1969, they crossed over one another. A clustering of trend lines based on the assumed parameters was not observed.

The Select dataset year effects for weaning weight are shown in Figure 16. The lines are roughly parallel throughout the selection experiment. However, from 1965 to 1969, there was greater fluctuation. The range of year effects is 1.6 times that of the Complete dataset analyses.

In summary, the results support the premise that the parameters assumed in the mixed-model method affect the solutions and thus estimates of genetic trends but not in an exclusive way since the data themselves have an impact on the estimates of genetic trend. The response lines for all parameter sets were parallel to that for the base run parameter set but they shifted up or down depending upon the assumed parameter combination. With the parameter sets arranged in order of decreasing genetic trend, the trends of environmental year effects on postweaning gain were concurrently increasing. In general, the weaning weight environmental trends also increased concurrently, though there was some variation. When EBV's of ten sires and ten yearling bulls were examined for each parameter set, and the Complete and Select datasets, the trait postweaning gain was most consistent in the ranking of animals across parameter sets and datasets, maternal weaning weight was most variable, and direct weaning weight was not quite as variable as maternal weaning weight. This likely reflects the interaction of the data and the assumed parameters; the estimated genetic trend of postweaning gain being

little affected by the direct-maternal correlation of weaning weight whereas this assumed parameter was the main influence on estimated trend in maternal weaning weight and the secondary influence on direct weaning weight.

Other Elements in the Model

Sex Effect

For the postweaning gain sex effect in the Complete dataset analyses, most of the parameter sets were within 1 kg of that for the base run. Sets 3, 7, and 11 were within 2 kg. In general, both male and female effect differences were consistent within parameter set. In the Select dataset, only sets 2, 6, and 10 were within 8 to 10 kg of the base run values. The other sets were within the 10 to 16 kg range. The range in values was 3.3 times that of the Complete dataset analyses. Female differences were slightly greater than male differences, up to 1 kg, within parameter set.

Weaning weight sex effects in the Complete dataset analyses were within 1.5 kg of the base run, except sets 4 and 5 which were within 2.5 kg and sets 11 and 12 which were between 4 and 4.5 kg. Sex differences were consistent between males and females within parameter set. In the Select dataset, values were within +5 kg of the base run, except for sets 11 and 12 which were within 7 to 8.5 kg. Female differences were slightly greater than male differences, up to 0.6 kg.

The Select dataset overestimated the sex effects for postweaning gain, with a tendency towards overestimation in weaning weight, compared to the Complete dataset. This sensitivity to using only select-line data to estimate the effects for postweaning gain

has been previously observed in the genetic and environmental trends. Another reason for the sensitivity of sex effect estimates may be an inadequacy of the model. In the Complete dataset, sex effects are assumed to be constant when in fact selection may be increasing the sex differences in the select line. These differences may be better accounted for when only select-line data is analyzed.

Calf Station of Origin

For postweaning gain station effects, estimates are expressed relative to the Indian Head station, i.e, all parameter sets, as a difference from the base run, are zero for Indian Head. In the Complete dataset, all solutions were within 1 kg of the base run. The station with the greatest difference was Melita which also was the station with the least amount of data, only 2 years worth. In the Select dataset, Brandon station differences were within -1 kg, and Melita differences were within -3 to -4.5 kg.

For weaning weight station effects in the Complete dataset analyses, values were within 1.3 kg of the base run. Brandon and Melita differences were equally varied. In the Select dataset, Brandon differences were within 1 kg, Melita differences were greater than Brandon and within 3.5 kg.

Station effects for postweaning gain and weaning weight indicate that the Select dataset analyses, without the control-line data, was not as effective in estimating the station effect for Melita as was the Complete dataset analyses. In the Complete dataset, there are more records present for the Melita station effect due to the inclusion of control-line data. When the number of records is small, an increase in the number of records would affect the precision of the estimates.

Implication of Results

The mixed-model estimates of genetic trends and EBV's discussed in the previous section are dependent upon the assumed genetic and environmental correlations; however, the data themselves also influence these estimates. Mixed-model methodology assumes constant genetic and environmental correlations and therefore these assumptions are also made in the beef cattle industry when this method is used. This assumption may not be correct, for even in the single herd analyzed here, the genetic and/or environmental correlations must change from year to year to produce the phenotypic correlations shown previously in Table 17. Analysis of the data without a control population, which is typical of the industry at large, was shown to affect the genetic trend estimates of postweaning gain but not the genetic trend estimates of direct and maternal weaning weight. The estimates obtained in postweaning gain may be due to an inadequacy of the model and method to account for selection effects and thereby accurately separate the genetic and environmental components. The fact that estimates for direct and maternal weaning weight were not affected may be due to the small environmental component of weaning weight (Olthoff et al., 1990b) or the relatively small correlated response in weaning weight compared to that in postweaning gain.

Using mixed-model methodology to estimate breeding values for all individuals is a common goal in industry analyses of beef cattle populations. These EBV's are then used in selection programs by individual producers. However, the results here indicate an important effect both of the assumed parameters and of the inclusion or exclusion of a control population. This was particularly noticeable in the

direct and maternal weaning weight EBV's of ten randomly chosen sires and yearling bulls. These traits were also affected by the direct-maternal correlation, whereas postweaning gain genetic trend estimates did not depend upon this correlation. In conclusion, the mixed-model methodology as used here with a reduced animal model, is likely to be not as accurate as one would wish for the estimation of breeding values, and genetic trends, in beef cattle populations.

SUMMARY

Mixed-model methodology was applied to the dataset used by Newman et al. (1973) and Olthoff et al. (1990b) to compare mixed-model estimates of yearly genetic and environmental changes to those estimated by the control-line method for the correlated traits, postweaning gain, direct weaning weight, and maternal weaning weight, in a line of beef cattle selected for yearling weight. Required estimates of genetic and environmental variances and covariances for the mixed-model methodology were obtained from the literature. The select and control lines were analyzed together (Complete) as one dataset, and separately as two subsets of the first dataset (Select dataset and Control dataset) to examine the sensitivity of the mixed-model estimates to the inclusion or exclusion of a control population. The Complete dataset and the assumed parameters of $+0.5$ for the genetic correlation of weaning weight and postweaning gain, -0.2 for the environmental correlation between weaning weight and postweaning gain, and 0.0 for the direct-maternal correlation of weaning weight, were used as the base run against which all other solutions were compared. Twelve solutions were obtained for each dataset based on all possible combinations of the assumed parameter values for the genetic correlation between weaning weight and postweaning gain ($+0.5$ or -0.1), the environmental correlation between weaning weight and postweaning gain ($+0.2$ or -0.2),

and the direct-maternal correlation of weaning weight (+.5, 0.0, or -.5) to examine the sensitivity of the mixed-model estimates to possibly incorrect assumed parameters.

The genetic trend estimates of the base run, over the ten-year selection period, were 2.52 kg yr⁻¹ for postweaning gain, 1.16 kg yr⁻¹ for direct weaning weight, and 0.30 kg yr⁻¹ for maternal weaning weight, all of which were significantly different from zero ($P < .05$). The yearling weight genetic trend estimate was 4.53 kg yr⁻¹, calculated from the sum of its parts (postweaning gain EBV of calf, direct weaning weight EBV of calf, maternal weaning weight EBV of dam, and permanent maternal environment EBV of dam) for each of the select and control lines, and then the yearly differences (select minus control) were regressed on year of birth. The trait with the greatest correlated response to yearling weight selection was postweaning gain. The postweaning gain genetic response was 93% of the estimate obtained from the control-line method (Olthoff et al., 1990b), direct weaning weight was 63%, and yearling weight was 96%. Maternal weaning weight genetic trend could not be estimated by the control-line method. The close approximation of the mixed-model genetic trend estimate of postweaning gain to the control-line method estimate indicates adequate separation of the genetic and environmental components by the mixed-model methodology. This was not the case with direct weaning weight, however, and may indicate that the assumed model and method were not sufficient, due perhaps to the relatively small correlated response compared to postweaning gain or the very small environmental component as found by Olthoff et al. (1990b).

The genetic response patterns found using the twelve parameter combinations and the Complete dataset were very similar to the base run for the three correlated traits. The genetic trend estimates clearly depended on the assumed correlations but were probably not significantly different from one another given the size of some of the standard errors. This similarity indicates a degree of robustness of the mixed-model methodology in estimating genetic trends given different assumed parameters. The same patterns and estimates were observed in the Select dataset for direct and maternal weaning weight. Postweaning gain genetic trend estimates were smaller than the base run estimates but the response pattern was similar. The effects of selection may not have been adequately accounted for in this situation. Arranging the parameter combinations in order of decreasing genetic trend estimates, arranges the environmental effect in increasing order for postweaning gain and for most of the parameter combinations of weaning weight.

The environmental effect estimates were affected by the inclusion or exclusion of the control population. When the control population was not part of the data, year effects were underestimated compared to the base run. In the Control dataset, year effects were overestimated. Year effect estimates from both datasets were lower than those found for the Complete dataset.

The effect of the assumed genetic parameters at an individual level was examined by randomly choosing ten sires and ten yearling bulls of the select line. These individuals were ranked by their EBV's for each trait for every parameter combination in both the Complete and Select datasets. For the trait postweaning gain, ranking of

individuals was slightly dependent on the assumed parameters though fairly consistent across parameter sets and datasets. The ranking of individuals for the traits direct and maternal weaning weight depended to a large degree on the assumed parameters and to a lesser degree on the dataset analyzed. Thus, the degree of robustness indicated in the estimation of genetic trends over all parameter combinations was not observed at the individual level. The variability of ranking of individuals, together with the genetic trend estimates, indicates an interaction of the assumed parameters and the data. The greater variability in weaning weight rankings may be due to the direct-maternal correlation which influenced both direct and maternal weaning weight, maternal more than direct, but not postweaning gain. In conclusion, the mixed-model methodology produces results for genetic and environmental trends which depend upon the assumed parameters and the individual EBV's were clearly affected by the assumed parameters, and also to some extent, the dataset analyzed.

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APPENDICES

Appendix A: Calculation of the base run (co)variances.

The (co)variance matrix was:

| Line no. | Matrices | | | Explanation | | | |
|----------|----------|-------|-----|----------------------------------|----|----|---|
| 1 | 144 | 0 | 0 | R: parent record, PWG missing | | | |
| 2 | 144 | -40 | 276 | R: parent record, PWG present | | | |
| 3 | 400 | 0 | 0 | R: nonparent record, PWG missing | | | |
| 4 | 400 | 3 | 797 | R: nonparent record, PWG present | | | |
| 5 | 112 | 83 | 0 | 245 | -8 | 64 | G: WWD, WWD•PWG, WWD•WWM, PWG, PWG•WWM, WWM |
| 6 | 30 | P: PE | | | | | |

For line 1 and line 2, the residual (R) (co)variance matrices are for parent records either with a weaning weight (WW) record only (line 1) or with a weaning weight and a postweaning gain (PWG) record (line 2). (See List of Abbreviations for definitions.)

$$V_{E:WW} = V_{P:WW} - V_{G:WWD} - V_{G:WWM} - COV_{G:WWD,WWM} - E_{WWPE}$$

$$= 350 - 112 - 64 - 0 - 30 = 144$$

$$V_{E:PWG} = V_{P:PWG} - V_{G:PWG} = 521 - 245 = 276$$

$$COV_{E:WW,PWG} = r_{E:WW,PWG} \sqrt{V_{E:WW} V_{E:PWG}} = -.2 \sqrt{144 \cdot 276} = -40$$

Similarly, lines 3 and 4 are for nonparent records:

$$V_{E:WW} = (V_{E:WW,parent} + \frac{1}{2}V_{G:WWD})^2 = (144 + \frac{1}{2} \cdot 112)^2 = 400$$

$$V_{E:PWG} = (V_{E:PWG,parent} + \frac{1}{2}V_{G:PWG})^2 = (276 + \frac{1}{2} \cdot 245)^2 = 797$$

$$\text{COV}_{E:WW,PWG} = (\text{COV}_{E:WW,PWG, \text{parent}} + \frac{1}{2}\text{COV}_{G:WWD,PWG})^2 = (-40 + \frac{1}{2}\cdot 83)^2 = 3$$

Line 5 is the genetic (G) (co)variance matrix and the values which vary are the genetic covariance between direct weaning weight and postweaning gain ($\text{COV}_{G:WWD,PWG}$) and the direct-maternal weaning weight covariance ($\text{COV}_{G:WWD,WWM}$).

$$V_{G:WWD} = h^2_{WWD} \cdot V_{P:WW} = .32(350) = 112$$

$$V_{G:PWG} = h^2_{PWG} \cdot V_{P:PWG} = .47(521) = 245$$

$$\text{COV}_{G:WWD,PWG} = r_{G:WWD,PWG}(\sqrt{V_{G:WWD} \cdot V_{G:PWG}}) = .5(\sqrt{112 \cdot 245}) = 83$$

$$V_{G:WWM} = h^2_{WWM} \cdot V_{P:WW} = .18(350) = 64$$

$$\text{COV}_{G:WWD,WWM} = r_{G:WWD,WWM}(\sqrt{V_{G:WWD} \cdot V_{G:WWM}}) = 0(\sqrt{112 \cdot 64}) = 0$$

$$\text{COV}_{G:PWG,WWM} = -8 \text{ (assumed)}$$

Line 6 is the assumed value of the permanent environmental variance.

Appendix B: Example of the RAM method of analysis.

The Dataset:

The example DATASET contains 11 calf records and is as follows:

| DATASET | | | | | | | | | | | |
|-------------|----|----|----|----|----|----|---|---|---|-----|-----|
| line no. | a | b | c | d | e | f | g | h | i | j | k |
| 1. | 4 | 53 | 1 | 56 | 8 | 59 | 1 | 0 | 1 | 474 | 0 |
| 2. | 5 | 57 | 1 | 56 | 9 | 59 | 1 | 0 | 2 | 369 | 690 |
| 3. | 6 | 56 | 2 | 55 | 10 | 59 | 2 | 0 | 1 | 410 | 836 |
| 4. | 7 | 54 | 2 | 55 | 11 | 59 | 2 | 0 | 2 | 333 | 0 |
| 5. | 7 | 54 | 1 | 56 | 12 | 60 | 2 | 1 | 1 | 425 | 818 |
| 6. | 6 | 56 | 3 | 58 | 13 | 60 | 1 | 2 | 1 | 447 | 0 |
| 7. | 4 | 53 | 3 | 58 | 14 | 60 | 1 | 2 | 2 | 356 | 727 |
| 8. | 5 | 57 | 1 | 56 | 15 | 61 | 1 | 1 | 1 | 359 | 757 |
| 9. | 11 | 54 | 1 | 56 | 16 | 61 | 1 | 1 | 2 | 407 | 732 |
| 10. | 9 | 59 | 10 | 59 | 17 | 61 | 1 | 2 | 1 | 415 | 813 |
| 11. | 4 | 53 | 10 | 59 | 18 | 61 | 1 | 2 | 2 | 378 | 0 |

From left to right, the information is:

- a) dam number to identify dam
- b) dam year of birth to calculate a priori adjustment of weaning weight for age of dam
- c) sire number to identify sire
- d) sire year of birth
- e) calf number to identify calf
- f) calf year of birth for fixed effect of birth year
- g) calf herd of origin for fixed effect of herd of origin
- h) calf line to separate the control and select lines for comparison of genetic trends
- i) sex of calf for fixed effect of sex
- j) weaning weight of calf (in lbs. - conversion to kg occurs in data preparation programs) as first trait of interest to calculate genetic trends in the direct and maternal components of weaning weight (WWD, WWM) and the permanent maternal environmental effect (WWPE)

k) yearling weight of calf (in lbs.) as second trait of interest to calculate genetic trend in direct component of postweaning gain (PWG)

In this dataset, three calves later become parents; calf number 9 and 11 become dams and calf number 10 becomes a sire.

The Data Preparation Program Outputs:

A series of six data preparation programs are run to create the files required by the RAM program as follows:

1. As each record is read, the sire and dam numbers are outputted to separate files (SIRE, DAM) and these files are sorted (SIRES, DAMS) (see below).

| | SIRE | DAM | SIRES | DAMS | SIRELIST | DAMLIST |
|-----|------|-----|-------|------|----------|---------|
| 1. | 1 | 4 | 1 | 4 | 1 | 4 |
| 2. | 1 | 5 | 1 | 4 | 2 | 5 |
| 3. | 2 | 6 | 1 | 4 | 3 | 6 |
| 4. | 2 | 7 | 1 | 5 | 10 | 7 |
| 5. | 1 | 7 | 1 | 5 | | 9 |
| 6. | 3 | 6 | 2 | 6 | | 11 |
| 7. | 3 | 4 | 2 | 6 | | |
| 8. | 1 | 5 | 3 | 7 | | |
| 9. | 1 | 11 | 3 | 7 | | |
| 10. | 10 | 9 | 10 | 9 | | |
| 11. | 10 | 4 | 10 | 11 | | |

2. The SIRES and DAMS files are reduced by listing each parent only once (SIRELIST, DAMLIST) (see above).

3. Program three uses the two previously created files, SIRELIST and DAMLIST, and the DATASET to create a data file, DATA, and a pedigree file, PEDIGREE, containing only the relevant information required by the RAM program.

The DATA file (see below) contains one record for each calf that later becomes a parent and 2 records for each calf that does not become a parent.

| DATA | | | | | | | | | | | | |
|------|----|---|----|---|---|---|---|---|---|---|-------|-------|
| | a | b | c | d | e | f | g | h | i | j | k | l |
| 1. | 1 | 0 | 11 | 5 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 2. | 5 | 0 | 11 | 1 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 3. | 9 | 1 | 9 | 0 | 1 | 6 | 2 | 1 | 1 | 2 | 19127 | 14561 |
| 4. | 4 | 1 | 4 | 0 | 2 | 7 | 1 | 1 | 2 | 2 | 20251 | 19323 |
| 5. | 10 | 1 | 10 | 0 | 2 | 8 | 2 | 1 | 2 | 1 | 15692 | 0 |
| 6. | 1 | 0 | 12 | 8 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 7. | 8 | 0 | 12 | 1 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 8. | 3 | 0 | 13 | 7 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 9. | 7 | 0 | 13 | 3 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 10. | 3 | 0 | 14 | 5 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |
| 11. | 5 | 0 | 14 | 3 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |

| | | | | | | | | | | | | |
|-----|----|---|----|----|---|----|---|---|---|---|-------|-------|
| 12. | 1 | 0 | 15 | 6 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 13. | 6 | 0 | 15 | 1 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 14. | 1 | 0 | 16 | 10 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |
| 15. | 10 | 0 | 16 | 1 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |
| 16. | 4 | 0 | 17 | 9 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 17. | 9 | 0 | 17 | 4 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 18. | 4 | 0 | 18 | 5 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |
| 19. | 5 | 0 | 18 | 4 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |

From left to right, the information is (also applies to program outputs 5 and 6, or files DATAIE and DATAD):

- a) individual evaluated: either the calf itself if it later becomes a parent or the sire and dam of the calf if the calf does not become a parent
- b) indicates whether the individual evaluated is a calf which later became a parent (1) or a nonparent (0)
- c) the calf which made the observation(s)
- d) indicates the other parent for nonparent records
- e) sire of calf which made the observation(s)
- f) dam of calf which made the observation(s)
- g) sex of the calf, coded 1 for male and 2 for female
- h) year of birth of the calf, coded 1 for 59, 2 for 60 and 3 for 61
- i) coded herd of origin
- j) code for residual variance-covariance matrix to use for the current animal, depending upon whether it becomes a parent or not, and whether both traits are present or either one of weaning weight or postweaning gain
- k) weaning weight adjusted for age of dam (in kg with two implied decimal places)
- l) postweaning gain (in kg with two implied decimal places)

The PEDIGREE file (see below) contains only parent animals, one record for parents without calf records, three records for calves which later became parents, and no record for any calf which did not become a parent.

From left to right, the information is (also applies to program output 4, or file PEDIE):

- a) the parent individual or individual evaluated
- b) indicates if the parent individual is a progeny of columns c and d (1) or is the sire (or dam) of column c and column d is then the mate of the parent individual (2)
- c) is the sire if the parent individual is a progeny or is the progeny of the parent individual
- d) is the dam if the parent individual is a progeny or is the mate of the parent individual

| | PED | | | | PEDIE | | | |
|-----|-----|---|----|---|-------|---|----|---|
| | a | b | c | d | a | b | c | d |
| 1. | 9 | 1 | 1 | 6 | 1 | 1 | 0 | 0 |
| 2. | 1 | 2 | 9 | 6 | 1 | 2 | 9 | 6 |
| 3. | 6 | 2 | 9 | 1 | 2 | 1 | 0 | 0 |
| 4. | 4 | 1 | 2 | 7 | 2 | 2 | 4 | 7 |
| 5. | 2 | 2 | 4 | 7 | 2 | 2 | 10 | 8 |
| 6. | 7 | 2 | 4 | 2 | 3 | 1 | 0 | 0 |
| 7. | 10 | 1 | 2 | 8 | 4 | 1 | 2 | 7 |
| 8. | 2 | 2 | 10 | 8 | 5 | 1 | 0 | 0 |
| 9. | 8 | 2 | 10 | 2 | 6 | 1 | 0 | 0 |
| 10. | 1 | 1 | 0 | 0 | 6 | 2 | 9 | 1 |
| 11. | 2 | 1 | 1 | 0 | 7 | 1 | 0 | 0 |
| 12. | 3 | 1 | 0 | 0 | 7 | 2 | 4 | 2 |
| 13. | 5 | 1 | 0 | 0 | 8 | 1 | 0 | 0 |
| 14. | 6 | 1 | 0 | 0 | 8 | 2 | 10 | 2 |
| 15. | 7 | 1 | 0 | 0 | 9 | 1 | 1 | 6 |
| 16. | 8 | 1 | 0 | 0 | 10 | 1 | 2 | 8 |

By sorting the DATA and PEDIGREE files, three of the four (DATAIE, DATAD, PEDIE, VCV) files required to run the RAM program are produced.

4. The PEDIGREE file is sorted by the 'individual evaluated' (PEDIE) (see above) and is used to solve for animal direct genetic solutions, and maternal and permanent maternal environmental effects.

5. Sorting the DATA file by the 'individual evaluated' (column a of file DATAIE and DATA) allows for the solving of the animal direct genetic solutions (WW , PWG).

| DATAIE | | | | | | | | | | | | |
|--------|---|---|----|----|---|----|---|---|---|---|-------|-------|
| | a | b | c | d | e | b | g | h | i | j | k | l |
| 1. | 1 | 0 | 16 | 10 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |
| 2. | 1 | 0 | 15 | 6 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 3. | 1 | 0 | 12 | 8 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 4. | 1 | 0 | 11 | 5 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 5. | 3 | 0 | 13 | 7 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 6. | 3 | 0 | 14 | 5 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |
| 7. | 4 | 1 | 4 | 0 | 2 | 7 | 1 | 1 | 2 | 2 | 20251 | 19323 |

| | | | | | | | | | | | | |
|-----|----|---|----|---|---|----|---|---|---|---|-------|-------|
| 8. | 4 | 0 | 17 | 9 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 9. | 4 | 0 | 18 | 5 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |
| 10. | 5 | 0 | 18 | 4 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |
| 11. | 5 | 0 | 11 | 1 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 12. | 5 | 0 | 14 | 3 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |
| 13. | 6 | 0 | 15 | 1 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 14. | 7 | 0 | 13 | 3 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 15. | 8 | 0 | 12 | 1 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 16. | 9 | 1 | 9 | 0 | 1 | 6 | 2 | 1 | 1 | 2 | 19127 | 14561 |
| 17. | 9 | 0 | 17 | 4 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 18. | 10 | 1 | 10 | 0 | 2 | 8 | 2 | 1 | 2 | 1 | 15692 | 0 |
| 19. | 10 | 0 | 16 | 1 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |

6. Sorting the DATA file by the 'dam of the calf which made the observation' (column f of file DATAD and DATA) allows for the solving of maternal and permanent maternal environmental effects (WW , PE).

| | DATAD | | | | | | | | | | | |
|-----|-------|---|----|----|---|----|---|---|---|---|-------|-------|
| | a | b | c | d | e | f | g | h | i | j | k | l |
| 1. | 5 | 0 | 18 | 4 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |
| 2. | 4 | 0 | 18 | 5 | 4 | 5 | 2 | 3 | 1 | 3 | 17145 | 0 |
| 3. | 5 | 0 | 14 | 3 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |
| 4. | 3 | 0 | 14 | 5 | 3 | 5 | 2 | 2 | 1 | 4 | 16208 | 16828 |
| 5. | 5 | 0 | 11 | 1 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 6. | 1 | 0 | 11 | 5 | 1 | 5 | 1 | 1 | 1 | 3 | 21757 | 0 |
| 7. | 9 | 1 | 9 | 0 | 1 | 6 | 2 | 1 | 1 | 2 | 19127 | 14561 |
| 8. | 1 | 0 | 15 | 6 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 9. | 6 | 0 | 15 | 1 | 1 | 6 | 1 | 3 | 1 | 4 | 17337 | 18053 |
| 10. | 7 | 0 | 13 | 3 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 11. | 4 | 1 | 4 | 0 | 2 | 7 | 1 | 1 | 2 | 2 | 20251 | 19323 |
| 12. | 3 | 0 | 13 | 7 | 3 | 7 | 1 | 2 | 1 | 3 | 21328 | 0 |
| 13. | 8 | 0 | 12 | 1 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 14. | 1 | 0 | 12 | 8 | 1 | 8 | 1 | 2 | 2 | 4 | 19534 | 17827 |
| 15. | 10 | 1 | 10 | 0 | 2 | 8 | 2 | 1 | 2 | 1 | 15692 | 0 |
| 16. | 4 | 0 | 17 | 9 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 17. | 9 | 0 | 17 | 4 | 4 | 9 | 1 | 3 | 1 | 4 | 21213 | 18053 |
| 18. | 10 | 0 | 16 | 1 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |
| 19. | 1 | 0 | 16 | 10 | 1 | 10 | 2 | 3 | 1 | 4 | 18522 | 14742 |

The (Co)Variance File:

An example of the (co)variance file is:

| | | | | | | | |
|----|-----|-----|-----|-----|----|----|--|
| 1. | 144 | 0 | 0 | | | | |
| 2. | 144 | -40 | 276 | | | | |
| 3. | 400 | 0 | 0 | | | | |
| 4. | 400 | 3 | 797 | | | | |
| 5. | 112 | 83 | 0 | 245 | -8 | 64 | |
| 6. | 30 | | | | | | |

which corresponds to:

1. R: parent record, postweaning gain record (G) missing
2. R: parent record, G and weaning records (W) present

3. R: nonparent record, G missing
4. R: nonparent record, G and W present
5. G: WW, WG, WM, GG, GM, MM
6. P: PE

or, descriptively:

Line 1 and 2 are the residual (co)variance matrices for parent records without or with a postweaning gain record, respectively. Line 3 and 4 are the residual (co)variance matrices for nonparent records without and with a postweaning gain record. Line 5 is the genetic (co)variance matrix and line 6 is the permanent maternal environmental matrix for dams.

The line numbers correspond to the code numbers in the data files. For example, line 1 of the data file sorted by dam (see column j of file DATAD) has a code 3 for the (co)variance matrix. This corresponds to line 3 of the (co)variance file where the individual is a nonparent with only a weaning weight record. That is:

$$\begin{pmatrix} 400 & 0 \\ 0 & 0 \end{pmatrix}$$

The RAM Program Output:

The RAM program takes the files DATAIE, DATAD, PEDIE, and VCV to produce solutions to the FIXED and ANIMAL effects. The animals are in sequential order and only dams have nonzero permanent maternal environmental effects solutions.

| FIXED effects solutions: | Weaning Weight | Postweaning Gain |
|--------------------------|-------------------|---------------------|
| sex - male | 151.9 | 154.2 |
| - female | 124.7 | 129.7 |
| year - 1 | 26.8 | 1.9 |
| - 2 | 24.1 | 24.6 |
| - 3 | 0 | 0 |
| herd - 1 | 38.7 | 18.3 |
| - 2 | 0 | 0 |

ANIMAL effects solutions:

| | Sequential Number | WW | PWG | WW | PE |
|--------|----------------------|-------|-------|------|------|
| sires: | 1 | 5.6 | 2.3 | .3 | |
| | 2 | 0 | 0 | 2.0 | |
| | 3 | - 2.9 | - 1.8 | 0 | |
| | 4 | 43.0 | 36.1 | -0.8 | |
| dams: | 5 | - 7.1 | -11.4 | -3.7 | -1.9 |
| | 6 | - 3.1 | - 0.7 | -2.9 | -1.4 |

| | | | | | |
|---------|----|-------|-------|------|------|
| | 7 | 1.1 | 0.8 | -3.9 | -2.0 |
| | 8 | 2.8 | 1.9 | 3.9 | 1.1 |
| | 9 | 1.6 | - 1.6 | -1.1 | 0 |
| | 10 | 2.4 | - 2.2 | 4.9 | 1.7 |
| calves: | 11 | 1.1 | - 3.2 | -1.7 | |
| | 12 | 6.8 | 3.4 | 2.1 | |
| | 13 | 0.7 | 0.6 | -2.0 | |
| | 14 | - 8.9 | - 8.9 | -1.9 | |
| | 15 | - 2.0 | 0.1 | -1.3 | |
| | 16 | 7.1 | 2.2 | 2.6 | |
| | 17 | 21.4 | 14.5 | -0.8 | |
| | 18 | 16.8 | 11.4 | -2.3 | |

Calculation of Genetic Trend:

To use the solutions produced by the RAM program to calculate genetic trends per year, a seventh data preparation program was run which takes the files SIRELIST, DAMLIST, and DATASET to produce a new file (CALF) with all animals assigned sequential numbers - sires first, dams second, and nonparents third - to match the output from the RAM program. The CALF file contains:

- calf sequential number (seq.) - corresponds to RAM program output and, can be merged with the RAM output file to calculate genetic gains per year,
- calf line - can be used to calculate genetic trends by line,
- and calf number in the original dataset (id.).

Genetic trend of calf breeding values (WW , PWG , WW) are obtained by plotting the average solutions per line per year (avg.) against year of birth. The calf information for WW and PWG is given below.

| <u>Calf No.</u> | | line | year | WW | avg. | PWG | avg. |
|-----------------|-----|------|------|-------------|------|-------------|------|
| seq. | id. | | | | | | |
| 11 | 8 | 0 | 1 | 1.1 | | -3.2 | |
| 9 | 9 | 0 | 1 | 1.6 | | -1.6 | |
| 4 | 10 | 0 | 1 | 43.0 | | 36.1 | |
| 10 | 11 | 0 | 1 | <u>2.4</u> | 12.0 | <u>-2.2</u> | 7.3 |
| 12 | 12 | 1 | 2 | <u>6.8</u> | 6.8 | <u>3.4</u> | 3.4 |
| 13 | 13 | 2 | 2 | 0.7 | | 0.6 | |
| 14 | 14 | 2 | 2 | <u>-8.9</u> | -4.1 | <u>-8.9</u> | -4.2 |
| 15 | 15 | 1 | 3 | -2.0 | | 0.1 | |
| 16 | 16 | 1 | 3 | <u>7.1</u> | 2.6 | <u>2.2</u> | 1.2 |
| 17 | 17 | 2 | 3 | 21.4 | | 14.5 | |
| 18 | 18 | 2 | 3 | <u>16.8</u> | 19.1 | <u>11.4</u> | 13.0 |

Note: Calf sequential numbers 9 and 10 became dams and 4 became a sire.