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Sire by region interactions for reproductive traits in Angus cattle

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Sire by region interactions for reproductive

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Reproductive traits are the most economically important traits in beef cattle production. Trenkle and Willham (1977) estimated that in terms of relative economic value, reproduction is at least five times as important in commercial operations as growth and milk production. Improving reproductive performance by selection, however, is more difficult than improving growth traits. Reproductive traits are expressed in the female, but most of the genetic improvement must be made by the use of sires that are currently being selected on different criteria. Genetic improvement is further impeded by the fact that reproductive traits are generally lowly heritable.

There exists a possibility that genetically superior sires for traits concerned with the reproductive complex could be identified through national sire evaluation programs. At present, breed associations generally have limited data available on reproductive traits. Since birth dates are recorded, however, such measures of reproduction as age at calving, date of calving, and calving interval can be calculated.

Bourdon and Brinks (1983) found calving date preferable to calving interval as a reproductive measure in beef cattle. Calving intervals were reduced .86 $\pm$ .02 days for each 1 day delay in previous calving date. If calving interval is used as a criteria for selection when fixed breeding seasons are employed, later calving cows would tend to be selected. With a fixed breeding season, a heifer that conceived on day one of the breeding season would not have had the opportunity to conceive again for at least

365 days. Heifers that conceived late in the season would either have had a shorter calving interval or would not have produced a calf. Lesmeister et al. (1973) reported that early calving heifers tended to calve early throughout their productive life and had significantly higher lifetime production of kilograms of calf weaned.

The purpose of this study was to examine age at first calving as a possible criteria for ranking sires. In order to make genetic progress in a trait, that trait must be heritable. A specific objective of this study was to estimate the heritability of age at first calving.

A second factor that should be addressed is the nature and importance of sire by environment interactions that may exist in field data. With the widespread use of artificial insemination, sires may produce female progeny that are used in a wide variety of environmental situations. The second objective of this study was to determine the importance of sire by region, sire by herd within region, and sire by contemporary group within herd and region interactions.

REVIEW OF LITERATURE

Genotype by Environment Interactions

Dickerson (1962) stated that in the broad sense there are no independent genetic and environmental variations in animal performance. Phenotypic expressions of genotypes require a specific sequence of environments, and environmental influences are only measurable in terms of changes made in the expression of viable genotypes. Several environmental factors which can modify the phenotypic expression of genetic difference and thus produce interactions were listed. These included (1) external physical influences such as temperature and humidity, (2) maternal effects, since a dam's influence on her offspring is due to both her own genotype and her environment, (3) the social environment, which is determined by the genetic constitution of the population and the physical environment, (4) effects of the "background" genotype, which includes internal influences such as epistatic effects, dominance deviation, and sex limited traits, and (5) economic forces, such as market preferences, that may change the importance of genetic differences.

Significant estimates of sire by contemporary group or sire by herd interactions may also occur due to nonrandom mating and preferential treatment of cows. Falconer (1960) regarded this as a genotype-environment correlation. Possible causes for this extra correlation among offspring of a sire not due to genetics were presented by Bereskin and Lush (1965). Correlated environmental effects, correlations between breeding values of the mates of the sires, correlations between the breeding values of the sire and his mates, and correlations involving both environmental and genetic effects were proposed causes. Evidence of these factors was observed in Angus herds by Wilson (1983). It was found that popular AI sires were more frequently mated to older dams than to younger dams. In addition, dams that were bred artificially had significantly higher breeding value ratios for weaning weight than natural service dams.

Many studies dealing with genotype by environment have been reported. An extensive review of the literature by Pani and Lasley (1972) showed evidence of genotype by environment interactions for a number of traits in beef cattle, dairy cattle, sheep, swine, dogs, cats, mice, and poultry. The remainder of this section will deal with genotype by environment interactions for reproductive traits in cattle.

An interregional study of genotype by environment interactions in Hereford cattle was conducted in Miles City, Montana, and Brooksville, Florida. Separate lines were developed in each environment. When lines were transferred, the line of local origin exceeded the introduced line by 6.7 percent for pregnancy percentage and 6.1 percent for weaning percentage. There was no significant interaction for calf survival (Kroger et al., 1979). Significant genotype by environment interactions for birth weight and annual production per cow were found by Burns et al. (1979).

In a study reported by Kress et al. (1971), 31 pairs of identical and fraternal Hereford and Holstein twins were fed high and low energy diets. No significant set by diet interactions was found for age at first calving, age at first heat, age at first conception, number of matings per conception, or first gestation length. Using data from the same cattle, Grass et al. (1982) studied the postpartum records of these cattle and observed no significant breed by diet interactions for postpartum interval to first estrus or interval to conception.

Studies by other researchers have shown significant breed by diet interactions for reproductive traits. Howes et al. (1963) reported an interaction for interval from first mating to calving in Hereford and Brahman cattle fed two levels of protein. Wiltbank et al. (1969) found an interaction for age and weight at puberty in Angus, Hereford, and crossbred heifers on high and low diets.

Cow breed by year interactions were reported by Kroger et al. (1962) for percent calving and percent calves weaned from Brahman and British breeds. Sagebiel et al. (1969) found significant cow breed by year interactions for dystocia score using Angus, Hereford, and Charolais breeds. Sire breed by year interactions were not significant.

There is a great deal of diversity in the use of the terms "genotype by environmental interaction" and "reproductive trait." In general, experiments that have been designed to study genotype by environment interactions for reproductive traits have focused on extreme environmental differences, such as high and low energy diets, and have used very broad definitions of genotype, such as breeds or lines. Little has been reported concerning sire by environment interactions for reproductive traits in beef cattle.

Heritability

After reviewing heritability estimates for numerous reproductive traits, Preston and Willis (1970) concluded that for all practical purposes fertility will not give sufficient response to justify selection. Freeman (1984) observed that heritabilities of reproductive traits in dairy cattle are low, generally $\leq .05$ and that gains from mass selection would be minimal. Selection of sires for daughter fertility, however, could be effective when a reasonably large data base is available.

Bourdon and Brinks (1982) obtained a heritability estimate for age at first calving of $.07 \pm .09$ from data on Angus, Red Angus, and Hereford cattle. Ramsay (1964) using identical twin Holsteins reported heritabilities for age at first calving in months of .24 (13 pairs) and .07 (14 pairs).

Very little has been published concerning the heritability of age at first calving in beef cattle. Age at first calving is determined by age at puberty, time of first service, the period from first service to conception, and gestation length. Of these component traits, gestation length appears to be the most heritable. Estimates in the range of .30 to .50 were common in papers reviewed by Preston and Willis (1970) and Brinks (1984). Estimates for services per conception and length of service period were generally less than .05 for dairy studies reviewed by Freeman (1984). Beef cattle studies reviewed by Preston and Willis (1970) showed similar results. Heritability estimates for age at puberty were moderately high in papers reviewed by Brinks (1984). Estimates ranged from .20 to .67.

MATERIAL AND METHODS

Regions of the United States

To study the effects of regional differences on reproductive performance, the United States was divided into distinct geographic regions using procedures developed by Leighton (1979). Nine regions of the United States were defined and are shown in Figure 1. These regions were developed by taking into account rainfall, temperature, forage production, management practices, and terrain. Zip codes (U.S. Postal Service, 1977) were used to assign a region to each record. This use of zip codes allowed geographic regions to be free of state line boundary restrictions. The nine regions were labeled for discussion in this study as Northeast, Cornbelt, South, Gulf Coast, Upper Plains, Lower Plains, Rocky Mountains, Desert Southwest, and Pacific.

Although these regions have been used in analyses of beef cattle data in the past (Leighton, 1979; Bertrand, 1983), descriptions of situations that exist in these regions have not been presented. In an effort to justify the use of these regional definitions and to assist in interpretation of results, a study of factors that contribute to regional differences was undertaken. Table 1 and Table 2 show ranges of normal daily minimum, maximum, and average temperatures for January and July. These ranges are based on maps prepared by the U.S. Department of Commerce (1966d,e) and the U.S. Department of the Interior (1970). In general, lower temperatures in the ranges presented correspond to higher elevations and more northern areas within a region. Higher temperatures are associated with lower

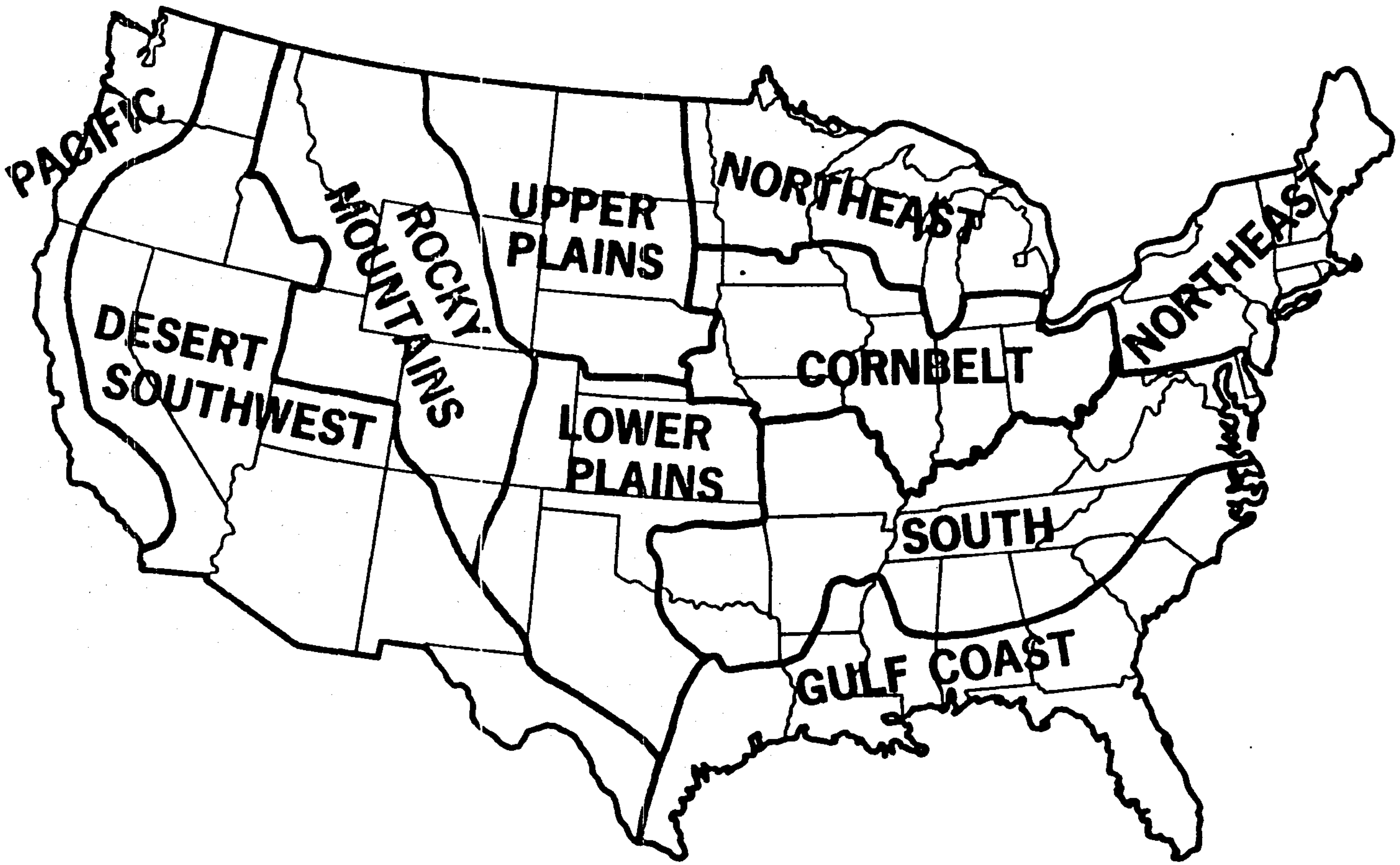

Figure 1. Boundary definitions for nine geographic regions of the United States

Table 1. Range of normal daily maximum, minimum, and average temperatures for each region in January (°F)

Region	Minimum	Maximum	Average
Northeast	0-25	20-40	10-35
Cornbelt	5-25	20-35	15-30
South	25-35	40-55	35-45
Gulf Coast	35-60	50-75	40-65
Upper Plains	-5-10	15-35	5-25
Lower Plains	15-35	35-60	30-50
Rocky Mountains	-5-15	20-35	10-25
Desert Southwest	10-50	30-70	20-60
Pacific	30-45	40-60	35-50

Table 2. Range of normal daily maximum, minimum, and average temperatures for each region in July (°F)

Region	Minimum	Maximum	Average
Northeast	55-65	75-85	60-80
Cornbelt	60-65	85-90	70-80
South	60-70	80-90	80-85
Gulf Coast	70-75	85-90	80-82
Upper Plains	55-65	80-90	70-75
Lower Plains	60-70	90-95	75-85
Rocky Mountains	40-60	70-90	55-70
Desert Southwest	45-70	70-100	60-90
Pacific	50-60	60-90	60-80

elevations and more southern areas. In addition, areas near large bodies of water tend to be less extreme in terms of both high and low temperatures. Table 3 shows ranges of normal annual total precipitation, total snowfall, and humidity for each region based on U.S. Department of Commerce (1966a,b,c) and U.S. Department of the Interior (1970) data. In

Table 3. Ranges of normal annual total precipitation, snowfall, and relative humidity for each region

Region	Precipitation[a]	Snowfall[a]	Humidity[b]
Northeast	24-48	12-100	70-80
Cornbelt	32-44	12-60	70-75
South	44-52	1-24	70-72
Gulf Coast	44-64	0-6	75-80
Upper Plains	12-20	24-36	60-70
Lower Plains	20-36	2-24	60-70
Rocky Mountains	16-32	24-100	60-70
Desert Southwest	8-24	0-100	20-70
Pacific	16-64	0-60	50-80

[a]Presented in inches.

[b]Presented as a percentage.

preparation for these tables, extreme values were encountered that are not typical for a given region. These values are associated with isolated areas such as mountain peaks and are not included in ranges presented.

Semple et al. (1934) divided the United States into five main pasture regions based on climatic adaptation of forage plants. These regions were subdivided to indicate adaptability of particular grasses and legumes. The United States can be divided by the 99th meridian into the arid west and the humid east. The arid west which includes the Upper Plains, Lower Plains, Rocky Mountains, Desert Southwest, and Pacific is characterized by predominantly native pastures. The humid east which includes the Northeast, Cornbelt, South, and Gulf Coast is characterized by introduced pasture plants. Of an estimated 865 million acres of land grazed in the United States, about 82 percent is located in the 17 states that are included in the arid west (Sprague, 1974). Most of the grazing land in the eastern United States is owned by private interest, while 48 percent of the land area of the 11 western states is federally owned, and domestic livestock graze on 73 percent of this area (Ensminger, 1976). More detailed descriptions of individual regions are given below.

Northeast

The Northeast is characterized by four main types of terrain: mountainous, upland plateau, lowland plain, and ridge and valley. This relatively rough topography makes small fields common. Soils are generally acidic and relatively infertile (Brady et al., 1957). The Northeast has a humid climate, with precipitation distributed throughout the year. Temperatures are cool through much of the year, and only the most winter-hardy forages may be safely grown in northern areas. Through most of the Northeast, the last freeze of the year occurs during May, and the first freeze occurs during late September or October (U.S. Department of the Interior, 1970). Kentucky bluegrass is the region's most important grass in improved permanent pastures and is often grown in combination with legumes such as red clover, white clover, and birdsfoot treefoil. Other important pasture grasses include timothy, orchardgrass, Reed canarygrass, and smooth bromegrass. Alfalfa, either alone or with grass, is used for hay production and to some extent for pasture (Heath et al., 1973). The western boundary of this region is also the western boundary of the major producing areas for birdsfoot treefoil, red clover, white clover, Kentucky bluegrass, and timothy.

Cornbelt

Most of the land in the Cornbelt is level to gently rolling. Soils are generally medium to fine in texture with good moisture holding capacity. They were formed primarily from glacial materials under prairie vegetation. They are high in organic matter and relatively fertile (Pierre and Riecken, 1957). As shown in Table 3, rainfall in the Cornbelt is 32-44 inches annually; however, the drier western section gets about 75 percent of its total from April to September while forages are growing. The last freeze normally occurs in late April or early May with the first freeze occurring in October (U.S. Department of the Interior, 1970). As in the Northeast, primarily cool season grasses and legumes are grown in the Cornbelt. Forage legumes include crown vetch, birdsfoot treefoil, alfafla, red clover, and white clover. Forage grasses are smooth brome, orchard grass, tall fescue, Reed canarygrass, timothy, and Kentucky bluegrass (Wedin and Vetter, 1970). Crop residues are also an important feed source in this region. A common management practice in the Cornbelt is to use land not suitable for grain production as summer pasture for cattle. After grain is harvested, cattle are allowed to glean stubble and cornstalk fields. Red clover, white clover, birdsfoot treefoil, Kentucky bluegrass, and timothy do not grow well west of the Cornbelt. Smooth brome, timothy, and birdsfoot treefoil are not common below the southern boundary of the region (Heath et al., 1973).

South

The topography of the South varies considerably from the mountainous Appalachians to the alluvial plain of the Mississippi Valley. Soils throughout most of the region developed under deciduous forest. These soils tend to have an acid surface layer that is light in color, low in organic matter, and relatively high in clay content. Subsoils are generally high in clay content (Winters, 1957). While total rainfall is greater than 40 inches, it is irregularly distributed, and droughts may be frequent. Most of the South experiences its last freeze in April with the first freeze of the fall in late October (U.S. Department of the Interior, 1970). In general, temperate species grow well throughout most of this region. Perennial mixes that include either Kentucky bluegrass or orchard grass along with legumes such as white clover and alfalfa are predominant in the northern areas; however, cool season plants such as Kentucky bluegrass can be injured by high soil temperatures in the southern areas. The boundaries of this region encompass the best growing areas in the United States for orchard grass and tall fescue. Bermudagrasses are common to the South. Midland bermudagrass grows up to the northern boundary while Costal, which is not as cold-hardy, only grows in southern areas. The grazing season in the South is often extended by the use of crimson clover and ryegrasses. Small grains can be planted for winter grazing in much of the lower South.

Gulf Coast

Topography of the Gulf Coast is gently rolling to hilly. Soils were developed predominantly from marine sands and clays. Upland soils have sandy surfaces with clay subsoils. These soils are low in organic matter, acid and relatively infertile (Pearson and Ensminger, 1957). Some areas of the Gulf Coast receive over 60 inches of rain annually, however, between 50 and 70 percent of this falls from October to March. This uneven distribution of rainfall along with the restricted water holding capacity of sandy soils mean that moisture is often deficient for forage growth in some periods of the summer. The last freeze normally occurs in March except for areas in southern Florida. The first freeze in the fall occurs in November (U.S. Department of the Interior, 1970). Of the warm-season perennial forages grown in the Gulf Coast, bermudagrass and bahiagrass are the most important. Costal and common bermudagrass are grown throughout the region while Costalcross-1 is winter-hardy only in the southern parts. Bahiagrass pastures are found in all areas of the Gulf Coast but are not commonly found outside of this region. Although johnsongrass is generally considered a weed in much of the region, it is an important source of forage in the Black Belt area of Alabama and Mississippi. Dallisgrass and carpetgrass are also widely grown (Heath et al., 1973). Due to the mild climate, temporary pastures of fall-sown grains are grown in the Gulf Coast for fall, winter, and early spring grazing. Over seeding crimson clover, arrowleaf clover, red clover, or ryegrass into perennial pastures for winter and early spring grazing is also common. Forages that are restricted to this region alone include carpetgrass, bahiagrass, and arrowleaf clover.

Upper Plains

Topography of the Upper Plains generally permits cultivation. Some steeply sloping land does occur in the Sandhills of Nebraska and around the Black Hills of South Dakota. Soils vary from dark brown in color with moderately high organic matter to sandy with relatively low organic matter (Norum et al., 1957). Of the less than 20 inches of annual precipitation, about 75 percent comes from April through September. In the Upper Plains, the normal freeze-free period extends from May into September (U.S. Department of the Interior, 1970). The eastern boundary of the Upper Plains is near the 99th meridian which divides the native short-grass country on the west from the regions of tall native and introduced grasses. Due to this combination of topography, soil, climate, and native vegetation, most agriculture is devoted to the production of spring wheat and range livestock. Grasses of this region may be divided into two categories based on the season in which they grow best. Bromegrasses, wheatgrasses, bluegrasses, and needlegrasses grow well during spring and fall. Bluestems, switchgrass, indiangrass, grama, and buffalograss are best suited for grazing during the warm summer months (Heath et al., 1973).

Lower Plains

Most of the Lower Plains is gently rolling. A diversity of soils has developed across the region. Reddish prairie soils of the east give way to lighter and shallower soils in the west (Hobbs, 1957). The climate is semiarid, but adequate moisture is available for the production of winter wheat. The Lower Plains has its last freeze during April or May. The first freeze of the fall normally occurs in October (U.S. Department of the Interior, 1970). Many of the grasses that grow well in the Upper Plains extend into the Lower Plains. Western wheatgrass, bluestems, grama, and switchgrass are common pasture grasses of this region. Costal and midland bermuda grass can be grown in the more southern areas. Large areas of land in the Lower Plains are under irrigation, and alfalfa represents the most important irrigated forage crop (Heath et al., 1973). The use of crop residues is common during the fall season. Winter wheat pastures are an important source of forage during the fall and winter.

Desert Southwest

Topography of the Desert Southwest is varied, ranging from desert areas to mountains. Soils are generally low in organic matter, light in color, and alkaline in reaction. Due to low levels of precipitation, very little leaching occurs, and soils are generally rich in minerals (Thorne, 1957). Most of this land is federally owned and is used for livestock production. Through most of the region, rainfall is inadequate for crop production. The last freeze occurs from April to June. The first freeze of the fall occurs from late September to November (U.S. Department of the Interior, 1970). Native vegetation over much of the rangelands consists of bunch grasses and shrubs. Cattle graze these rangelands during the appropriate season, and supplemental feed is grown under irrigation. Alfalfa is the most important irrigated forage crop. Many different types of sorghums are also grown under irrigation. Perrenials that are grown under irrigation include bermuda grass, wheat grasses, and brome.

Rocky Mountains

The Rocky Mountains can best be described as a land of extremes. Great variations in topography occur within short distances. Almost every major soil group in the United States exists in this region (Thorne, 1957).

Fluctuations in temperature and precipitation are also greater than in other regions. In general, the last freeze of the spring occurs from May to June, and the first freeze of the fall normally occurs in September. Many mountain rangelands are only accessible in summer. Cattle usually winter at the home ranch in lower elevations. They are pastured during the spring and fall on hay meadows at slightly higher elevations. During summer, cattle are moved to higher elevation rangeland. Common forage grasses include wheat grasses, bluestems, and other native grasses. Alfalfa is the most important seeded hay crop and is produced on both irrigated land and dryland. In recent years, many grasses and legumes common in the eastern United States have been introduced for use under irrigation.

Pacific

Topography of the Pacific is mountainous in the north giving way to more gently sloping land in the south. Soils of the northern sections are acidic. Alkaline soils appear in southern sections (Cheney, 1957; Aldrich, 1957). Much of the northern area may be classified as subhumid while the southern areas are more arid. Even in the areas of higher rainfall, however, summers are usually very dry. The last freeze of spring occurs from late March to May with the first freeze of fall occurring from October to December. Throughout the Pacific region, forested rangelands provide a considerable amount of grazing. Due to the subhumid climate, many of the forages common to the eastern United States, such as orchard grass, fescue, rye grass, timothy, birdsfoot treefoil, and white clover, can be grown in the northern Pacific region. Irrigated pastures are common throughout the region. In the more arid southern areas, bermuda grass, annual rye grasses, and sorghums are grown under irrigation. Alfalfa is an important hay crop throughout the Pacific.

Description of Data

Performance records and pedigree information for 805,922 Angus calves born between 1972 and 1982 were provided for statistical analysis by the American Angus Association. These data were recorded by cattleman participating in the Angus Herd Improvement Record program.

The objectives of this study were to examine the effects of sire by region, sire by herd within region, and sire by contemporary group within herd and region interactions and to estimate the heritability of age at first calving.

Age at first calving was defined as the total number of days between the birth date of a dam and the birth date of her first calf. Records with age at first calving values of less than 1,004 days were used for estimation of variance components. These values were consistent with the 2-year-old age of dam classification recommended by the Beef Improvement Federation (1981).

Contemporary groups were defined by herd code and weaning date of the calf. No direct indiction of breeding season was available. It was assumed that calves within a herd that were weaned on the same date were products of the same breeding season.

A series of steps was required to produce the final data set used for estimation of variance components. Data were first edited to remove embryo transfer and twin records, and records with missing dam registration, birth date, herd code, sex code, zip code or weaning date information. Pedigree information was then used to match sires to records of their daughters. Region codes were assigned based on zip codes. Records from outside the contiguous United States were detected. The data were then edited to include only records from sires with daughters in at least two regions. In addition, each contemporary group was required to contain records from at least two sires with at least two records per sire. Editing the data in this manner reduced the size of the data set without removing cells that would contribute to the estimation of interaction and error variance components. Table 4 contains the number of sires, herds, contemporary groups within herd, herd by sire cells, contemporary group within herd by sire cells, and total records in each region after the data were edited.

Table 4. Description of data for the estimation of variance components

Region	Records[a]	Herds	Contemporary groups	Sires[b]	Herd by sire cells	C. group by sire cells
Northeast	1540	36	136	163	230	357
Cornbelt	3814	66	297	301	552	890
South	1722	37	155	178	260	434
Gulf Coast	927	11	67	79	88	193
Upper Plains	4142	67	265	285	507	815
Lower Plains	2164	53	217	241	382	569
Rocky Mountains	2413	41	149	167	265	443
Desert Southwest	1104	20	79	115	147	240
Pacific	126	6	18	25	26	38

[a]Number of records in each region after the data were edited.

[b]Total number of sires across regions = 590.

Model

In this study, the following model was used:

$$Y_{ijklm} = \mu + R_i + H_{ij} + C_{ijk} + S_l + RS_{il}$$
$$+ HS_{ijl} + CS_{ijkl} + e_{ijklm}$$

Y_{ijklm} = the observation of the m^{th} daughter of the l^{th} sire in the k^{th} contemporary group in the j^{th} herd in the i^{th} region,

μ = overall mean,

R_i = the fixed effect of the i^{th} region,

H_{ij} = the fixed effect of the j^{th} herd in the i^{th} region,

C_{ijk} = the fixed effect of the k^{th} contemporary group in the j^{th} herd in the i^{th} region,

S_l = the random effect of the l^{th} sire,

RS_{il} = the random effect of the interaction of the i^{th} region and the l^{th} sire,

HS_{ijl} = the random effect of the interaction of the j^{th} herd in the i^{th} region and the l^{th} sire,

CS_{ijkl} = the random effect of the interaction between the k^{th} contemporary group in the j^{th} herd in the i^{th} region and the l^{th} sire,

e_{ijklm} = random error.

It was assumed that:

$E[Y] = XB$ where B represents the fixed effects of the model.

$E[S_l] = E[RS_{il}] = E[HS_{ijl}] = E[CS_{ijkl}] = E[e_{ijklm}] = 0.$

$$\mathrm{Var}\begin{bmatrix} S \\ RS \\ HS \\ CS \\ e \end{bmatrix} = \begin{bmatrix} I\sigma_S^2 & 0 & 0 & 0 & 0 \\ & I\sigma_{RS}^2 & 0 & 0 & 0 \\ & & I\sigma_{HS}^2 & 0 & 0 \\ & & & I\sigma_{CS}^2 & 0 \\ & & & & I\sigma_e^2 \end{bmatrix}$$

Statistical and Computational Procedures

Variance components were estimated using an approximate procedure outlined by Henderson (1980), referred to as Henderson's New Method. Additional information was obtained from Schaeffer (1983) and Henderson (1984). The computational advantage of using Henderson's New Method in this study was that inverses of large nondiagonal matrices were not required. A brief, general outline of the steps required for the estimation of variance components by Henderson's New Method is as follows:

Step 1: Obtain prior estimates of the ratio of σ_e^2 to the components of interest.

Step 2: Compute an estimate for σ_e^2.

Step 3: Set up the least squares equations.

Step 4: Absorb the fixed effects into the random effects.

Step 5: Select an approximation to the best linear unbiased predictors.

Step 6: Compute quadratic forms from the vector of approximations in Step 5.

Step 7: Find the expectations of the quadratic forms of Step 6.

Step 8: Equate the quadratic forms to their expectations and solve for the variance component estimates.

Step 9: If an iterative solution is desired, use the estimates found in Step 8 to replace those in Step 1. Continue the iterative process until the estimates converge.

Details of the specific procedures used in this thesis are given below. Left of diagonal elements are not displayed for symmetric matrices.

Prior estimates of variance components

Prior estimates are often obtained from previous research. Prior estimates of variance components could not be found in the literature for the model used in this study. For this reason, estimates of σ_e^2/σ_S^2, σ_e^2/σ_{RS}^2, σ_e^2/σ_{HS}^2, and σ_e^2/σ_{CS}^2 had to be obtained using a procedure that does not require prior estimates. A small data set containing 1700 records was created from the edited data. Components of variance were estimated by MIVEQUE(0) (SAS, 1982) from the mixed model previously listed. Estimates for σ_e^2/σ_S^2, σ_e^2/σ_{HS}^2, and σ_e^2/σ_{CS}^2 were 50, 15, and 2, respectively. A negative estimate for σ_{RS}^2 was obtained. It was assumed that the true value of σ_{RS}^2 was near zero, therefore, a relatively high value of 100 was used for σ_e^2/σ_{RS}^2.

Estimation of error variance

Estimation of error variance is independent of estimates of other variance components when Henderson's new method is used. Henderson (1980) states that any logical estimator of σ_e^2 may be used. In this study, the within smallest subclass mean square was an appropriate estimator. This estimate for σ_e^2 is given by the following equation:

$$\sigma_e^2 = \frac{\sum_{ijklm}(Y_{ijklm} - Y_{ijkl\cdot}/N_{ijkl\cdot})^2}{\sum_{ijkl}(N_{ijkl\cdot} - 1)}$$

Least squares equations and absorption

Least squares equations for the model are given by equation 1, where

X_R = the incidence matrix for region effects,

X_H = the incidence matrix for herd within region effects,

X_C = the incidence matrix for contemporary group within herd effects,

Z_S = the incidence matrix for sire effects,

Z_{RS} = the incidence matrix for region by sire effects,

Z_{HS} = the incidence matrix for herd within region by sire effects,

Z_{CS} = the incidence matrix for contemporary group within herd by sire effects,

$\hat{b}_R$, $\hat{b}_H$, $\hat{b}_C$, $\hat{u}_S$ $\hat{u}_{RS}$, $\hat{u}_{HS}$, $\hat{u}_{CS}$ = the vector of solutions corresponding to the subscripts,

Y = the vector of observations.

$$\begin{bmatrix} X_R'X_R & X_R'X_H & X_R'X_C & X_R'Z_S & X_R'Z_{RS} & X_R'Z_{HS} & X_R'Z_{CS} \\ & X_H'X_H & X_H'X_C & X_H'Z_S & X_H'Z_{RS} & X_H'Z_{HS} & X_H'Z_{CS} \\ & & X_C'X_C & X_C'Z_S & X_C'Z_{RS} & X_C'Z_{HS} & X_C'Z_{CS} \\ & & & Z_S'Z_S & Z_S'Z_{RS} & Z_S'Z_{HS} & Z_S'Z_{CS} \\ & & & & Z_{RS}'Z_{RS} & Z_{RS}'Z_{HS} & Z_{RS}'Z_{CS} \\ & & & & & Z_{HS}'Z_{HS} & Z_{HS}'Z_{CS} \\ & & & & & & Z_{CS}'Z_{CS} \end{bmatrix} \begin{bmatrix} \hat{b}_R \\ \hat{b}_H \\ \hat{b}_C \\ \hat{u}_S \\ \hat{u}_{RS} \\ \hat{u}_{HS} \\ \hat{u}_{CS} \end{bmatrix} = \begin{bmatrix} X_R'Y \\ X_H'Y \\ X_C'Y \\ Z_S'Y \\ Z_{RS}'Y \\ Z_{HS}'Y \\ Z_{CS}'Y \end{bmatrix} \tag{1}$$

In a hierarchical analysis, absorption of the lowest order fixed effects will eliminate any higher effects in the hierarchy. Therefore, it was only necessary to absorb contemporary group effects in this analysis. Absorption of contemporary group effects resulted in the following equations:

$$\begin{bmatrix} Z_S'MZ_S & Z_S'MZ_{RS} & Z_S'MZ_{HS} & Z_S'MZ_{CS} \\ & Z_{RS}'MZ_{RS} & Z_{RS}'MZ_{HS} & Z_{RS}'MZ_{CS} \\ & & Z_{HS}'MZ_{HS} & Z_{HS}'MZ_{CS} \\ & & & Z_{CS}'MZ_{CS} \end{bmatrix} \begin{bmatrix} \hat{u}_S \\ \hat{u}_{RS} \\ \hat{u}_{HS} \\ \hat{u}_{CS} \end{bmatrix} = \begin{bmatrix} Z_S'MY \\ Z_{RS}'MY \\ Z_{HS}'MY \\ Z_{CS}'MY \end{bmatrix} \qquad (2)$$

where

$$M = I - X_C'(X_C'X_C)^{-1}X_C' \ .$$

Since $X_C'X_C$ was a diagonal matrix, $(X_C'X_C)^{-1}$ was easy to calculate. It was possible to derive formulas for all of the coefficients in the submatrices of equation 2.

$$Z_S'MZ_S = \text{Each } S_1S_1 \text{ element} = \sum_{ijk}\left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}}\right) .$$

$$\text{Each } S_1S_{1'} \text{ element} = -\sum_{ijk} \frac{N_{ijkl\cdot}N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} \ .$$

$$Z_S'MZ_{RS} = \text{Each } S_1R_iS_1 \text{ element} = \sum_{jk}\left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}}\right) .$$

$$\text{Each } S_1R_iS_{1'} \text{ element} = -\sum_{jk} \frac{N_{ijkl\cdot}N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} \ .$$

$$Z_S'MZ_{HS} = \text{Each } S_l H_{ij} S_l \text{ element} = \sum_k \left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} \right).$$

$$\text{Each } S_l H_{ij} S_{l'} \text{ element} = -\sum_k \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z_S'MZ_{CS} = \text{Each } S_l C_{ijk} S_l \text{ element} = N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} .$$

$$\text{Each } S_l C_{ijk} S_{l'} \text{ element} = - \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z_{RS}'MZ_{RS} = \text{Each } R_i S_l R_i S_l \text{ element} = \sum_{jk} \left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} \right).$$

$$\text{Each } R_i S_l R_i S_{l'} \text{ element} = - \sum_{jk} \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z_{RS}'MZ_{HS} = \text{Each } R_i S_l H_{ij} S_l \text{ element} = \sum_k \left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} \right).$$

$$\text{Each } R_i S_l H_{ij} S_{l'} \text{ element} = -\sum_k \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z_{RS}MZ_{CS} = \text{Each } R_i S_l C_{ijk} S_l \text{ element} = N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} .$$

$$\text{Each } R_i S_l C_{ijk} S_{l'} \text{ element} = - \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z_{HS}'MZ_{HS} = \text{Each } H_{ij} S_l H_{ij} S_l \text{ element} = \sum_k \left(N_{ijkl\cdot} - \frac{N_{ijkl\cdot}^2}{N_{ijk\cdot\cdot}} \right).$$

$$\text{Each } H_{ij} S_l H_{ij} S_{l'} \text{ element} = -\sum_k \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z'_{HS}MZ_{CS} = \text{Each } H_{ij}S_lC_{ijk}S_l \text{ element} = N_{ijkl\cdot} - \frac{N^2_{ijkl\cdot}}{N_{ijk\cdot\cdot}} .$$

$$\text{Each } H_{ij}S_lC_{ijk}S_{l'} \text{ element} = - \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z'_{CS}MZ_{CS} = \text{Each } C_{ijk}S_lC_{ijk}S_l \text{ element} = N_{ijkl\cdot} - \frac{N^2_{ijkl\cdot}}{N_{ijk\cdot\cdot}} .$$

$$\text{Each } C_{ijk}S_lC_{ijk}S_{l'} \text{ element} = - \frac{N_{ijkl\cdot} N_{ijkl'\cdot}}{N_{ijk\cdot\cdot}} .$$

$$Z'_{S}MY \text{ elements} = \sum_{ijk} \left(Y_{ijkl\cdot} - \frac{N_{ijkl\cdot}}{N_{ijk\cdot\cdot}} Y_{ijk\cdot\cdot} \right) .$$

$$Z'_{RS}MY \text{ elements} = \sum_{jk} \left(Y_{ijkl\cdot} - \frac{N_{ijkl\cdot}}{N_{ijk\cdot\cdot}} Y_{ijk\cdot\cdot} \right) .$$

$$Z'_{HS}MY \text{ elements} = \sum_{k} \left(Y_{ijkl\cdot} - \frac{N_{ijkl\cdot}}{N_{ijk\cdot\cdot}} Y_{ijk\cdot\cdot} \right) .$$

$$Z'_{CS}MY \text{ elements} = Y_{ijkl\cdot} - \frac{N_{ijkl\cdot}}{N_{ijk\cdot\cdot}} Y_{ijk\cdot\cdot} .$$

All elements not listed for the above submatrices were equal to zero. All of the elements of the left hand side matrix in equation 2 can be derived from sums of rows and columns of $Z'_{CS}MZ_{CS}$. All of the elements of the right hand side of equation 2 can be derived from $Z'_{CS}MY$. Therefore, it was not necessary to build the matrices of equation 1 in this study, and the task of building submatrices of equation 2 was simplified.

Approximation of predictors

To obtain the best linear unbiased predictor of u_i, the inverse of a large matrix would be required. An approximate solution to $\hat{u}_i$ in equation 2 is:

$$\tilde{u}_i = D_i^{-1} Z_i' MY$$

where

$$D_i = \text{Diagonal } (Z_i' MZ_i + I\sigma_e^2/\sigma_i^2)$$

for $i = 1,\ldots,4$.

Quadratic forms and expectations

There are several kinds of quadratic forms that may be used to obtain unbiased estimates. Some of these are presented by Schaeffer (1983). The quadratic forms $\tilde{u}_i'\tilde{u}_i$ were used in this study. Development of the expectations for $\tilde{u}'\tilde{u}$ follows:

$$\tilde{u}_i'\tilde{u}_i = Y'MZ_i D_i^{-2} Z_i' MY$$

$$= r_i' D_i^{-2} r_i'$$

$$= r' Q_i r$$

where

$$r = (r_i' \quad r_2' \quad r_3' \quad r_4')$$

and Q_i is a 4 x 4 partitioned matrix with D_i^{-2} in the i^{th} diagonal position and null matrices in all other positions.

$$E(r'Q_i r) = E(r')Q_i E(r) + \text{trace } (Q_i \text{Var}(r))$$

$$E(r) = E(Z'MY)$$

$$= Z'ME(Y)$$

$$
\begin{aligned}
&= Z'MXb \\
&= Z'(I - X(X'X)^{-1}X')Xb \\
&= Z'(Xb - Xb) \\
&= \phi \\
\mathrm{Var}(r) &= \mathrm{Var}(Z'MY) \\
&= Z'M\,\mathrm{Var}(Y)MZ \\
&= Z'MV(Z_1u_1 + Z_2u_2 + Z_3u_3 + Z_4u_4 + e)MZ \\
&= \sum_{i=1}^{4} Z'MZ_iZ_i'MZ\sigma_i^2 + Z'MZ\sigma_e^2 \\
&= \sum_{i=0}^{4} C_i\sigma_i^2
\end{aligned}
$$

where

$$C_i = Z'MZ_iZ_i'MZ\sigma_i^2 \ ,$$

$$\sigma_0^2, \sigma_1^2, \sigma_2^2, \sigma_3^2, \sigma_4^2 = \sigma_e^2, \sigma_S^2, \sigma_{RS}^2, \sigma_{HS}^2, \sigma_{CS}^2$$

respectively.

$$
\begin{aligned}
E(r'Qr) &= 0 + \mathrm{trace}(Q_i \sum_{i=0}^{4} C_i\sigma_i^2) \\
&= \sum_{j=0}^{4} \mathrm{trace}(Q_iC_j\sigma_j^2)
\end{aligned}
$$

Solutions

Solutions were obtained by solving the following set of simultaneous equations:

$$\begin{bmatrix} tr(Q_1C_1) & tr(Q_1C_2) & tr(Q_1C_3) & tr(Q_1C_4) & tr(Q_1C_0) \\ tr(Q_2C_1) & tr(Q_2C_2) & tr(Q_2C_3) & tr(Q_2C_4) & tr(Q_2C_0) \\ tr(Q_3C_1) & tr(Q_3C_2) & tr(Q_3C_3) & tr(Q_3C_4) & tr(Q_3C_0) \\ tr(Q_4C_1) & tr(Q_4C_2) & tr(Q_4C_3) & tr(Q_4C_4) & tr(Q_4C_0) \end{bmatrix} \begin{bmatrix} \hat{\sigma}^2_S \\ \hat{\sigma}^2_{RS} \\ \hat{\sigma}^2_{HS} \\ \hat{\sigma}^2_{CS} \\ \hat{\sigma}^2_e \end{bmatrix} = \begin{bmatrix} \tilde{u}_1'\tilde{u}_1 \\ \tilde{u}_2'\tilde{u}_2 \\ \tilde{u}_3'\tilde{u}_2 \\ \tilde{u}_4'\tilde{u}_4 \end{bmatrix} \tag{3}$$

Because Q_i is a diagonal matrix, only the diagonal element of C_j must be calculated to obtain the necessary traces. Development of trace (Q_1C_1) is as follows:

$$Q = \left[\begin{array}{cccc:c:c:c} q_{11} & & & & & & \\ & q_{22} & & & \Phi & \Phi & \Phi \\ & & \ddots & & & & \\ & & & q_{nn} & & & \\ \hdashline & & \Phi & & \Phi & \Phi & \Phi \\ \hdashline & & \Phi & & \Phi & \Phi & \Phi \\ \hdashline & & \Phi & & \Phi & \Phi & \Phi \end{array}\right]$$

$$= \left[\begin{array}{c|c|c|c} D_1^{-2} & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 \end{array}\right]$$

$$C_1 = Z'MZ_1Z_1'MZ$$

$$= \begin{bmatrix} Z_1'MZ_1Z_1'MZ_1 & Z_1'MZ_1Z_1'MZ_2 & Z_1'MZ_1Z_1'MZ_3 & Z_1'MZ_1Z_1MZ_4 \\ Z_2MZ_1Z_1'MZ_1 & Z_2'MZ_1Z_1'MZ_2 & Z_2'MZ_1Z_1'MZ_3 & Z_2'MZ_1Z'MZ_4 \\ Z_3MZ_1Z_1'MZ_1 & Z_3'MZ_1Z_1'MZ_2 & Z_3'MZ_1Z_1'MZ_3 & Z_3'MZ_1Z_1'MZ_4 \\ Z_4MZ_1Z_1'MZ_1 & Z_4'MZ_1Z_1'MZ_2 & Z_4'MZ_1Z_1'MZ_3 & Z_4'MZ_1Z'MZ_4 \end{bmatrix}$$

The trace of Q_1C_1 may be expressed as

$$\text{trace}(Q_1C_1) = \text{trace}(D_1^{-2}Z_1'MZ_1Z_1'MZ_1).$$

In a similar fashion, the trace of any Q_iC_j can be shown to be

$$\text{trace}(Q_iC_j) = \text{trace}(D_i^{-2}Z_i'MZ_jZ_j'MZ_i).$$

Since Q_j is a diagonal matrix, only the diagonal of $Z_i'MZ_jZ_j'MZ_i$ is needed to calculate trace (Q_iC_j). Note also that diagonal elements of $Z_i'MZ_jZ_j'MZ_i$ are simply the sum of the squared elements in each row of $Z_i'MZ_j$. Using values calculated for elements in equation 2, the coefficient of σ_j^2 in the i^{th} row of equation 3 was calculated as follows: elements of each row of the appropriate submatrix of equation 2 were squared and summed; these quantities were divided by the square of the corresponding diagonal element to which σ_e^2/σ_i^2 had been added; these quotients were then summed across rows. The coefficient of σ_e^2 in the i^{th} row of equation 3 was simply the sum of quotients produced by dividing the diagonal elements of the i^{th} diagonal submatrix of equation 2 by the square of that diagonal to which σ_e^2/σ_i^2 had been added.

Iterative solutions

Iterative solutions may be obtained using Henderson's new method; however, iteration is not required. First round solutions are unbiased while properties of variance components obtained iteratively are unknown. For this reason, both first solutions and iterative solutions are presented. First solutions were obtained using prior estimates of 50, 100, 15, and 2 for σ_e^2/σ_S^2, σ_e^2/σ_{RS}^2, σ_e^2/σ_{HS}^2, and σ_e^2/σ_{CS}^2, respectively. First solutions were used as priors for the next round of iteration. This was repeated until convergence was reached. Henderson's new method, like other unbiased procedures, can yield negative estimates. Since it is illogical to use a negative prior estimate, effects with negative variance component estimates were set equal to 0 before the next round of iteration.

Heritabilities and genetic correlations

Variance component estimates were used to estimate across region, within region, within herd, and within contemporary group heritabilities. These estimates were calculated using the following formulas:

$$\frac{4\sigma_S^2}{\sigma_P^2} = \text{across region } h^2,$$

$$\frac{4(\sigma_S^2 + \sigma_{RS}^2)}{\sigma_P^2} = \text{within region } h^2,$$

$$\frac{4(\sigma_S^2 + \sigma_{RS}^2 + \sigma_{HS}^2)}{\sigma_P^2} = \text{within herd } h^2,$$

$$\frac{4(\sigma_S^2 + \sigma_{RS}^2 + \sigma_{HS}^2 + \sigma_{CS}^2)}{\sigma_P^2} = \text{within contemporary group } h^2,$$

where

$$\sigma_P^2 = \sigma_S^2 + \sigma_{RS}^2 + \sigma_{HS}^2 + \sigma_{CS}^2 + \sigma_e^2 .$$

Dickerson (1962) suggested that when large numbers of environments are involved, it is most convenient to estimate the average degree of genetic correlation by an intraclass method. The intraclass correlation was given by Dickerson as $r_G = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2}$. In this study, the average genetic correlation of sire breeding values in different regions was estimated by $\frac{\sigma_S^2}{\sigma_S^2 + \sigma_{RS}^2 + \sigma_{HS}^2 + \sigma_{CS}^2}$. The correlation between sire breeding values in different herds within regions was estimated by $\frac{\sigma_S^2}{\sigma_S^2 + \sigma_{HS}^2 + \sigma_{CS}^2}$, and the correlation between sire breeding values in different contemporary groups within levels was estimated by $\frac{\sigma_S^2}{\sigma_S^2 + \sigma_{CS}^2}$.

Alternate models

Estimates of variance components are often obtained using simpler models than the one used in this study. Sire evaluation models usually do not contain herd, region, sire by region, or sire by herd effects. For comparison, estimates were calculated from a model including only contemporary group and error. Development of estimation procedures under this model followed the same steps outlined for the full model. Due to the hierarchical nature of the full model, the same coefficients and right hand sides for σ^2_S, σ^2_{CS}, and σ^2_e in Equation 3 could be used.

Solutions for sire variance and error variance were also obtained from a model containing only sire, contemporary group, and error. As in the above case, development of expectations and equations followed the same steps as the full model. However, estimation of error variance was accomplished in a different manner. Since interactions were no longer included, the within smallest subclass error was not appropriate. Error was estimated simultaneously with sire variance using $Y'MY$ where

$$Y'MY = Y'(I - X(X'X)^{-1}X')X$$

and

$$E(Y'MY) = tr(Z_1'MZ_1)\,{}^2_S + tr(M)\sigma^2_e .$$

The second equation needed was

$$\tilde{u}_1\tilde{u}_1 = tr(Q_1C_1)\sigma^2_S + tr(Q_1C_1)\sigma^2_e .$$

These are the same values listed in row 1 of Equation 3.

RESULTS AND DISCUSSION

Summary Statistics

In explaining the results of variance component estimation, it is helpful to know something about the population from which they arose. For this reason, a brief summary of reproductive performance in the Angus breed is presented. These summary statistics could also be useful to researchers interested in linear programming for beef systems.

Table 5 gives the distribution of age at calving in the Angus breed. The entire unedited data set was used. All of the dams of calves with recorded weaning weights in the Angus breed from 1970 to 1982 are included. Ages in years are given in whole numbers and include dams from 3 months younger than the given year to 9 months older. Percentages given in Table 5 are in close agreement with those presented by Greer et al. (1980) for dams at the Livestock and Range Research Station in Miles City, Montana. The average dam of the Angus breed is relatively young. About 60 percent of recorded calves were out of dams 5 years of age or younger, and only 6.72 percent were out of dams older than 10 years of age. Percent of previous age group in Table 5 gives an indication of the rate at which cow numbers decline with age. These percentages may be used to approximate the probability that a cow of a given age will produce a calf in the next year. This is only an approximation since dams are not necessarily culled for reproductive failure in all herds and since not all calves are registered.

Table 5. Distribution of dams in the Angus breed by age at calving

Age in years	Number observed	Percent of total	Percent of previous age group
2	140,788	17.47	-
3	130,755	16.22	92.87
4	115,430	14.32	88.28
5	97,719	12.13	84.66
6	80,959	10.01	82.85
7	65,434	8.12	80.82
8	51,659	6.06	78.95
9	39,667	4.92	76.79
10	29,258	3.63	73.76
11	20,474	2.54	69.96
12	14,047	1.74	68.61
13	8,982	1.11	64.92
14	5,324	.66	59.27
15	2,924	.36	54.92
16	1,431	.18	48.94
17	629	.08	43.96
18	263	.03	41.81
19	90	.01	34.22
$\geq$20	87	-	-

Table 6 gives the age at first calving in months for dams 20 to 40 months of age in each of the nine regions. Table 7 gives the month of the year in which calves were born. Data listed in these tables show that regional differences do exist for reproductive performance in young dams. In the Northeast, Cornbelt, Upper Plains, and Rocky Mountains, calves were produced by 58 percent, 62 percent, 69 percent, and 68 percent, respectively, of the dams listed in Table 6 by the age of 25 months. Only 30 percent of the dams in the Gulf Coast and 31 percent of the dams in the South had produced a calf in 25 months. Dams in the Lower Plains, Desert Southwest, and Pacific were intermediate with 45 percent, 53 percent, and

Table 6. Numbers of observed first calvings for dams 20 to 40 months of age by age of dam and region

Age (months)	NE	CB	S	GC	UP	LP	RM	SW	P
20	48	96	52	27	106	115	87	35	15
21	261	524	205	104	713	549	374	185	39
22	1025	2319	717	304	3405	2100	1742	772	203
23	2952	6891	1982	969	9480	5423	4993	2131	544
24	2956	6297	2469	1071	7706	5664	4051	2155	567
25	1309	2803	1966	573	2215	3180	1493	1020	421
26	590	1055	1557	470	567	1991	440	483	259
27	335	510	1404	450	200	1675	171	390	211
28	224	464	1483	406	217	1707	168	443	242
29	188	411	1361	476	309	1787	146	447	196
30	178	441	1275	487	261	1521	97	302	139
31	231	329	1084	503	153	1084	109	242	118
32	208	350	886	527	226	774	112	191	90
33	325	574	867	564	414	869	232	230	126
34	520	1076	950	603	1006	1239	553	381	161
35	1186	2386	1365	805	2884	2156	1386	752	257
36	1163	2219	1314	666	2921	2160	1584	784	256
37	593	1065	1034	396	1060	1376	641	414	192
38	263	522	733	289	280	842	200	241	145
39	153	255	542	200	121	635	78	152	98
40	124	173	547	205	81	669	66	158	91

41 percent, respectively. In regions where a large proportion of dams calved before 25 months of age, very few calved at 26 to 33 months of age. Only 16 percent, 13 percent, 7 percent, and 8 percent of the first calf dams in the Northeast, Cornbelt, Upper Plains, and Rocky Mountains, respectively, produced calves at 26 to 33 months. Calves out of 26 to 33 month-old dams accounted for 42 percent of the total in the South and 38 percent in the Gulf Coast. Again dams from the Lower Plains, Desert Southwest, and Pacific were intermediate with 30 percent, 23 percent, and 32 percent,

Table 7. Numbers of observed first calvings for dams 20 to 40 months of age by month and region

Month	NE	CB	S	GC	UP	LP	RM	SW	P
January	397	550	2564	1783	773	2025	1189	762	326
February	1007	2101	3360	1270	5539	4588	5891	2145	536
March	4234	8011	4846	1105	13611	9833	6995	3465	905
April	5009	11037	3244	485	10346	7327	3265	2078	688
May	2425	5589	1631	194	2809	4221	884	859	379
June	710	1647	581	71	413	1353	187	292	161
July	424	641	284	78	68	804	69	219	112
August	177	318	376	93	182	841	51	485	146
September	208	438	1816	1312	381	3008	98	726	486
October	103	237	1937	1206	155	1799	39	440	245
November	79	128	1616	1272	38	1088	29	279	236
December	64	98	1582	1271	30	698	38	181	157

respectively. These differences may be explained by use of data presented in Table 7, which are summarized in Table 8, and descriptions of regional differences presented earlier in this dissertation. In the Northeast, Cornbelt, Upper Plains, and Rocky Mountains, 85 percent, 87 percent, 94 percent, and 91 percent, respectively, of the dams produced a first calf during the four-month period from February through May. Only 55 percent of the dams in the South and 30 percent of those in the Gulf Coast calved during this period. In the Lower Plains, Desert Southwest, and Pacific, first calves were produced by 70 percent, 72 percent, and 57 percent, respectively, of the dams during these four months. In those regions with a higher proportion of dams calving first near two years of age, there is a well-defined calving season. Due to climatic limitations and short growing seasons for forage crops, spring calving is optimum. In these regions,

Table 8. Dams 20 to 40 months of age in each calving season as a percent of the regional total

Season	NE	CB	S	GC	UP	LP	RM	SW	P
Winter (Dec.-Jan.)	3	2	17	30	2	7	6	8	11
Early spring (Feb.-March)	35	33	35	23	56	38	69	47	33
Late spring (April-May)	50	54	20	7	38	31	22	25	24
Summer (June-Aug.)	9	8	5	2	2	8	2	8	10
Fall (Sept.-Nov.)	3	3	23	38	2	16	1	12	22

heifers that are not bred to calve as two-year-olds are unlikely to be bred until the following year. In the more southern regions, winter forages can be successfully produced, and weather is not a limitation for fall or winter calving. In these regions, heifers may be bred to calve in a different season from the one in which they were born. These management differences that exist across regions would suggest that age at first calving may have a different economic value in different regions.

Concern about maternal performance has prompted the American Angus Association to develop the Pathfinder Cow program. To be listed as a Pathfinder Cow, a dam must produce at least three calves with an average weaning weight ratio of at least 105. Reproductive requirements are that she produces a calf every 12 months and that her age at first calving is less than the herd average. Regional differences found in this study support the practice of using herd averages as a minimum standard as opposed to using a fixed age for the entire nation.

Variance Components

Variance components were estimated using Henderson's New Method. Table 9 contains estimates for sire, sire by region, sire by herd within region, sire by contemporary group within herd and region, and error variance for age at first calving. The results of iteration are also presented.

Initial estimates obtained for sire by herd within region and sire by contemporary group within herd and region variances were very large in comparison to the sire variance. These sire by environment interactions could be due to biological causes or to nonrandom treatment of daughters. The magnitude of the sire by herd within region and sire by contemporary group within herd and region interactions would suggest that daughters of different sires may not receive equal opportunities to calve at an early age. It is logical to assume that daughters of one sire may be mated to a different bull than daughters of another sire in the same contemporary group. If service sires are used at different times or if some service sires are used in natural service while others are used for artificial insemination, sire by management interactions may result. Contemporary group definitions were based on weaning dates of the calves. A better definition of contemporary groups could probably be found which would reduce the sire by contemporary group interaction. At the present time, information on time of breeding is not recorded.

Table 9. Variance components from Henderson's New Method and results of iteration

	Variance Components				
	σ^2_S	σ^2_{RS}	σ^2_{HS}	σ^2_{CS}	σ^2_e
Initial estimate[a]	20.1	-212.7	293.9	581.8	1532.6[b]
	Interative Estimates				
Round 2	-59.0	0[c]	319.6	406.0	1532.6
Round 3	0	0	321.7	320.6	1532.6
Round 4	0	0	351.9	275.7	1532.6
Round 5	0	0	619.1	-1.1	1532.6

[a]Prior values used were: $\sigma^2_e/\sigma^2_S = 50$, $\sigma^2_e/\sigma^2_{RS} = 100$, $\sigma^2_e/\sigma^2_{HS} = 15$, $\sigma^2_e/\sigma^2_{CS} = 2$.

[b]Error variance was estimated by the within smallest subclass mean square.

[c]Negative component from previous round was set to 0.

A large negative sire by region variance component was found. The same problem was reported by Bertrand (1983) for sire by region estimates for birth weight and postweaning gain from Polled Hereford field data. Negative components are possible with any of the unbiased estimation procedures. A negative estimate for sire by region is probably due to large sampling error. Schaeffer (1983) stated that the preferred option in dealing with negative estimates is to leave the results as they are. Setting negative estimates to zero, removing the factor from the model, or using another estimation procedure will bias future summaries of estimates.

Variance estimates failed to converge to positive values when iteration was attempted. Properties of iterative solutions to Henderson's New Method are unknown. There is nothing inherent in the procedure that would guarantee convergence to positive estimates. Peculiarities probably existed in the data set used that caused this divergence. Data were highly unbalanced, and there were large numbers of missing subcells. These factors can cause problems in any iterative procedure. A wide range of prior values was used to determine if convergence could be obtained. Using priors of 2 for all of the variance ratios and priors of 200 for all of the variance ratios was tried. The variance component estimates for sire were small. The variances of sire by contemporary group within herd and region were large. Sire by herd within region estimates were intermediate, and sire by region estimates were negative. Iteration on these values did not produce convergence. In general, use of a wide range of prior values resulted in low or negative estimates for sire variance, negative estimates for sire by region variance, and relatively large estimates for sire by herd within region and sire by contemporary group within herd and region. While these results show that different estimates may be produced by the use of different priors, these estimates would lead to the same general conclusions as estimates in Table 9.

Sire evaluation models often include contemporary group, sire, sire by contemporary group, and error. Estimates of sire and sire by contemporary group variances are needed for these models. Since the fixed effects in the model used in this thesis are nested, a reduced model containing only contemporary group, sire, sire by contemporary group, and error yielded the same estimate for sire variance as presented in Table 9 when the same priors for sire and sire by contemporary group were used. The sire by contemporary group estimate from the reduced model was equal to the sum of the interaction variance components.

Sire variance was obtained using a model containing only sire, contemporary group, and error. An initial prior value for σ_e^2/σ_s^2 of 50 was used. Initial estimates for sire and error were 132 and 1872, respectively. After six rounds of iteration, estimates converged to 272 for sire variance and 1783 for error variance. The increase in sire variance from previous models was probably due to the failure to account for sire by environment interactions. Sire variance in this case would contain variance due to management practices in addition to genetic variance.

Data used in this study were highly unbalanced, subclasses were small, and there were many missing subcells. Variance component estimates may reflect these problems. With nonorthogonal data, the precision of estimates for higher effects is not as great as the precision of estimates for lower effects in a nested model. This may account for negative estimates of variance for sire by region interaction and for inflated estimates of sire by contemporary group interaction. These problems may also account for the failure of components to converge during iteration. Sampling variances of the estimates would be high due to the structure of the data.

The estimation procedure used in this thesis is only one of several available procedures. Henderson's New Method was chosen because inverses of large matrices were not required. This allowed for the use of a large proportion of the available data. Editing in this study was restricted to the removal of data that did not contribute to the estimation of sire by region and error components. Estimations of variance components are often made using small, selected data sets. This has the advantage of reducing computational effort or allowing for the use of elaborate models or procedures. A disadvantage of this practice is that estimates may not be applicable to the entire population. Use of the entire data set also has disadvantages. Many records in field data do not contribute to the estimation of variance components. Subcells with single records are lost in absorption routines, therefore, use of the entire data set often requires unnecessary computations. Editing procedures used in this study were chosen as a compromise between the two extremes.

Heritability

Heritability of age at first calving across regions was .04. This is near the estimate of .07 reported by Bourdon and Brinks (1982) and is consistent with generally low heritability estimates for reproductive traits summarized by Preston and Willis (1974) and Freeman (1984). The estimate of across herd heritability was -.35. A negative estimate was due to the large negative sire by region variance component estimate. Within herd and within contemporary group heritability estimates were .18 and 1.23, respectively. These estimates are probably not a true reflection of genetic parameters for the Angus breed. For estimation of within herd and within contemporary group heritability, sire by herd within region, and sire by contemporary group within herd and region variance components were included as part of the genetic variance. These interactions are probably due in part to nonrandom treatment of daughters. This would tend to produce an upward bias in the estimates.

Heritability of age at first calving, using variance components from a model with no interaction effects, was .53. This estimate is larger than would be expected and may be due to unequal management of daughters of sires.

Intraclass Correlations

Dickerson (1962) recommended an intraclass correlation method for the estimation of genetic correlations. An estimate of -.10 for the correlation of sire breeding value estimates across regions was obtained. The negative value is due to a negative estimate for sire by region interaction. The genetic correlations among sire breeding values across herds within a region and across contemporary groups within a herd were .20 and .03, respectively. These results indicate that estimation of breeding values would be highly unsatisfactory if sire by environment interaction effects are not included in an evaluation model. These estimates may be biased due to the unbalanced structure of the data and unequal variance across regions.

CONCLUSIONS AND SUGGESTIONS

Reproductive traits are generally lowly heritable. Progress from mass selection would be minimal; however, evaluation of superior sires through progeny testing may be possible. To develop such an evaluation, estimates of genetic parameters and evaluations of the nature and importance of sire by environment interactions are needed. In the study, the across region heritability for age at first calving was .04. Large sire by herd within region and sire by contemporary group within herd interactions were observed.

A general conclusion that may be drawn from this study is that age at first calving, from available field data, would be a poor choice of traits for use in sire evaluation. Many problems would exist in the use of age at first calving. Since the trait is only observed on first calf dams, only about 17 percent of the performance records could be used for the evaluation, and these records are poorly distributed. This along with a low heritability would make high accuracies difficult to obtain. Sire by environment interactions would also have to be considered. Part of the large sire by contemporary group interaction may be due to an incorrect definition of contemporary groups. Angus performance records were designed for the evaluation of growth traits, and information that would allow for good contemporary group definitions for age at first calving is lacking. Information on the date at which a heifer was first exposed would be helpful.

More work is needed before suitable evaluations of reproductive performance are possible. Information that exists in Angus field data on reproduction is generally related to the birth dates of calves. Date of first calving is a component of age at first calving and would probably produce some of the same types of problems in analysis. Calving intervals may also present problems. As shown in this study, there is a rapid decline in cow numbers as age increases. Cows may be removed for reasons other than reproductive failure, therefore, reproductive traits observed on older cows may be biased due to selection for other traits. The fact that a cow is still in the herd at an advanced age indicates that previous reproductive selection has taken place. It is doubtful that calving interval on young dams is the same trait as calving interval on old dams, because of this selection. An evaluation of calving intervals and selection bias associated with age of dam is needed.

A major problem that exists in the evaluation of reproductive performance is that field data are not designed for this purpose. Any dam listed in field data has achieved reproductive success. Dams that currently are not recorded may be the key to successful evaluation. The reproductive failure of daughters of a sire has a larger economic impact than the relative time at which successful daughters calve. Recording systems for use in the evaluation of reproductive performance should include records on all heifers and cows that are exposed. Data that would be useful would include: birth date of the dam, date of first exposure, date of last exposure, breeding date if known, birth date of calf or reason that calf was not produced, type of service, and service sire. Most of the above data is easy to obtain and is already recorded on many farms. An effort needs to be made to get these data into central data banks. This would be of great benefit for any future work on reproduction.

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