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DWAYNE D. FAIDLEY

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B. Dennis Banks
Major professor

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GENETIC AND COMPOSITION EFFECTS ON REPRODUCTIVE FITNESS TRAITS IN YEARLING LIMOUSIN CATTLE

By

Dwayne D. Faidley

A THESIS

Submitted to Michigan State University in partial fulfillment of the requirements
for the degree of

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ABSTRACT

GENETIC AND COMPOSITION EFFECTS ON REPRODUCTIVE FITNESS TRAITS IN YEARLING LIMOUSIN CATTLE

By

Dwayne D. Faidley

Fertility, fleshing ability, and muscularity are three traits vital to breeders of Limousin cattle. While muscularity is a recognizable breed strength, fertility traits and fleshing ability are considered breed deficiencies in many production settings. Breeders are striving to improve inherent fertility through genetic selection, realizing reproductive traits are low to moderately heritable. Expressed reproductive efficiency is being stressed through a combination of genetic selection and management using body condition scores. Although enhanced reproductive fitness is a primary objective, breeders have determined beef industry necessities dictate preservation of Limousin muscularity advantages.

Age, weight, and increased body condition favorably affected many phenotypic measures of reproductive traits in both bulls and heifers. Moderate and heavy muscled heifers were superior to light muscled heifers for yearling fertility traits. Muscular bulls, however, had the smallest scrotal circumferences. Genetic effects of sire were important in their male progeny and comparable to similar analyses. Bivariate analyses provided methods to estimate sire effects on male and correctly account for female traits simultaneously. Heritability estimates were low, but in the range found in the literature. Genetic correlations between fertility indicators in yearling heifers and bulls were low.

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Dr. Rob Tempelman has been an invaluable committee member who has challenged me, yet never withheld assistance regarding the statistical analyses. Thanks to Dr. Tempelman, I have a deeper understanding and appreciation for all those who seek to quantify and explain what others merely speculate about.

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CHAPTER 1

INTRODUCTION and OBJECTIVES

Breeders of Limousin cattle took a hard look at breed strengths and weaknesses in the summer and fall of 1990 through their Directions Symposium. Known as the "Carcass Breed", both domestically and in their native France, the relative leanness, muscularity and efficiency advantages of Limousin cattle are well documented. Likewise, among other relative weaknesses of the breed, fertility was identified as a major concern through research trials and production experience. The breed has experienced rapid growth and industry acceptance due to the ability of Limousin bulls to add muscle and feed efficiency to a calf crop. However, Limousin enthusiasts realized continued breed expansion depended on their ability to overcome breed shortcomings. Therefore, Limousin breeders have targeted reproductive fitness for improvement while maintaining breed muscle advantages.

Breeding for improved fertility is complicated by the fact that underlying genetic merit for fertility is often not expressed on a continuous scale. Pregnancy status, for instance, allows for only two possible outcomes: pregnant or nonpregnant; degrees of pregnancy are not observable. The side of the pregnant/nonpregnant threshold on which an individual record falls also depends on environmental influences, such as plane of nutrition and length of breeding season.

Bourdon and Brinks (1986) reported potentially more important factors are genotype x environment and genotype x genotype x environment interactions. All else being equal, the expression of inherent fertility differences is more pronounced in poor environments than in favorable environments. Differing levels of genetic merit for other traits, such as milk produc

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production and calf growth rate, often obscure inherent and expressed fertility. For instance, heavy-milking cows with high inherent fertility will calve regularly in good environments, but in stressful environments they will have poorer reproductive performance than inherently less fertile, but lighter-milking cows.

Genetic antagonisms between production traits, such growth vs. calving ease, lean yield vs. carcass quality, and maintenance cost vs. milk/growth pose major challenges to beef cattle breeders. Fertility traits are likewise related, often adversely, with other traits of economic importance. What sets fertility traits apart, however, is the degree to which they are affected by environment. Inclusion of composition traits, such as body condition and muscularity, among those receiving emphasis will undoubtedly complicate multiple-trait selection efforts.

Therefore, the objectives of this project were to:

1) model the phenotypic effects of composition on indicators of fertility in yearling Limousin cattle,
2) determine if composition effects differ between males and females,
3) account for composition differences in a genetic analysis of reproductive trait indicators in yearling cattle,
4) estimate a genetic correlation between scrotal circumference and cycling status utilizing a bivariate threshold – continuous model in an attempt to correctly account for the discrete nature of the female fertility trait,
5) provide practical information to the industry that merits consideration as selection decisions are made.

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CHAPTER 2

REVIEW OF LITERATURE

REPRODUCTIVE TRAITS IN BEEF FEMALES

Age at Puberty

Age at puberty (AP) of heifers is an important early indicator of potential reproductive ability, casting significant implications on cow longevity. Provided adequate nutrition and management, most heifers have the potential to reach puberty and breed satisfactorily at yearling ages. However, management and nutritional levels required to support estrous vary greatly among breeds and heifers within a breed. Heifers with the inherent ability to reach puberty at early ages may breed at less cost than heifers with later inherent AP.

Age at puberty is the only known fertility trait expressed in a heifer before she is in production, and therefore relatively immune from many interactions with other traits. Her level of milk production in a given environment, for example, is obviously unlikely to affect her AP because at the time of puberty she has yet to lactate. Consequently, AP appears to be a sensible measure of inherent fertility in young cattle, providing the earliest indication of potential reproductive performance. However, AP in females is a time and labor intensive trait to measure. Other indicators of reproductive fitness, such as pregnancy status following a fixed breeding season or age at first calving, are more easily measured traits. Breeders wishing to place selection pressure on fertility may prefer the convenience advantages of those other traits over AP, realizing the additional expense and labor required to identify heifers which may ultimately prove to have inferior and unacceptable fertility levels.

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levels. The objective here is to summarize AP, its influences on fertility, productivity, longevity, and relationships with growth and composition traits. For a complete review of the endocrinological mechanisms of puberty, see Kinder et al. (1987).

Pregnancy and Reproductive Performance

Age at puberty (age of first behavioral estrus) has been shown to be favorably and at least moderately associated with pregnancy percentage (Laster et al., 1979), percent calving during the first 25 days (Laster et al., 1979; Doornbos et al., 1983), and estrous cycles prior to conception for the first, second, and fourth lactation (Werre and Brinks, 1986). Several researchers have reported a favorable correlation of AP with yearling pregnancy rates on both a between and within-breed basis. Laster et al. (1979) reported correlations among AP breed means with percentage calving the first 25 days of -.75 and for AP with pregnancy percentage of -.42. These values indicate that earlier AP resulted in earlier conception dates and more numerous pregnancies between breeds. Doornbos et al. (1983) reported a residual correlation of -.40 between AP and percentage pregnant for Hereford cattle. Werre and Brinks (1986) reported correlations among line of sire AP means with heat cycle of conception (1 = early, 3 = late) of .54, .34, -.06, and .47 for the first four lactations respectively. Thus, heifers from lines with early puberty also tended to conceive earlier each year, except for the third lactation (Table 2.1). Furthermore, these correlations may indicate a genetic relationship.

Numerous beef cattle studies reported between and within-breed differences in age and weight at puberty related to subsequent reproduction in beef cattle (Laster et al., 1976; Gregory et al., 1979a; Dow et al., 1982; Cundiff et al., 1986; Gregory et al., 1991; Gregory et al., l

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et al., 1992; Cundiff et al., 1993). Most of the work was conducted as a component of the Germ Plasm Evaluation project (GPE) at the Meat Animal Research Center (MARC), Clay Center, Nebraska. Even so, contradictions exist over time regarding the influence of AP on pregnancy percentage, percent calf crop born and weaned, etc. For instance, during the first three cycles of the GPE project AP differed significantly among breeds, but pregnancy rate in yearling heifers did not differ between breed groups that were oldest at puberty and those breed groups that reached puberty at the youngest ages (Laster et al., 1976; Laster et al., 1979; Young et al., 1978; Gregory et al., 1979a). Heifers in all breed groups at MARC were grown and developed under drylot conditions on a moderately high-energy diet (approximately 2.2 Mcal ME/kg) and pregnancy rates were not limited by variation observed among breed groups in AP. It has been shown that heifers developed more slowly on diets with lower energy density, reached puberty at significantly older ages, and had lower pregnancy rates than did heifers developed more rapidly when both were exposed to breeding as yearlings (Wiltbank et al., 1966; Wiltbank et al., 1969; Ferrell, 1982). Moreover, Gregory et al. (1991, 1992) and Cundiff et al. (1993) have subsequently reported significant differences in pregnancy percentage following a fixed breeding season that were reflective of differences in AP. In all cases, Limousin cattle have been shown to be among the latest breeds to reach sexual maturity.

Gregory et al. (1992) reported the correlation between AP in heifers and reproduction rate in all ages was -.79 among pure breed means. Relationships among purebred means are higher than those among F_1 crosses in the GPE program. This is due to a higher percentage of F_1 crosses observed in estrus by 490 days of age in the GPE program (Laster et al., 1976;

Laster et al., 1979; Gregory et al., 1979) than were observed in estrus among pure breeds by 490 days (Gregory et al., 1991), possibly because of favorable effects of heterosis on AP.

Productivity and Longevity

Cundiff et al. (1986) also found AP to have favorable relationships with milk production and progeny weaning weights. Lesmeister (1973) reported early calving heifers had higher average annual lifetime calf production than late calving heifers, demonstrating reproductive performance of primiparous cows is dependent on the time of first calving. Age at puberty has a significant effect on beef production when heifers are bred to calve as 2-year-olds, particularly in systems that utilize restricted breeding seasons (Ferrell, 1982). In addition, heifers that calved as 2-year-olds produced more calves during their lifetime than did heifers that calving for the first time as 3-year-olds (Núñez-Dominquez et al., 1991). Werre (1980) reported favorable correlations (by line of sire means in Hereford cattle) between AP and adjusted weaning weight and most probable producing ability (MPPA) through four lactations (Table 2.1). Thus, earlier age at puberty was associated with heavier offspring weaning weights and higher accumulative MPPA values, presumably through higher milk production.

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TABLE 2.1: Correlation of heifer age at puberty with productivity traits[a]

Age at Puberty	HCC[b]	AWWR[c]	MPPA[d]
1st Lactation	.54	-.65	-.62
2nd Lactation	.34	-.11	-.38
3rd Lactation	-.06	-.24	-.10
4th Lactation	.47	-.11	.25

[a]Werre, 1980.
[b]Heat cycles of conception (1 = early, 3 = late)
[c]Adjusted 205 day weaning weight ratio
[d]Most probable producing ability

A favorable relationship of earlier age at puberty with higher milk production has also been observed from correlations among breed means. Laster et al. (1979) reported a correlation of -.88 between AP and milk production, indicating a favorable relationship between breeds. Similarly, Gregory et al. (1991) reported that breeds historically selected for milk production reached puberty at significantly younger ages than breeds of comparable mature size and retail yield that had not been selected for milk production. Thus, knowledge of the relationships between puberty traits and measures of productivity is important for effective utilization of selection, heterosis, and complementarity to achieve an optimum production level.

Heritability

Heritability estimates for AP average about 40%, slightly lower than SC in yearling bulls, but still relatively high compared with many other reproductive traits. Heritability estimates for age at puberty range from .07 $\pm$ .17 reported by McInerney (1977) to .67 reported by Werre and Brinks (1986). Heritability estimates for AP are listed in Table 2.2.

Table 2

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Table 2.2: Heritability estimates for age at puberty (AP)

Source	Heritability ± SE
Arije and Wiltbank, 1971	.20 ± .16
Smith et al., 1976	.64 ± .31
McInerney, 1977	.07 ± .10
Laster et al., 1979	.41 ± .17
Lunstra, 1982	.41
King et al., 1983	.48 ± .18
MacNeil et al., 1984	.61 ± .18
Werre and Brinks, 1986	.67 ± .68
Smith et al., 1989a	.10 ± .09
Gregory et al., 1995	.31 ± .04
AVERAGE	**.39**

Relationships with Growth

The genetic correlations of AP with growth traits are similar to those between SC and growth traits in yearling bulls. Estimates of genetic correlations of AP with various weights are listed in Table 2.3. Negative correlations with AP (favorable) indicate that heifers with more genetic strength for growth from birth to yearling reach puberty earlier.

Genetic relationships of AP with growth traits indicate a relatively low, but favorable, correlation with birth weight, whereas the relationships with weaning and yearling weights are slightly stronger and complementary. These genetic correlation estimates suggest an advantageous relationship between measures of puberty and the growth curve (i.e., increasing early growth rate and reaching a higher percentage of mature weight at earlier ages without increasing birth weight).

Table 2.3: Genetic correlations of age at puberty with growth traits.

Source	Birth weight	Weaning weight	Yearling weight	Mature weight
Smith et al., 1976	-.07	-.52	-.29	-.20
Werre & Brinks, 1986	-.16	-.31	-.25	
Smith et al., 1989a	.58	-.04	-.14	
Gregory et al., 1995	.03	-.14	-.05	-.05
Average	**.1**	**-.25**	**-.18**	**-.13**

Other studies have reported a positive genetic correlation between age and weight at puberty. Arije and Wiltbank (1971), Smith et al. (1976) and Laster et al. (1979) reported values of .36, .67 and .52 indicating that, genetically, heifers reaching puberty at later ages were also heavier, or vice versa. These studies seem to be in conflict with the findings described above. However, the latter relationships were calculated at the point in time when first behavioral estrus was observed. When one considers that the correlations reported in Table 2.3 were reported for weights adjusted to an age constant, the favorable relationship of AP with the growth curve remains plausible.

Similarly, Martin et al. (1992), reported heifers of faster gaining breed groups with large mature size (e.g., Charolais, Chianina) tended to be older and heavier at puberty than did heifers sired by breeds with smaller mature size (e.g., Hereford, Angus). Correlations between mature size and AP are .57 for *Bos taurus* breeds and .25 when *Bos indicus* breeds are included. Both between and within-breed sources of genetic variation were large and important for age or weight at puberty. Heavier milking breeds seem to reach puberty earlier than breeds of similar mature size and retail product that do not have a history of selection for milk production (e.g. Simmental and Gelbvieh vs. Charolais and Limousin).

Relationships with Body Condition

Body condition (degree of fatness) is reportedly favorably correlated with rebreeding performance of beef cattle. Gregory et al. (1995) reported a favorable genetic correlation for body condition score and age at puberty in yearling females of -.09. The phenotypic relationship between body condition and age at puberty, although favorable, was small and unimportant. Furthermore, Limousin heifers were shown to be the leanest of nine breed groups in the GPE Project and among the latest for age at puberty.

Ritchie et al. (1992) has described the 9-point body condition scoring system that is the most widely adopted in industry:

1. **Severely emaciated.** Rarely seen. All ribs and bone structures easily visible. Very little visible muscle tissue. Physically weak.
2. **Emaciated.** Similar to Condition Score 1, but not weakened. Little visible muscle tissue.
3. **Very thin.** No fat over ribs or in brisket. More apparent muscling than on Condition Score 2. Backbone easily visible.
4. **Thin.** Ribs usually visible with shoulders and hindquarters showing modest muscling. Backbone visible.
5. **Moderate.** Last two or three ribs can be seen. Little evidence of fat in brisket, over ribs or around tailhead.
6. **High moderate.** Smooth appearance throughout. Slight fat deposition in brisket and over tailhead. Ribs covered, and back appears slightly rounded.
7. **Good.** Brisket full. Tailhead shows pockets of fat. Back appears well rounded due to fat. Ribs appear very smooth.

8. **Obese.** Back square due to fat. Brisket distended. Heavy fat pockets around tailhead. Neck thick.
9. **Very obese.** Rarely seen. Similar to Condition Score 8, but more extreme. Heavy disposition of udder fat.

Relationships with Muscularity

Relationships between muscularity and female age at puberty are not well defined. Objective methods of measuring differences for either muscle or fertility traits in live animals are inherently difficult, expensive and often imprecise. Coupling two such traits in any analysis requires additional time, labor, and assumptions regarding the validity of the raw data. While not a perfect solution, subjectively assigned muscle scores were used prior to the onset of more advanced technology and continue to be in use. Gregory et al. (1995) reported an intermediate genetic relationship of a subjective muscle score with measures of carcass composition, suggesting visual evaluation of differences in muscle thickness has value in contributing to making changes in carcass composition. Characterization of biological types by researchers at the MARC indicates tendencies among *Bos taurus* breeds with greater retail product to be later maturing cattle that are significantly older at first detectable estrus (Gregory et al., 1992; Gregory et al., 1995).

Reproductive Tract Score

Several researchers have studied AP in beef heifers when defined as the age at first behavioral estrus. However, because AP is difficult and labor-intensive to measure, direct selection for age at puberty in females is seldom practiced. A method for evaluating the reproductive tract of yearling heifers has been developed at Colorado State University (Andersen et al., 1991). The reproductive tract scoring (RTS) system was designed to estimate pubertal status via rectal palpation of the uterine horns and ovaries. Each heifer is assigned a score of 1 (immature) through 5 (cycling) as described in Table 2.4.

Table 2.4: Description of reproductive tract scores[a]

		Ovaries (approx. size)			
Repro. tract scores	Uterine horns	Length (mm)	Height (mm)	Width (mm)	Ovarian structures
1	Immature < 20 mm diameter - no tone	15	10	8	No palpable follicles
2	20-25 mm diameter - no tone	18	12	10	8 mm follicles
3	25-30 mm diameter - slight tone	22	15	10	8-10 mm follicles
4	30 mm diameter - good tone	30	16	12	< 10 mm follicles corpus luteum possible
5	> 30 mm diameter - good tone, erect	>32	20	15	>10 mm follicles corpus luteum present

[a]Reproductive tract score was determined approximately one month pre-breeding by rectal palpation. Andersen et al., 1987.

Evaluation System

The reproductive tract scoring system estimates pubertal status via rectal palpation of the uterine horns and ovaries as described in Table 2.4 (LeFever and Odde, 1986). A RTS of 1 is assigned to heifers with infantile tracts as indicated by small, toneless uterine horns and small ovaries devoid of significant structures. Heifers scored as 1 are likely the furthest from cycling at the time of examination. Heifers given a RTS of 2 are closer to cycling than those scoring 1 due primarily to the presence of small follicles and slightly larger uterine horns and ovaries. Those heifers assigned a RTS of 3 are on the verge of cycling based on slight uterine tone in addition to the presence of follicles. Heifers assigned a score of 4 are presumably cycling as indicated by good uterine tone, uterine size, and follicular growth. However, heifers with tract scores of 4 lack an easily distinguished corpus luteum due to the stage of the estrous cycle. Heifers with tract scores of 5 are similar to those scoring 4 except for the presence of a palpable corpus luteum.

Pregnancy and Reproductive Performance

Synchronization trials and other studies at Colorado State University indicate that reproductive tract scoring one month prior to breeding can help identify heifers less likely to become pregnant during a short breeding season (LeFever and Odde, 1986; Brown, 1986; Andersen, 1987; Andersen et al., 1987; Odde et al., 1989). This prompted study of the genetic aspects of RTS and other traits used in selecting replacement heifers. Genetic analysis results prompted an investigation of the relative importance of RTS, condition score, age, and weight to predict estrous response to synchronization (RS), pregnancy rate to synchronized breeding (PS), pregnancy rate at the end of the breeding season (PBS), and conce

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conception date (Andersen, 1987). The reproductive tract scoring system was more useful as an indicator of pregnancy rate (PS and PBS) than as an indicator of RS and conception date as evidenced by significance levels (Andersen, 1987). Inclusion of condition score, age, and weight along with RTS in models used for analysis provided little additional accuracy over RTS alone for the reproductive traits analyzed.

The relationship of RTS to reproductive performance information from a series of studies is presented in Table 2.5. Generally, means in Table 2.5 indicate a 5-22% advantage in PS for tract scores of 4 and 5 versus tract scores of 3. Rates of pregnancy to synchronized breeding for RTS 1 were 41-48% lower than for RTS of 4 and 5.

Differences in breeding season pregnancy rates for RTS 4 and 5 versus scores of 3 suggest anywhere from a 5-20% advantage. Heifers with RTS 3 prior to the breeding season seem to have little apparent advantage over RTS 2 in terms of pregnancy rates at the end of the breeding season. Heifers scoring 1 tended to have a 31-67% lower pregnancy rate at the conclusion of the breeding season than heifers scoring 3. These results indicate that heifers scoring 1 should be eliminated from the breeding group or managed differently. Of heifers that conceived, conception dates for heifers with scores of 3, 4, and 5 were, on average, about 10 days earlier than heifers with a RTS of 1 and 2.

The RTS values were predictive of reproductive performance of yearling heifers, especially for pregnancy rates to synchronized breeding and to breeding season pregnancy rates. Heifers with more mature reproductive tracts had higher pregnancy rates and calved earlier.

Table 2.5: Effect of reproductive tract score on reproductive trait means[a]

Reproductive measure	Reproductive tract score 1	2	3	4	5
Response to synchronization, %[b]					
LeFever and Odde, 1986	50.0	79.7	79.3	93.1	96.8
Brown, 1986 (MGA-PGF_2)[c]	3.4	63.6	82.2	95.3	92.4
Brown, 1986 (SMB)[c]	76.0	100.0	92.0	95.4	93.2
Andersen, 1987	56.0	63.0	69.0	79.0	76.0
Average	46.3	76.6	80.4	90.7	89.4
Pregnancy rate to synchronized breeding, %[b]					
LeFever and Odde, 1986	0.0	17.0	37.0	62.1	54.0
Odde et al., 1989	0.0	23.0	32.0	55.0	54.0
Brown, 1986	4.5	23.4	35.8	52.3	50.0
Andersen et al., 1987			58.8	56.6	70.9
Andersen, 1987	6.0	27.0	34.0	48.0	46.0
Average	2.6	22.6	39.5	54.6	55.0
Pregnancy rate at end of breeding season, %[b]					
Odde et al., 1989	38.0	61.0	70.0	93.0	85.0
Brown, 1986 (MGA-PGF_2)[c]	18.8	70.7	85.8	95.2	89.6
Brown, 1986 (SMB)[c]	16.2	100.0	80.2	90.9	82.4
Andersen et al., 1987			74.1	99.4	86.1
Andersen, 1987	40.0	65.0	74.0	92.0	82.0
Average	28.2	74.2	76.8	94.1	85.0
Conception date[d]					
Odde et al., 1989	22.0	12.0	4.0	2.0	0
Andersen et al., 1987			1.0	9.0	0
Andersen, 1987	16.0	8.0	3.0	2.0	0
Average	19.0	10.0	2.0	4.3	0

[a]Means presented by LeFever and Odde (1986; 1989) are raw means. All other means are least-square means.
[b]Number responding or conceiving divided by the number treated at the start of the breeding season.
[c]Synchronization method.
[d]Average conception dates represent the average number of days into the breeding season that conception occurred compared to the average number of heifers which had reproductive tract scores of 5.

Productivity

Considerable apparent breed differences were reported between both purebreds and composite crossbreds for RTS as well as for other traits (Andersen et al., 1988). Purebred Herefords exhibited the lowest mean RTS (2.78), while Angus and Simmental had the highest means (4.14 and 4.07, respectively). Generally, the purebreds known for higher milk production also had higher RTS. These findings agree with Cundiff et al. (1986), and others who have reported the favorable relationship between age at puberty and milk production.

Genetic Aspects of RTS

Reproductive tract scores were included in a study that evaluated genetic aspects of several performance traits in beef heifers (Andersen et al., 1988). For RTS, the effects of line of sire, sire within line of sire, birth year, inbreeding, and age were all significant ($P < .05$) sources of variation while age of dam was not significant. For all dependent variables except birth weight, increased inbreeding had detrimental effects while increased age had favorable effects on all traits analyzed as indicated by regression coefficients (Table 2.6).

Table 2.6: Regression coefficients for heifer performance traits[a]

	BW[b] (lb.)	WW (lb.)	YW (lb.)	RTS (units)	CS (units)	PA (cm^2)	PH[c] (cm)	PW[c] (cm)
Regression on inbreeding	-.16[d]	-2.21[d]	-2.45[d]	-.019[d]	-.013[d]	-.27[d]	-.011[d]	-.016[d]
Regression on age	.03	1.57[d]	1.67[d]	.02[d]	.009[d]	.37[d]	.012[d]	.018[d]

[a]Andersen et al., 1988
[b]BW = birth weight; WW = weaning weight; YW = yearling weight; RTS = reproductive tract score; CS = condition score; PA = pelvic area; PH = pelvic height; and PW = pelvic width.
[c]Pelvic height and width regression coefficients were calculated from a subset of the data used for pelvic areas because of missing data from 1987.
[d]$P < .05$.

Heritability estimates for RTS were lower than AP estimates, as might be expected because this measure of puberty is less precise and the distribution of RTS depends on when the heifers are examined. Although moderate, the average heritability estimate of .28 (Table 2.7) for RTS seems feasible (Andersen et al., 1991; Andersen, 1991). The heritability estimate for RTS is within the range of estimates for age at puberty and suggests that RTS should respond favorably to selection. Heifers in the studies cited were measured approximately one month prior to breeding.

Table 2.7: Heritability estimates for reproductive tract score (RTS).

Source	Heritability $\pm$ SE
Andersen et al., 1991	.32 $\pm$ .17
Andersen, 1991	.24 $\pm$ .13
AVERAGE	**.28**

Relationships with Growth

Positive correlations are favorable for RTS with measures of growth. Heifers in these studies were raised under limited feed resources from weaning until breeding.

Genetic correlations (Table 2.8) between RTS and growth and pelvic traits were all favorable (Andersen et al., 1988). These correlations suggest that favorable correlated response would occur in all traits evaluated, given selection for improved RTS. However, a follow-up study also conducted by Andersen (1991) reported genetic relationships between RTS and birth weight, weaning weight, and yearling weight as .05 $\pm$ .39, -.01 $\pm$ .43, and .24 $\pm$ .35, respectively. Phenotypic correlations between RTS and other traits were all positive and moderate in magnitude, except for birth weight, which was slightly negative.

Table 2.8: Heritabilities and genetic, phenotypic, and environmental correlations for heifer growth and reproductive traits [a]

	BW	WW	YW	RTS	CS	PA	PH	PW
Birth Weight								
G[b]	.09	.98	.74	-.37		.14	-.06	.62
SE (G)[c]	.16	.95	.75	.95		.79	.61	.59
E[d]		.10	.36	.07		.18	.18	-.07
P[e]		.30	.33	-.02	.07	.15	.05	.23
Weaning Weight								
G		.58	.93	.20	.16	.64	.53	.75
SE(G)		.20	.07	.39	.44	.23	.29	.18
E			.67	.60	.62	.27	-.83	.08
P			.82	.41	.39	.47	.25	.58
Yearling Weight								
G			.87	.31	.40	.72	.47	.95
SE(G)			.21	.32	.31	.17	.28	.13
E				.94	1.60	.32	-.05	-.56
P				.44	.45	.57	.35	.63
Reproductive Tract Score								
G				.32	-.06	.53	1.01	.30
SE(G)				.17	.49	.34	.77	.55
E					.71	.31	-.35	1.08
P					.37	.39	.28	.39
Condition Score								
G					.42	.61	.59	.77
SE(G)					.22	.37	.47	.36
E						-.10	-.64	.72
P						.26	.18	.36
Pelvic Area								
G						.53	.78	.75
SE(G)						.19	.12	.13
E							.81	1.08
P							.78	.78
Pelvic Height								
G							.82	.16
SE(G)							.26	.29
E								.84
P								.22
Pelvic Width								
G								.91
SE(G)								.26

[a] Anderson et al., 1988.

[b]G = genetic (correlation between breeding values); [c]SE(G) = standard error of genetic parameter; [d]E = environmental (correlation between environmental effects on two traits); [e]P = phenotypic (correlation between phenotypic values).

Other Factors which Influence RTS

Another study was undertaken to evaluate how contemporary group (location, year, and synchronization treatment combinations), age, weight, and condition score influence RTS (Andersen, 1988; unpublished data). Approximately 45% of the variation in RTS was accounted for by the above four factors. Contemporary group, condition score, and weight were highly significant ($P < .005$) sources of variation. In this study, age did not account for a significant portion of the variation in RTS.

Timing and Appropriate Use

The distribution of RTS for a group of heifers depends upon when the heifers are examined. Variation within a group of heifers is temporary. If taken before a year of age, most heifers will not be cycling and receive tract scores of 1 and 2. Conversely, if scores are taken too late, most heifers will be cycling and scored 4 or 5. The time or age at which heifers are examined depends upon the desired use of the scoring system and the particular group of heifers to be evaluated.

It is my belief that when tract scoring is to be used as an indicator of a heifer's ability to conceive early during the first breeding season, scoring should be done about one month before breeding or earlier. If RTS is used as a tool to place selection pressure on age at puberty, the best time to evaluate is when 25-50% of the heifers are thought to have begun cycling based on age, weight, and casual estrus observation. Depending upon management, maturing rate, and age uniformity, heifers may only have to be scored once to take full advantage of the system. If heifers are cycling more than one month before the start of the breeding season, they should be scored earlier while greater variation exists. A RTS taken

30 to 60 days prior to the start of the breeding season can also serve as a check for the heifers nutritional development program. Then, according to the resultant scores, the ration or start of the breeding season may be adjusted.

Discussion

Widespread use of the reproductive tract scoring system depends upon overcoming special problems associated with this trait. Training personnel that can palpate and assign scores proficiently is perhaps the major obstacle. It seems likely that veterinarians should be able to adapt to the scoring system and provide clients with a useful service.

The usefulness and resulting economic value of this scoring system in specific selection and management systems is difficult to assess, at least partially because of the threshold nature of most measures of reproductive performance. Breeds, lines, or crossbreds characterized as later maturing may profit more from scoring than earlier maturing types. Because of the favorable relationship between sire scrotal circumference and daughters age at puberty (Brinks et al., 1978; King et al., 1983; Lunstra, 1982), operations that have practiced sire selection for scrotal circumference may already have high levels of fertility built into their herds. In such cases, RTS may provide little additional benefit. Regardless of how inherent fertility is improved, through decreased age at puberty from the male and/or female side, it can be thought of as an insurance policy for expressed fertility. This should provide greater flexibility when matching mature size and milk production to management and environmental constraints.

Breeding heifers several weeks before the cow herd permits concentration of time and labor during breeding and calving and allows for a longer postpartum interval the following year. Unfortunately, this practice may be futile if a large proportion of heifers are expected to conceive at pubertal estrus, which is often less fertile than subsequent estrus (Byerley et al., 1987). The utility of this management practice can be evaluated using RTS to predict pubertal status before starting the breeding season. If non-cycling heifers can be identified and eliminated from the breeding group, higher first service pregnancy rates and other benefits of this management practice can be more fully realized.

There is justification for feeding heifers so that less than a maximum proportion are allowed to express their genetic potential for cyclic activity one month before breeding. If less total weight has to be maintained during winter feeding months, the associated feed costs could be reduced and weight could be gained more cost effectively on grass after breeding. A one-time tract score would then allow selection for both age at puberty and reproductive performance during the first breeding season. Also, only heifers capable of adequate consumption and (or) efficient conversion of feed will achieve weights that allow them to cycle. Heifers that cycle at lighter weights or lower condition scores on less feed relative to their age could be assumed the most inherently fertile.

Summary

In summary, RTS appears to be moderately heritable and favorably related to lower birth weight as well as pelvic and higher growth traits. Tract scores have also been found to be favorably associated with response to synchronization, pregnancy rate to synchronized breeding, pregnancy rate at the end of the breeding season, and conception date. Usefulness of the tract scoring system depends upon timing, previous selection practices, management, and environmental factors. Tract scores can be used to evaluate the status of heifer development, time synchronization programs and the start of the breeding season, and place selection pressure on age at puberty and related traits. The scoring can be done in conjunction with collection of yearling weights, condition scores, pelvic measures, and general processing as part of a yearling heifer evaluation and health program.

Threshold Trait Considerations

Reproductive tract score, like most reproductive traits expressed in the female, is an example of a threshold trait. Threshold traits are those which vary in a discontinuous manner but aren't inherited in simple Mendelian fashion. Because characteristics such as reproductive tract score, pregnancy, etc. are typically measured in discrete terms; they appear to be indescribable as quantitative traits. Genetic analysis reveals however, these traits are indeed inherited in the same was as continuously varying characters. Reproductive tract score has an underlying continuous distribution of both genetic and environmental origin and a threshold that imposes discontinuity on the observable scale. When the underlying variable effects on the animal are greater than the threshold for puberty, the animal scores a 4 or 5 in the previously described RTS system. By contrast, if the sum of effects is less than the threshold value, the heifer is scored 1, 2, or 3 as she has not yet completed her first estrous cycle.

Incidences of the threshold for puberty being met and the trait being expressed are coded as "1" and a failure to have cycled is coded as "0". Thus, despite the fact a continuous distribution is assumed for the factors that control age at puberty, observable differences and corresponding codes allow for only binomial or multinomial distrib

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distributions. Therefore, linear model procedures are inappropriate for estimating the variance components for threshold traits such as pubertal status because their use violates the assumption of a continuous, normal distribution required by these methods. Gianola and Foulley (1983) and Hoeschele et al. (1995) noted that linear model procedures couldn't account for the non-normal distribution of error commonly associated with categorically observed traits. Threshold model procedures that assume the existence of an underlying continuous variable (Gianola and Foulley, 1983) have overcome this dilemma. Analytical methods that account for the binomial nature of female fertility traits will be discussed further in the next section.

Logistic Regression

Most genetic analyses of reproductive traits with discrete categories have utilized linear model procedures for variance component estimation. As previously stated, such methods are inappropriate due to the violation of the required assumption that the response variable be normally distributed. Logistic regression is a form of statistical modeling that is often appropriate for categorical outcome variables (Selvin, 1996). Like standard linear modeling, it describes the relationship between a response variable and a set of explanatory variables. The response variable is usually dichotomous; in which case it follows the binomial distribution. However, logistic regression also fits polytomous variables, that is variables having more than two response levels, which then follows a multinomial distribution. These multiple-level response variables can be scaled nominally or ordinally. The explanatory variables may be categorical or continuous.

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On a phenotypic level, researchers may be interested in the likelihood that a fertility trait of interest is expressed given an array of explanatory variables such as weight, age, body condition, etc. Logistic regression is advantageous to standard linear modeling in this instance as it guarantees the probability of success will range between 0 and 1. Moreover, the logistic function has a sigmoid curve, which more accurately reflects the threshold nature of fertility traits. The logistic function is described as: $f(z) = \frac{1}{1+e^{-z}}$.

The value of logistic function is dependent on the value of z. To obtain the logistic model from logistic function z is written as a function of independent variables (X's).

$z = \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$

The logistic model for the conditional probability of cycling given characteristics $X_1,\ldots,X_k$, i.e. $P(1|X_1,\ldots,X_k)$ is written as follows:

$f(z) = \frac{1}{1+e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = \frac{e^{(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}}{1+e^{(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = \frac{1}{1+e^{-(\alpha+\sum_{i=1}^{k}\beta_i X_i)}}$ where α, β_1, $\beta_2,\ldots,\beta_k$ are parameters to be estimated (e.g. age, season). Parameter estimation is performed through maximum likelihood techniques.

An important aspect of logistic regression to remember is that it was developed in the context of follow-up studies. Therefore, in fields such as epidemiology it is used to describe the probability of developing disease as a function of independent variables measured at the start of some follow-up period. There may be some concern regarding the validity of parameter estimates calculated on traits measured at the same time as the response variable. However, logistic regression appears to be the best analysis tool for categorical outcome variables

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Obtaining odds and odds ratios from logistic regression

Another feature of the logistic regression function is the interpretation of the coefficient β_i through estimation of the odds in favor of an event and the odds ratio. The odds ratio is interpreted as the increase in odds for a unit increase in the independent variable(s). To do this the logistic model must be rewritten in the logit form. By definition, if p is the probability than an event will occur then:

Odds is defined as the probability an event will occur divided by the probability the event will not occur, i.e. $\frac{p}{1-p}$ and,

logit $(p) = \ln\left(\frac{p}{1-p}\right) = \ln(\text{odds})$. In logistic model

$$\mathrm{P(C|X_1,\ldots,X_k)}\frac{1}{1+e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = \mathrm{P_{(C|X)}}$$

$$\therefore 1 - \mathrm{P(C|X_1,\ldots,X_k)} = \frac{e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}}{1+e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = 1 - \mathrm{P_{(C|X)}}$$

$$\therefore \text{Odds} = \frac{\mathrm{P_{(C|X)}}}{1 - \mathrm{P_{(C|X)}}} = \frac{1}{1+e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = e^{\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k}$$

$$\therefore \text{logit(P)} = \ln(\text{odd}) = \ln\left(\frac{p}{1-p}\right) = \ln\left(e^{\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k}\right)$$

$$= \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$$

The most common correct way of writing the model in the logit form.

$$\ln\left(\frac{p}{1-p}\right) = \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$$

Thus, the logit form of the logistic model offers an expression for log odds of an event for an individual with a specific set of X's.

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Interpretation of coefficients from the logit form of the logistic model

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If all X's are set to zero then $\text{logit(P)} = \alpha + \beta_1 X_1 + \beta_2 X_2 + ... + \beta_k X_k = \alpha$

i.e. α is the log odds for an individual with zero values for all X's. This interpretation has limitations for naturally occurring continuous variables such as age or weight.

A more appealing alternative is to interpret the intercept as the baseline odds i.e. odds that would be estimated if no X's were considered at all.

(β_i's)

Interpretable in terms of odds and/or odds ratios. Consider the following example of a model that fits both weight and muscle score. If weight remains fixed and muscle scores vary from 1 to 2, the data would appear as follows:

y = yearling reproductive tract score (0 = non-cycling, 1 = cycling)

X_1 = muscle score 1 (1: MS = 1, 0: MS ≠ 1)

X_2 = muscle score 2 (1: MS = 2, 0: MS ≠ 2)

X_3 = muscle score 3 (1: MS = 3, 0: MS ≠ 3)

X_4 = weight

Denote by A_1, the collection of X's for a light muscled individual (MS 1), and let A_2 specify the collection of X's that characterize an average muscled individual (MS 2).

$A_1 = (X_{11} = 1, X_{12} = 0, X_{13} = 0, X_{14} = 0)$

$A_2 = (X_{21} = 0, X_{22} = 1, X_{23} = 0, X_{24} = 0)$

If it is assumed to be known that:

$$\ln\left(\frac{p_{A1}}{1 - p_{A1}}\right) = \ln(oddsA_1) = \alpha + \beta_1 X_{11} + \beta_2 X_{12} + \beta_3 X_{13} + \beta_4 X_{14}$$

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$$\ln\left(\frac{p_{A2}}{1-p_{A2}}\right) = \ln(oddsA_2) = \alpha + \beta_1 X_{21} + \beta_2 X_{22} + \beta_3 X_{23} + \beta_4 X_{24}$$

then

$$e^{\ln(oddsA_2)} = e^{\alpha+\beta_1 X_{21}+\beta_2 X_{22}+\beta_3 X_{23}+\beta_4 X_{24}}$$

and

$$e^{\ln(oddsA_1)} = e^{\alpha+\beta_1 X_{11}+\beta_2 X_{12}+\beta_3 X_{13}+\beta_4 X_{14}}$$

$$OR_{(A_2,A_1)} = \frac{\text{odds}(X_2)}{\text{odds}(X_1)} = \frac{e^{\alpha+\beta_1 X_{21}+\beta_2 X_{22}+\beta_3 X_{23}+\beta_4 X_{24}}}{e^{\alpha+\beta_1 X_{11}+\beta_2 X_{12}+\beta_3 X_{13}+\beta_4 X_{14}}}.$$

Rules of algebra indicate that $\frac{e^a}{e^b} = e^{a-b}$

Therefore, $OR_{(A_2,A_1)}$ can be rewritten as

$$OR_{(A_2,A_1)} = e^{[(\alpha+\sum_{i=1}^{k}\beta_i X_{2i})-(\alpha+\sum_{i=1}^{k}\beta_i X_{1i})]} = e^{\sum_{i=1}^{k}\beta_i (X_{2i}-X_{1i})}$$

Thus, for the example

$$A_1 = (X_{11}=1, X_{12}=0, X_{13}=0, X_{14}=0)$$

$$A_2 = (X_{21}=0, X_{22}=1, X_{23}=0, X_{24}=0)$$

then

$$OR_{(A_2,A_1)} = e^{[\beta_1(0-1)+\beta_2(1-0)+\beta_3(0-0)+\beta_4(0-0)} = e^{-\beta_1+\beta_2}$$

Where β_1 and β_2 are coefficients in the model: logit $P_{(C|X)} = \alpha + \beta_1 MS1 + \beta_2 MS2 + \beta_3 MS3 + \beta_4 Wt$.

For a continuous variable such as weight, the odds of cycling for a heifer 45 kg heavier than the mean are four times the odds of cycling for a heifer 45 kg lighter than the mean according to the following calculation $e^{\beta_4(\text{difference})} = e^{0.0156(90)} = 4.071$.

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REPRODUCTIVE TRAITS IN BEEF MALES

Bull Fertility

Brinks (1991) stated that nearly 90% of the genetic improvement within a cowherd are derived from the sire side of the pedigree. Thus, the largest potential improvements in a herd's inherent fertility levels are made through sire selection. One method to determine a bull's reproductive capacity is the breeding soundness evaluation (BSE). The exam is a test standardized by the Society of Theriogenology and is used on yearling bulls to identify males unfit for breeding. It consists of a reproductive organ examination, semen evaluation, and structural soundness test. A bull that fails to satisfy all exam requirements fails the test. Yearling bulls are often re-evaluated as their additional nutrient requirements for growth sometimes prevent reproductive maturation, and not all bulls reach reproductive ability as yearlings. The BSE requires a minimum scrotal circumference of 30 cm.

Genetic factors, which will be discussed in subsequent sections that influence inherent bull fertility, are additive effects, breed, heterosis, inbreeding and correlations with other performance traits, such as growth, maternal, and composition. Indicator traits for bull fertility, genetic merit and breeding capacity that will be described in forthcoming sections include: age at puberty, semen quality, daughter age at puberty, and yearling scrotal circumference.

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Puberty

Male puberty is defined and evaluated by the following criteria: 50 x 10^6 spermatozoa per ejaculate, a minimum of 10% motility, an average scrotal circumference of 27 to 28 cm, and sheath detachment (Lunstra et al., 1978; Lunstra et al., 1982). Davis (1993) described an alternative evaluation for puberty using increased serum testosterone with GnRH stimulation. Either this method or the previously described criteria will describe a bull's sexual maturity status, although the hormonal array may change as sexual maturity approaches. Luteinizing hormone and testosterone serum levels increased in bulls prior to reaching puberty, and breeds known for higher testosterone levels reached age at puberty earlier (Lunstra et al., 1978).

Obviously, it is necessary for a bull to reach puberty prior to breeding. Scrotal circumference and semen evaluations are the standard indicators for bull fertility and age at puberty status. Neely et al. (1982) reported that 365 d scrotal circumference measurements were better indicators of yearling bull fertility than those taken at other ages were. Heritabilities of 205 and 365 d scrotal circumference were .08 ± .20 and .44 ± .24, respectively. The 205 d scrotal circumference was associated with changes in a bull's live weight rather than developed semen-producing tissue. The 365 d scrotal circumference measurement was favorably correlated with semen quality and testes size. Smith and Brinks (1989) showed that as age increased, seminal quality improved. A linear regression analysis on age for all traits showed significant results for motility, percent normal, scrotal circumference, breeding soundness exam, and primary abnormal percentage. Thus, aging appears to increase semen quality, motility, concentration, and percent normal sperm and decrease abnormalities (Abadia et al., 1976).

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Scrotal Circumference and Bull Fertility

Scrotal circumference is a standard indicator of fertility in yearling bulls. Palasz et al. (1994) showed that bulls with scrotal circumference measurements greater than 31 cm had greater sperm producing capability than those bulls with less than 30 cm. Smaller scrotal circumference bulls (<30 cm) exhibited a higher incidence of germinal epithelial loss and damaged testicular tissue. Madrid et al. (1988) reported that bulls with scrotal circumferences less than 32 cm had a higher incidence of semen abnormalities and testicular lesions. However, other research has shown that the relationship between scrotal circumference and bull fertility has not been established. Thompson et al. (1992) reported no significant associations between the loss of germinal epithelium and spermatozoa production. Additional studies found scrotal circumference to be a poor predictor of semen output (Carter et al., 1980; Knights et al., 1984; Makarechian et al., 1985; Thompson et al., 1992). While these differing results may be disconcerting from a practical standpoint, the relevant question involves the general relationship between yearling scrotal circumference and inherent fertility in collateral relatives and offspring. These issues will be addressed in a following section.

Scrotal Circumference Relationships with Age at Puberty

Results from the Roman L. Hruska Meat Animal Research Center, (Lunstra, 1982) indicated that SC was a more accurate predictor of bull puberty than either age or weight regardless of breed or breed cross. Martin et al. (1992) reported that among breed group means, high absolute correlations were observed between AP and SC in males (-.92).

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Smith et al. (1989b, c) reported that for each centimeter increase in a sire's SC there was a .31 cm increase in sons' SC, which is more than expected based on average heritability estimates. Hough (1991) reported preliminary results from a high versus low selection study utilizing scrotal circumference EPD in Hereford cattle. High SC sires had 2.4 ± .03 larger EPD values than low SC sires. Bull progeny of the high-EPD sires averaged 2.2 ± .7, 3.5 ± .9, and 2.6 ± 1.0 cm larger SC than their contemporaries by low-EPD sires at weaning, yearling and 15 months, respectively. Consequently, it seems apparent that sire SC impacts AP in his male progeny.

Breed Effects

There are differences between breeds in age at puberty and the ability to produce viable spermatozoa at an early age. Lunstra et al. (1978) reported that Hereford bulls had the oldest age at puberty and the lightest weight at puberty compared to Red Poll, Angus, and Brown Swiss. Gregory et al. (1991) reported breed differences for scrotal circumference using MARC data. Breed group was a highly significant fixed effect for scrotal circumference and paired testicular volume least square means. Least square means for scrotal circumference ranged from 29 cm for Limousin to 34 cm in Gelbvieh. Gregory et al. (1995) stated there was a reduction in variation for scrotal circumference with 368 d weight as a covariate, but there were still differences between breeds.

Fields et al. (1979) reported the breed effect to be a significant source of variation for testicular volume, semen volume, motility, sperm concentration, and seminal fructose. The breeds evaluated were Hereford, Angus, Santa Gertrudis, and Brahman. Brahman bulls had smaller scrotal circumferences and later ages at puberty than the other breeds. Sperm concentration and motility were lower for the Brahman and Santa Gertrudis, and higher for Angus and Hereford. Smith and Brinks (1989) reported that breed was a highly significant factor for percent motility and primary abnormalities. Red Angus bulls had the highest breeding soundness results while Brangus bulls charted the lowest BSE scores.

Heterosis Effects

Heterosis has been shown to have positive effects on bull fertility. Composite MARC data showed that scrotal circumference was partially influenced by breed group and showed heterosis as an additional source of variation. Heterosis differences were significant for scrotal circumference and paired testicular volume in all composite-breeding generations, and reflected heterosis values for weight (Gregory et al., 1991). However, Gregory et al. (1995) followed up by stating that heterosis effects on scrotal circumference occur because of additional factors in addition to weight. When the covariate 368 d weight was included, a high percentage of heterosis effects were removed (Gregory et al., 1991).

Inbreeding Effects

In contrast to heterosis, inbreeding can be detrimental to bull fertility and has been unfavorably associated with semen quality traits and scrotal circumference. Abadia et al. (1976) reported that inbred bulls were at greater risk for testicular and seminal vesicular inflammation, and specific inbred lines showed a higher incidence. Palasz et al. (1994) showed results of increased testicular hypoplasia and damaged seminiferous tubules because a high percentage of the testicle was composed of germinal epithelium. This decreased the percentage of normal sperm because of the significant negative correlation

with degree of germinal epithelium loss. Smith et al. (1989b) reported that inbreeding was significant and detrimental for semen quality traits, except for secondary abnormalities.

Relationships with Growth

Scrotal circumference can be favorably associated with most measures of growth according to genetic and phenotypic correlations reported in the literature. Bourdon and Brinks (1986) reported weight had a greater effect on scrotal circumference than the other covariates, age and height. Furthermore, any factor that caused an increase in weight tended to increase scrotal circumference. Knights et al. (1984) reported that bulls with increased growth sired male progeny with larger scrotal circumferences. Smith et al. (1989b) showed favorable genetic correlations for scrotal circumference with weaning and yearling weights of .56 and .63, respectively. Knights et al. (1984) reported a .68 genetic correlation between SC and yearling weight, a 0 correlation with weaning weight, and .15 for birth weight. A partial listing of genetic correlations found in the literature are presented in Table 2.9.

The genetic correlation between SC and birth weight appears to be relatively low whereas the correlation between SC and yearling weight is relatively high. This suggests that larger SC (earlier puberty) and faster growth rate is compatible in young bulls. These relationships suggest a favorable growth curve, i.e., reaching a higher percent of mature weight at earlier ages while maintaining or increasing early growth rate and possibly holding mature weight in check.

TABLE 2.9: Genetic correlations between scrotal circumference and measures of growth

Source	Birth Weight	Weaning Weight	Post-Weaning Gain	Yearling Weight
Bourdon & Brinks (1985)	.18	.29	.35	.44
Bourdon & Brinks (1986)	.22	.20		.39
Knights et al. (1984)	.10	.00		.68
Neely et al. (1982)		.86	.22	.52
Smith (1989a)	.08	.56	.59	.63
Lunstra, Gregory & Cundiff (1988)	-.02	.00	.00	.10
Keeton et al. (1996)		.14		
Kriese et al. (1991)	.02	.08	.35	
Kriese et al. (1991)	-.04	.34	.12	

Relationships with Composition

Moser et al. (1996) studied correlated responses in progeny reproduction and growth to selection for scrotal circumference in Limousin bulls. Bulls were grouped initially into large (mean = 36.3 cm) and small (mean = 28.5 cm) lines, and subsequently regrouped according to non-parent SC expected progeny differences into low, average and high EPD categories. Weaning ribeye area was greater for progeny of sires with average scrotal circumference EPD's than those of low SC EPD's. No other differences in composition were reported. Gregory et al. (1995) reported genetic and phenotypic relationships between 368 d SC, body condition score and muscle score. Scrotal circumference genetic and phenotypic relationships with body condition were .1 and .08±.07 respectively. Genetic and phenotypic relationships between SC and muscle score were .0 and -.17± .07.

Keeton et al. (1996) and Neely et al. (1992) reported that ultrasonic measures of backfat were not significant sources of variation in SC.

Heritability

There are several reports in the literature relating to the heritability of SC in yearling beef bulls on both an age and weight adjusted basis (Table 2.10).

These studies indicate that SC in yearling bulls is a moderate to highly heritable trait (approximately 50%) and that selection should be very effective in changing SC.

TABLE 2.10: Heritability estimates for scrotal circumference in yearling beef bulls

Source	Heritability	SE
Age Adjusted		
Bourdon and Brinks (1986)	.49	.06
Coulter and Foote (1979)	.78	.07
Keeton et al. (1996)	.46	.04
Knights et al. (1982)	.36	.06
Latimer et al. (1982)	.38	.16
Lunstra (1982)	.52	
Lunstra, Gregory and Cundiff (1987)	.41	.06
Neely et al. (1982)	.44	.24
Smith et al. (1989a)	.40	.09
Nelsen (1986)	.55	.21
Average	**.48**	
Weight Adjusted		
Bourdon and Brinks (1985)	.46	.06
Lunstra (1982)	.69	
Lunstra, Gregory and Cundiff (1987)	.50	.06
Neely et al. (1982)	.44	.24
Kriese et al. (1991)	.16	
Kriese et al. (1991)	.53	
Average	**.46**	

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Relationships of Scrotal Circumference to Female Reproductive Traits

A heifer's underlying fertility is associated with male reproductive measures. Until recently, heritability estimates for direct measures of fertility were very lowly heritable and unworthy of selection pressure as a means of improving reproductive fitness. Therefore, indicator traits such as scrotal circumference, which is more highly heritable and correlated with female fertility measures, were used in an effort to make genetic progress. The genetic correlation between heifer age at puberty and sire yearling scrotal circumference and has been estimated at -.71, -1.07, -.39, and -.91 (Hoehenboken et al., 1971; King et al., 1983; Gregory et al., 1991; Morris et al., 1992). Lunstra (1982) reported a correlation of .98 among breed means (8 breeds) for SC of bulls with age at puberty in heifers. Hough (1991) reported a 60 ± 28 day advantage in AP for heifer progeny of sires with SC EPD values 2.4 ± .3 cm. larger than those of other sires. Genetic correlation estimates between SC in yearling bulls and age at puberty in half-sib heifers of -.71 and -1.07 (favorable) have been reported by Brinks et al. (1978) and King et al. (1983). In all mentioned studies, heifers related to larger scrotal circumference bulls were more likely to attain early puberty than heifers related to bulls with smaller scrotal circumferences. These very strong genetic relationships, coupled with Lunstra's (1982) data has led others to speculate that heifer age at puberty and SC are essentially the same trait.

Toelle and Robinson (1985) also reported that SC was favorably related genetically to several measures of female reproductive traits. Martin et al, (1992) reported among breed group means, high absolute correlations were observed between SC in males and pregnancy rate in heifers (.97). Smith et al. (1989b, c) reported regressions of -.80 days in age at puberty, -.67 days in day of first calving, and -.83 days in age of first calving of female offspring per centimeter of sire SC. The change in age at puberty is less than that expected based on genetic parameter estimates. Possibly, there is a greater change in inherent age at puberty than in expressed age at puberty due to seasonal or daylight length effects of other environmental limitations such as nutrition. King et al. (1983) reported that although heifers born later in the calving season reached puberty at an earlier age, heifers born earlier in the calving season reached puberty at an earlier date the following year.

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MIXED MODELS

The general mixed model embraces the vast majority of estimation problems encountered from highly unbalanced family sizes and fragmentary data from numerous types of relationships common to many agricultural species. Data sets from which individuals have been eliminated by natural and/or artificial selection may deviate substantially from the base population about which one wishes to make inferences. Further culling of the data to accommodate a conventional statistical technique, such as analysis of variance, even if nonselective, still leads to an inefficient use of information. General mixed models allow the efficient estimation of quantitative genetic parameters under arbitrary settings, including those involving extended pedigrees, unequal family sizes, assortative mating, and selection.

Mixed model theory has existed for a number of years (Eisenhart 1947), and generally describes a model that jointly accounts for fixed and random effects. Fixed effects typically include the population mean and other factors such as birth year, gender, experimental treatment and so forth. Random effects are usually genetic effects such as additive genetic values. The mixed linear model with one random factor is generally described as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where: $\mathbf{y}$ is an N x 1 vector of phenotypic observations,

$\mathbf{b}$ is a p x 1 vector of fixed effects associated with $\mathbf{y}$,

$\mathbf{u}$ is a q x 1 vector of random effects associated with $\mathbf{y}$,

$\mathbf{X}$ is a known incidence matrix of order N x p relating elements of $\mathbf{b}$ to elements of $\mathbf{y}$, expe

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Z is a known incidence matrix of order N x q that relates elements of **u** to elements of **y**, and

E is an N x 1 vector of residual effects.

Additional attributes of the general form of mixed linear models include the expectations of the random variable, which include:

$$E(\mathbf{y}) = \mathbf{Xb},$$

$$E(\mathbf{u}) = \mathbf{0}, \text{ and}$$

$$E(\mathbf{e}) = \mathbf{0}.$$

The (co)variance structure is:

$$Var\begin{bmatrix}\mathbf{y}\\ \mathbf{u}\\ \mathbf{e}\end{bmatrix} = \begin{bmatrix}\mathbf{ZGZ'+R} & \mathbf{ZG} & \mathbf{R}\\ \mathbf{GZ'} & \mathbf{G} & \mathbf{0}\\ \mathbf{R} & \mathbf{0} & \mathbf{R}\end{bmatrix}$$

The Best Linear Unbiased Prediction (BLUP) developed by Henderson (1953) utilizes the mixed model to predict random effects, such as breeding values. A similar procedure, adopted to estimate fixed effects, is referred to as the Best Linear Unbiased Estimator. The procedures are similar in the sense that they share three important functions. They are best by minimizing sampling variance, linear as they are linear functions of observed phenotypes **y**, and unbiased in the sense that E[BLUE(**b**)] = **b** and E[BLUP(**u**)] = **u**. BLUP is primarily used to identify individuals with high estimated genetic merit in selection programs, monitor response to selection and has become the dominant methodology for estimating breeding values. The literature collection describing BLUP methodology is voluminous and extensive (Henderson, 1977a, 1984a, 1988a; Schaeffer, 1991; Kennedy, 1991; Searle et al., 1992; and Mrode, 1996). BLUP methodology is useful to estimate breeding values for a single trait in a strictly additive model, expandable to include estimation of dominance values and maternal effects, and can accommodate repeated records and multiple traits (Lynch and Walsh, 1998).

SIRE MODELS

General linear mixed models form the fundamental framework for BLUP analysis, yet there are numerous ways in which this model can be formulated and applied. Of note to animal breeders is the animal model, which predicts breeding values for each measured individual, the gametic model, which describes breeding values of measured in terms of parental contributions. The reduced animal model developed by Quaas and Pollak (1980) combines aspects of both the animal and gametic models in specific applications in which parental breeding values are of primary interest. The objective here is to focus on the gametic model, specifically as it is used to evaluate sires for important traits.

The gametic model is often used when parental breeding values are of more concern than offspring values, as when one is attempting to estimate the breeding value of bulls from large arrays of descendants (Lynch and Walsh, 1998). In this model, the additive genetic value of each offspring is expressed in terms of its parents' breeding values. The sire model is a variation of the gametic model wherein the dam contribution is ignored and incorporated into the error term.

Variations in the sire model primarily concern whether relationships among sires are considered. Kemp et al. (1984) indicated additive genetic relationships between sires are important as their inclusion reduces standard errors of prediction.

BIVARIATE MODELS

Several traits of interest in animal breeding appear as categorical variables. Analysis of such variables by linear methodology violates several assumptions of the linear model and is not optimal (Gianola 1982). A more satisfactory method is based on the threshold model concept (Wright, 1934). Statistical treatment of the threshold model has been developed for sire evaluation by Gianola and Foulley in a Bayesian setting, and equivalently by Harville and Mee (1984) from a classical viewpoint.

Janss and Foulley (1993) attempted to perform a genetic evaluation of French beef bulls for calving difficulty which includes a bivariate analysis of birth weight in an attempt to increase accuracy of prediction. Birth weight was included due to its high genetic and residual correlation with calving difficulty (Philipsson, 1976; Meijering, 1985). Simianer and Schaeffer (1989) have described bivariate analyses for evaluation of a binary and continuous variable. However, their methods lack general applicability when missing records exist and/or different fixed effects influence each trait. Janns and Foulley (1993) described general bivariate analyses that successfully accommodated unequal design matrices for a binary and continuous variable. The usefulness of the information matrix to obtain standard errors, loss of information when records with missing data are not included, and ability of this analysis to correct for selection on one of the traits were investigated by simulation.

Observations for the continuous trait followed the linear model:

Model 1: $\mathbf{y_1} = \mathbf{X_1 b_1} + \mathbf{Z_1 u_1} + \mathbf{e_1}$

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where **X** and **Z** were incidence matrices, relating records to fixed effects (**b**) and to sire-effects (**u**) for birth weight. The error variance is given as σ^2_{e1}.

Observations for the threshold trait calving difficulty was modeled as:

Model 2: $\mathbf{y_2 = X_2b_2 + Z_2u_2 + E(e_2 \mid e_1) + e^*_2}$

where all terms are similar to those in Model 1 and E denotes expectation. Model 2 conditions observations for calving difficulty on birth weight, so that the remaining error, $\mathbf{e}^*_2$, is uncorrelated with the error for the continuous trait. This enables writing the joint likelihood of the data. The variance on the underlying scale is arbitrary (=1).

The variance structure for sire effects is given as:

$$V\begin{bmatrix}\mathbf{u}_1\\ \mathbf{u}_2\end{bmatrix} = G = \begin{bmatrix}\mathbf{G}_{11} & \mathbf{G}_{12}\\ \mathbf{G}_{21} & \mathbf{G}_{22}\end{bmatrix} = \begin{bmatrix}\mathbf{I}\sigma^2_{U11} & \mathbf{I}\sigma^2_{U12}\\ \mathbf{I}\sigma^2_{U21} & \mathbf{I}\sigma^2_{U22}\end{bmatrix} \ldots\text{and}\ldots \mathbf{G}^{-1} = \begin{bmatrix}\mathbf{G}^{11} & \mathbf{G}^{12}\\ \mathbf{G}^{21} & \mathbf{G}^{22}\end{bmatrix}$$

Sires in this analysis were assumed unrelated, but an extension to include relationships between sires is straightforward by defining **G** differently.

Accuracy of evaluation improved for both traits in bivariate analysis. The increase in accuracy is particularly substantial for the discrete trait when all data are included. The relative increase in accuracy ranged between 15 and 30%. The most significant aspect of this methodology is the ability to account correctly for the information content of a discrete observation.

SUMMARY OF LITERATURE

Significant genetic and phenotypic variation exists within and between breeds of beef cattle for age at puberty (AP). In general, faster-gaining breed groups of larger mature size reach puberty at a later age than do slower-gaining breed groups of smaller mature size. Breeds selected for milking ability reach puberty at younger ages than do those breeds not selected for milk production. Heterosis, independent of heterosis effects on weight, influences most measures of puberty in females and scrotal circumference (SC) in males. Crossbred heifers reach puberty at younger ages and heavier weights than their straightbred counterparts. Age at puberty in both bulls and females appears to be a good indicator of inherent fertility and expressed reproductive efficiency, especially in the early productive years. Scrotal circumference is an excellent measure of age at puberty in yearling bulls. Furthermore, a favorable genetic relationship exists between SC in bulls and AP of female offspring. Scrotal circumference is relatively easy to obtain, highly heritable and is favorably related to seminal characteristics and measures of early growth. Reproductive tract score, although not as specific a measure as age at puberty, possesses many of the same attributes regarding measurability and repeatability as scrotal circumference in yearling bulls. Thus, AP appears to be a feasible and good selection criterion in yearling heifers. Limousin cattle are consistently older at puberty and less reproductively efficient throughout their lifetime than many other breeds.

Selection to improve threshold traits, such as fertility, becomes particularly challenging because of the strong influence of environment and importance of genotype x environment interactions. Furthermore, genetic antagonisms that exist between expressed fertility and milk/growth in certain environments create still greater challenges. Age at puberty, however, is expressed in a female before potential interactions with traits like milking ability have the opportunity to be expressed. Therefore, age at puberty may be the most reliable indicator of inherent fertility. Consequently, selection for age at puberty or more easily measured traits such as age of first calving or scrotal circumference may provide the most feasible strategy for making genetic improvement at this time.

IMPLICATIONS

Limousin breeders can choose from multiple strategies to attempt selection for improved fertility. The first involves direct selection for fertility traits. Scrotal circumference, because it is relatively highly heritable and easy to measure, is a likely candidate for selection. Other possibilities include traits mentioned earlier, as well as age at first calving, calving interval and longevity. The utility of any prospective fertility trait depends on its ease of measure and relationship with inherent fertility. Furthermore, breed associations that gather complete and accurate reproductive data from breeders are able to provide substantial information and service to aid producers in their genetic improvement efforts. Obviously, the value of the information generated is highly dependent on the extent of breeder participation.

The indirect approach to breeding for improved fertility involves selection for an array of traits that have favorable correlated effects on fertility. These include milk production, calving ease, growth rate, and body condition. By selecting for optimum combinations of these traits, breeders create a favorable "genetic environment" for fertility. The objective would be simply to set the levels of other traits in such a way that expressed fertility is optimized. This is the point at which genotype x environment interactions are of major concern, and producers must be aware of management level required to achieve desired fertility levels.

The success of either approach to seedstock breeding will depend on the extent to which traits of interest are incorporated into national genetic evaluations. With potentially vast amounts of family and progeny data available, it is possible to accurately identify sires with exceptional breeding values for even lowly heritable traits. Many breed associations currently report expected progeny differences (EPD) for scrotal circumference and additional indicators of fertility traits, such as longevity (Limousin, Gelbvieh, Red Angus). Obviously, whole herd reporting and comparable efforts by breeders regarding data collection and submission to the breed association are critical if reliable accuracies are to be generated. Used correctly, this information accommodates a rate of progress inconceivable through traditional phenotypic selection.

As with other traits, genetic improvement in fertility traits will come largely through sire selection. Strict culling regimens based on expectations of heifer and cow reproductive performance will satisfactorily eliminate the problem females from the herd. However, dam selection, as a method for improving fertility, suffers from poor accuracy of breeding value prediction and low selection intensity. The key to genetic improvement of fertility is identifying and using superior sires.

The direct and indirect approaches to breeding for improved fertility are appropriate for commercial herds as well. Commercial breeders generally have more flexibility, however, of being able to apply each approach on a between and within-breed basis. Using the direct

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approach, they can choose outstanding sires for SC and AP within breeds, utilize them according to knowledge of breed differences for fertility and other economic traits, and reap the additional advantages of heterosis on reproductive fitness. Commercial breeders can also use the indirect approach, once the proper economic balance of milk, growth, mature size and fertility has been determined. More importantly, although reliance on heterotic effects in the crossbred cow to provide ample expressed fertility is justified, sire selection remains critical.

Limousin breeders have the opportunity to improve the reproductive ability of their cattle and maintain breed strengths of muscling and efficient growth. The extent to which they prioritize this task will largely determine the role Limousin cattle play in the beef industry of the future.

Chapter 3

Phenotypic relationships between reproductive fitness and composition traits of Limousin cattle.

D. D. Faidley[1], B. D. Banks[1], R. J. Tempelman[1], H. D. Ritchie[1], K. J. Andersen[2], and D. G. LeFever[3]

[1]Michigan State University, E. Lansing, [2]North American Limousin Foundation, Englewood, CO, [3]Colorado State University, Fort Collins.

Abstract

Phenotypic relationships between composition traits and indicators of fertility were evaluated from Limousin field data collected at Running Creek Ranch, Elizabeth, CO. Yearling reproductive tract score (RTS) of 1,575 heifers and scrotal circumference (SC,) of 1,247 bulls were analyzed separately. Traits measured included yearling weight (WT, kg), RTS of heifers, SC (cm) of bulls, body condition score (BCS), and muscle score (MS). For RTS analyses, heifers were either grouped as cycling (n=1134, RTS≥4) or non-cycling (n=442, RTS≤3). Logistic regression analyses were performed on heifers using SAS® to model the dichotomous response variable (cycling vs. non-cycling) as a function of the main effects of heifer age (AGE, days), age of dam (AOD), WT, percent Limousin (PL), year (YR), MS, BCS. The model for SC was similar, with the addition of the WT by MS interaction. Percent Limousin, additional interactions, and quadratic

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terms for WT and AGE were not important in either model (P>.1). In general, increases in WT, AGE and BCS favorably affected both the probability of cycling and SC. Odds ratio estimates for cycling of BCS 6 and BCS 7 heifers relative to BCS 5 were 8.272 ($p<.001$) and 3.333 ($p<.001$), respectively. Regression coefficients for SC on WT and AGE were .021, cm/kg and .015, cm/day, respectively. Solutions for SC on BCS increased .6 cm for a BCS increase from 5 to 6 and 1.2 cm for an increase from 5 to 7 ($p<.05$). There were sex effects of muscularity on reproductive fitness traits. Favorable odds ratio estimates for MS 2 and MS 3 heifers on RTS were 1.905 and 1.896 relative to MS 1 ($p<.05$). Average and heavy muscled heifers did not differ in probability of cycling (p>. 5). However, heavier muscled bulls had significantly smaller scrotal measurements than average and light muscled bulls ($p<.05$). Solutions of SC for light and average muscled bulls were $.783 \pm .335$ and $.485 \pm .136$, cm. Regression coefficients for SC on WT by MS were $.018 \pm .005$ and $.007 \pm .003$, cm/kg for MS 1 and MS 2, respectively. These results pose selection and management concerns for Limousin breeders wishing to improve fertility and maintain muscularity of their cattle.

Introduction and Objectives

Breeders of Limousin cattle have targeted reproductive fitness for improvement while maintaining inherent breed muscle advantages. Relationships between fertility and carcass composition traits are not well defined, but represent important considerations in breeding stock selection.

The dichotomous nature of fertility traits (e.g. cycling vs. non-cycling, pregnant vs. non-pregnant) does not facilitate distinction of the subtle differences in inherent fertility that exist between females. Furthermore, poor accuracy of breeding values for fertility traits coupled with lower selection intensity in female populations restrict progress through dam selection. Consequently, sire selection for fertility traits, such as scrotal circumference, is considered the most rapid method for improving inherent fertility in beef cattle.

Some have speculated that age at puberty in heifers is influenced by the same genes as scrotal circumference in yearling bulls due to strong, favorable genetic correlations (Brinks et al., 1978; King et al., 1983). Correlations among breed means (Lunstra, 1982; Gregory et al, 1991; Gregory et al, 1992; Cundiff, et al., 1993) have supported this conclusion, and indicated phenotypic expression of scrotal circumference, age at puberty and other fertility traits were lower in Limousin cattle than other breeds. Moreover, both female age at puberty and scrotal circumference have been shown to be favorably related to growth, reproduction and maternal performance. (Laster et al., 1979; Werre, 1980; Bourdon and Brinks, 1986; Werre and Brinks, 1986; Smith et al., 1989)

Gregory et al. (1995) reported small favorable genetic and phenotypic correlations for body condition score with scrotal circumference in yearling bulls and age at puberty in yearling females. Limousin heifers were shown to be the leanest of nine breed groups in the Germ Plasm Evaluation Project (GPE) at the Meat Animal Research Center, Clay Center, NE, and among the latest for age at puberty (Gregory, et al., 1991).

Subjective muscle scores (1 = extremely light muscled to 9 = extremely heavy muscled) were assigned to yearling bulls in the GPE project (Gregory et al., 1995) and shown to have a negative genetic relationship (-.17±.07) with scrotal circumference, but no phenotypic relationship. Moser et al. (1996), reported no difference in composition among yearling crossbred progeny of Limousin sires with high and low adjusted yearling scrotal circumferences (difference=8 cm). However, sires with average SC expected progeny differences (EPD) had progeny with significantly larger weaning ultrasonic ribeye area measurements than those of low SC EPD sires.

Therefore, the objectives of this study were to:

1) model the effects of composition on indicators of fertility in yearling cattle and,
2) determine if those relationships (if any) were different between males and females.

Materials and Methods

Heifer Population.

Data. Field data collection was initiated in 1990 on 2179 yearling Limousin heifers as part of ongoing research at Running Creek Ranch, Elizabeth, CO. Traits measured included yearling weight (WT, kg), body condition score (BCS) as described by Ritchie et al. (1992), reproductive tract score (RTS as described by Andersen et al. (1991), and muscle score (MS) which will be described later. All data collection was performed by the same, trained technician. Herdbook information for Running Creek Ranch was provided by the North American Limousin Foundation (NALF), Englewood, CO. Heifer age (AGE, days), age of dam (AOD, years), and percent Limousin (PL) information was obtained from the NALF herd file.

Heifer Management. The heifers included in this analysis were recorded in mid-May when the majority were approximately 13 months of age. Calves were not creep fed. Following weaning, heifers were wintered in a single contemporary group under dry-lot conditions. No healthy heifers were culled or removed from the replacement heifer group until after they had been measured as yearlings. Heifers were fed a silage-based ration adequate for maintenance and approximately .8 kg/day gain. The herd objective is to retain or sell as many replacement females as possible. Consequently, the feeding objective was to maximize the number of heifers cycling at the time of measurement. Therefore, heifers were grown at a rate sufficient to ensure that optimum weight and body condition levels for cycling were reached. Cycling heifers were implanted with Syncro-Mate B at the time of recording to synchronize estrus at the start of the breeding season.

Reproductive Tract Scoring System. Several researchers have studied age at puberty (AP) in beef heifers when defined as the age at first behavioral estrus. However, because AP is difficult and labor-intensive to measure, direct selection for age at puberty in females is seldom practiced. Andersen et al. (1991) described the reproductive tract scoring (RTS) system developed at Colorado State University which estimates pubertal status via rectal palpation of the uterine horns and ovaries. Each heifer is assigned a score of 1 (infantile) through 5 (palpable corpus luteum) as described in Table 3.1.

A RTS of 1 is assigned to heifers with infantile tracts as indicated by small, toneless uterine horns and small ovaries devoid of significant structures. Heifers scored as 1 are likely the furthest from cycling at the time of examination. Heifers given a RTS of 2 are thought to be closer to cycling than those scoring 1 due primarily to the presence of small follicles and slightly larger uterine horns and ovaries. Those heifers assigned a RTS of 3 are thought to be on the verge of cycling based on slight uterine tone in addition to the presence of follicles. Heifers scoring 4 are presumably cycling as indicated by good uterine tone, uterine size, and follicular growth. However, heifers with tract scores of 4 lack an easily distinguished corpus luteum due to the stage of the estrous cycle. Heifers with tract scores of 5 are similar to those scoring 4 except for the presence of a palpable corpus luteum.

Table 3.1. Description of reproductive tract scores[a]

		Ovaries (approx. size)			
Repro. tract scores	**Uterine horns**	**Length (mm)**	**Height (mm)**	**Width (mm)**	**Ovarian structures**
1	Immature < 20 mm diameter - no tone	15	10	8	No palpable follicles
2	20-25 mm diameter - no tone	18	12	10	8 mm follicles
3	25-30 mm diameter - slight tone	22	15	10	8-10 mm follicles
4	30 mm diameter - good tone	30	16	12	< 10 mm follicles corpus luteum possible
5	> 30 mm diameter - good tone, erect	>32	20	15	>10 mm follicles corpus luteum present

[a] Reproductive tract score was determined less than 1 mo. prior to start of breeding season.

Muscle Score. Numerous studies have reported use of a scoring system to describe musculary differences between cattle (Gregory et al., 1995; Koch et al., 1995; Wolfe et al., 1990). Subjective scores were assigned utilizing visual appraisal of an animal's topline, hip, rear quarter, and base width. For these analyses ordinal scores ranged between 1 and 3.5 with higher levels indicating greater muscularity as follows:

1.0) Light muscled. Narrow loin, hip and stance and tapered through the quarter. Little visible muscle tissue.

1.5) More apparent muscling than in muscle score 1, yet flat quartered and narrow throughout.

2.0) Average muscling. Moderate muscle shape in topline and rear.

2.5) Above average muscularity.

3.0) Heavily muscled. Wide stance, thick and expressive quarter and hip, broad loin with visible muscle shape throughout topline.

3.5) Very heavily muscled. Abundant visible muscular shape and dimension throughout.

Data Editing. For these analyses heifers were either grouped as cycling (72%, RTS≥4) or non-cycling (28%, RTS≤3). Thus, RTS was used to simply distinguish between pre-pubertal heifers and heifers who had reached puberty. Yearling MS ranged from 1 to 3.5 and were grouped as light (MS<2), average (MS 2) or heavy muscled (MS>2). All heifers had BCS between 5 and 8. Percent Limousin (PL) was included to account for potential heterosis effects. Initially, PL was grouped according to NALF specifications as: 37-50, 51-75, 76-87, 88-93, 94-100. However, due to the existence of predominantly high percentage cattle and resulting small class sizes in the lower percentage categories, PL was regrouped: < 75, 75-87, > 87. Year and PL effects were reparameterized to sum to zero, so reported solutions are for the mean YR and mean PL. Age of dam (AOD) was stratified for 2, 3, 4-10, and greater than 10 year old dams. The mean age and actual weight at time of recording were subtracted from each record on age and weight respectively, to minimize computer round off error. Heifers with missing responses or explanatory covariates (n=603) were removed from the analysis. Only those females with a complete array of response and explanatory variables remained.

Table 3.2. Data description for Running Creek Ranch females

Trait		Mean	Percent	Range
Age (days)		398		308-473
Weight (WT, kg)		380		210-525
Percent Limousin (PL)				
	< 75%		15%	
	76-87%		28%	
	> 87%		57%	
Age of dam (AOD)				
	2		18%	
	3		16%	
	4-10		58%	
	>10		8%	
Reproductive Tract Score (RTS)		4.6		1-5
	Cycling (≥ 4)		72%	
	Non-cycling (< 4)		28%	
Muscle Score (MS)		2.2		1-3.5
	Light (≤ 1.5)		15%	
	Average (= 2)		60%	
	Heavy (≥ 2.5)		25%	
Body Condition Score (BCS)		6.2		5-8
	5		2.5%	
	6		57%	
	7		39%	
	8		1.5%	

Bull Population.

Data. Data collection on 1,472 yearling Limousin bulls at Running Creek Ranch, Elizabeth, CO was also initiated in 1990. Traits measured were the same as those for the heifer analysis with the substitution of SC for RTS.

Bull Management. Bulls were reared under similar conditions as their heifer mates, though an unknown number were culled at weaning, presumably due to lack of performance. The important distinction is that after weaning, bulls were grown at proportionately slower rates relative to their gain potential than were females. Running Creek Ranch has a substantial number of repeat and potential customers who prefer 18-month old bulls for use in fall calving programs, and two-year old bulls that can be exposed to more cows. Cost of gain is a more important economic factor than maximum early growth to their bull production efforts. Consequently, there were no apparent rate of gain targets for the bulls. Therefore, bull development strategies utilized lower quality, more cost effective feeds. Bulls that met NALF recommendations for adjusted yearling scrotal circumferences (≥32 cm.) could be sold in the spring as yearlings or later. Bulls that failed to meet Society of Theriogenology criteria for breeding soundness examinations at sale time (SC<30 cm.) were culled.

Data Editing. Procedures followed when grouping, AOD, PL, and MS for RTS analysis were replicated prior to modeling SC. In this case, however, final PL classes were 51 to 75, 76 to 87, 88 to 93, 94 to 100. All bulls had BCS between 4 and 7. Bulls with missing data (n=225) were removed from the analysis. Only those males with a complete array of response and explanatory variables remained.

Table 3.3. Data description for Running Creek Ranch males

Trait		Mean	Percent	Range
Age (days)		383		308-473
Weight (WT, kg)		429		260-732
Percent Limousin (PL)				
	< 75%		15%	
	76-87%		21%	
	> 87%		64%	
Age of dam (AOD)				
	2		13%	
	3		16%	
	4-10		63%	
	>10		8%	
Scrotal Circumference (SC, cm)		32.1		22-42.3
	≥ 34		25%	
	≤ 30		25%	
Muscle Score (MS)		2.3		1-3.5
	Light (≤ 1.5)		8%	
	Average (= 2)		56%	
	Heavy (≥ 2.5)		36%	
Body Condition Score (BCS)		5.8		4-7
	4		.3%	
	5		27%	
	6		70%	
	7		2.4%	

n = 1247

Reproductive Tract Score Analysis.

Logistic regression analyses were conducted using SAS® (Proc Logistic, 1995) to model the dichotomous response variable (RTS) grouped as cycling (1) and non-cycling (0) as a function of continuous and fixed categorical explanatory variables. Cycling status was assumed to follow a binomial distribution with the probability of the i^{th} heifer cycling equaling P_i. Logistic modeling is advantageous over standard linear modeling in this instance as it guarantees the estimates obtained for probability of cycling will range between 0 and 1 and allows a more tenable distributional assumption. The logistic function is described as follows: $f(z) = \frac{1}{1+e^{-z}}$. The value of logistic function is dependent on the value of z. To obtain the logistic model from the logistic function, z is written as a linear function of independent variables (X's).

$$z = \alpha + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$$

The logistic model for the conditional probability of cycling given characteristics $X_1,\ldots,X_k$, i.e. $P(CY|X_1,\ldots,X_k)$ is written as follows:

$$f(z) = \frac{1}{1+e^{-(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = \frac{e^{(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}}{1+e^{(\alpha+\beta_1 X_1+\beta_2 X_2+\ldots+\beta_k X_k)}} = \frac{1}{1+e^{-(\alpha+\sum_{i=1}^{k}\beta_i X_i)}}$$

where α, β_1, $\beta_2,\ldots,\beta_k$ are parameters to be estimated. Parameter estimation is performed through maximum likelihood techniques.

The final model included the main effects of AGE, WT, PL, year (YR), MS, and BCS.

P(Cycling) = natural log probability of cycling

- a intercept
- YR year (1990, 1991, 1992, 1993, 1994, 1995, 1996)
- PL percent Limousin (< 75, 75-87, > 87)
- AOD age of dam (2, 3, 4-10, >10)
- MS muscle score (1, 2, 3)
- BCS body condition score (5, 6, 7, 8)
- AGE age at recording deviation from the mean age
- WT actual weight at recording deviation from the mean weight

Note the absence of a normally distributed error term. Variability is defined by the binomial distribution as:

$$Var(p_i) \equiv p_i\,(1 - p_i)$$

Scrotal Circumference Analysis.

Regression analyses were conducted using PROC MIXED of SAS®. No random effect was fitted, but PROC MIXED was selected for two reasons. First, general linear models produced the same results as mixed model methodology in the absence of random effects. Second, mixed models account for fixed and random effects, such as genetic effects, and thus this phenotypic analysis serves as a precursor to a genetic analysis. The fixed effects model used in this analysis is given by the following expression: $y = \mathbf{X}\boldsymbol{\beta} + \mathbf{e}$ where **y** denotes the vector of observed scrotal circumferences, **X** is the known matrix of explanatory variables, **β** is the unknown fixed effects parameter, and **e** is the unknown vector of independent and identically distributed Gaussian random errors.

The final model included main effects: year (YR), PL, AOD, AGE, WT, MS, BCS and YR by MS interaction. Additional interactions and PL were not important (P>.1). Keeton et al. (1996) suggested either bull age or bull weight should be fit to a scrotal circumference model, as the traits were highly and favorably correlated (.91). In these data however, bull AGE and WT were related only a modest r=.37 (p<.0001).

Linear Model - Bulls

SC=

- a — intercept
- YR — year (1990, 1991, 1992, 1993, 1994, 1995, 1996)
- PL — percent Limousin (< 76, 76-87, 88-93, >93)
- AOD — age of dam (2, 3, 4-10, >10)
- MS — muscle score (1, 2, 3)
- BCS — body condition score (4, 5, 6, 7)
- AGE — age at recording deviation from the mean age
- WT — actual weight at recording deviation from the mean weight
- WT*MS — weight by muscle score interaction
- e — random error $N \sim (0, I\sigma^2_e)$

Results

Probability of cycling.

Parameter estimates for probability of cycling are given in Table 3.4. The baseline predicted probability of cycling for heifers was .27. This value corresponds to a heifer of mean percent Limousin, born in the mean year to a >10 year old dam, of average age and weight, with body condition score 5 and muscle score 1. As expected, heifer age was the most significant source of variation ($p<.000$), and had the largest chi-square value. Although WT was not as important ($p = .067$), the authors felt it was questionable enough to remain in the model. Furthermore, each kg increase in weight increases probability of cycling by one-tenth of a percent. The effects of age and weight are depicted graphically in figure 3.1.

Effects of composition on probability of cycling. In general, heavier muscled and fatter heifers were more likely to be cycling than their lighter muscled and/or leaner counterparts. Predicted cycling status was not different among average and heavy muscled heifers according to Wald tests ($p>.1$), but both groups were advantageous to light muscled heifers regarding probability of cycling ($p<.05$). These muscle score effects are depicted in figure 3.2.

Although muscle score effects were significant, body condition score was a more important factor affecting predicted probability of cycling. Increases in BCS had favorable affects on reproductive tract maturity. Obese heifers (BCS 8) were the exception, as their odds for cycling were lower numerically than those heifers in good condition (BCS 7). However, Wald tests for significant differences between body condition scores revealed

BCS 8 heifers were not different than BCS 6 or BCS 7 ($p>.05$). Heifers recording body condition scores of 8 were a relatively small percentage of the population and associated parameter estimates had a larger standard error than other reported solutions. All other body condition score classes were significantly different from each other ($p<.05$). Body condition score effects are plotted in figure 3.3.

The combined effects of muscularity and body condition indicate the relative importance of each trait on predicted probability of cycling. Fatter and heavier muscled heifers were the most likely to be cycling. The leanest and lightest muscled heifers were the least likely to be cycling. Figure 3.4 indicates that the combination of fatter and lighter muscled heifers is preferable to lean, heavy muscled heifers regarding reproductive tract maturity.

Some may be concerned about possible confounding of muscle score and body condition scores. Logic dictates muscle and fat accretion accompany increases in age and weight under conventional management practices. Subjectively assigned scores such as these are certainly more prone to bias than are objectively measured traits. Step-wise selection procedures were utilized to test interactions between composition and continuous traits. As previously mentioned, no interactions explained significant variation above and beyond that described by the main effects model. Likewise, model fit statistics indicated the main effects model sufficiently described the relationships of age, weight, body condition and muscularity with reproductive fitness. The combined effects of age, weight, body condition and muscularity are described in figure 3.5.

These data suggest that selection of heavier muscled replacement heifers, given adequate weight and body condition score, is not detrimental to reproductive fitness.

Table 3.4. Parameter estimates for probability of cycling.[a]

Variable	Parameter Estimate	SE	Chi-Square	Pr < Chi-Square	Odds Ratio
Intercept	-1.012	.378	7.177	.007	-
Weight[b] (kg)	.004	.002	3.348	.067	1.004
Age[b] (days)	.018	.003	29.634	.000	1.018
Muscle Score[c]					
3	.640	.262	5.947	.015	1.896
2	.645	.231	7.822	.005	1.905
1	-	-	-	-	-
Body Condition Score[d]					
8	1.862	1.111	2.827	.093	6.476
7	2.113	.395	28.549	.000	8.272
6	1.204	.355	12.912	.000	3.333
5	-	-	-	-	-
Age of Dam					
2	-.085	.135	.391	.532	.919
3	.408	.146	7.797	.005	1.504
4-10	.176	.100	3.087	.079	1.193
>10	-	-	-	-	-

[a] Year and percent Limousin were reparameterized to sum to zero; thus estimates are provided for the mean year calved and percent Limousin.
[b] Expressed as deviations from the mean.
[c] MS; 3 = heavy muscled, 2 = average muscled, 1 = light muscled.
[d] BCS; 8 = Obese, 7 = Good, 6 = High Moderate, 5 = Moderate

Figure 3.1. Probability of cycling for heifers with composition differences as both age and weight are increased.

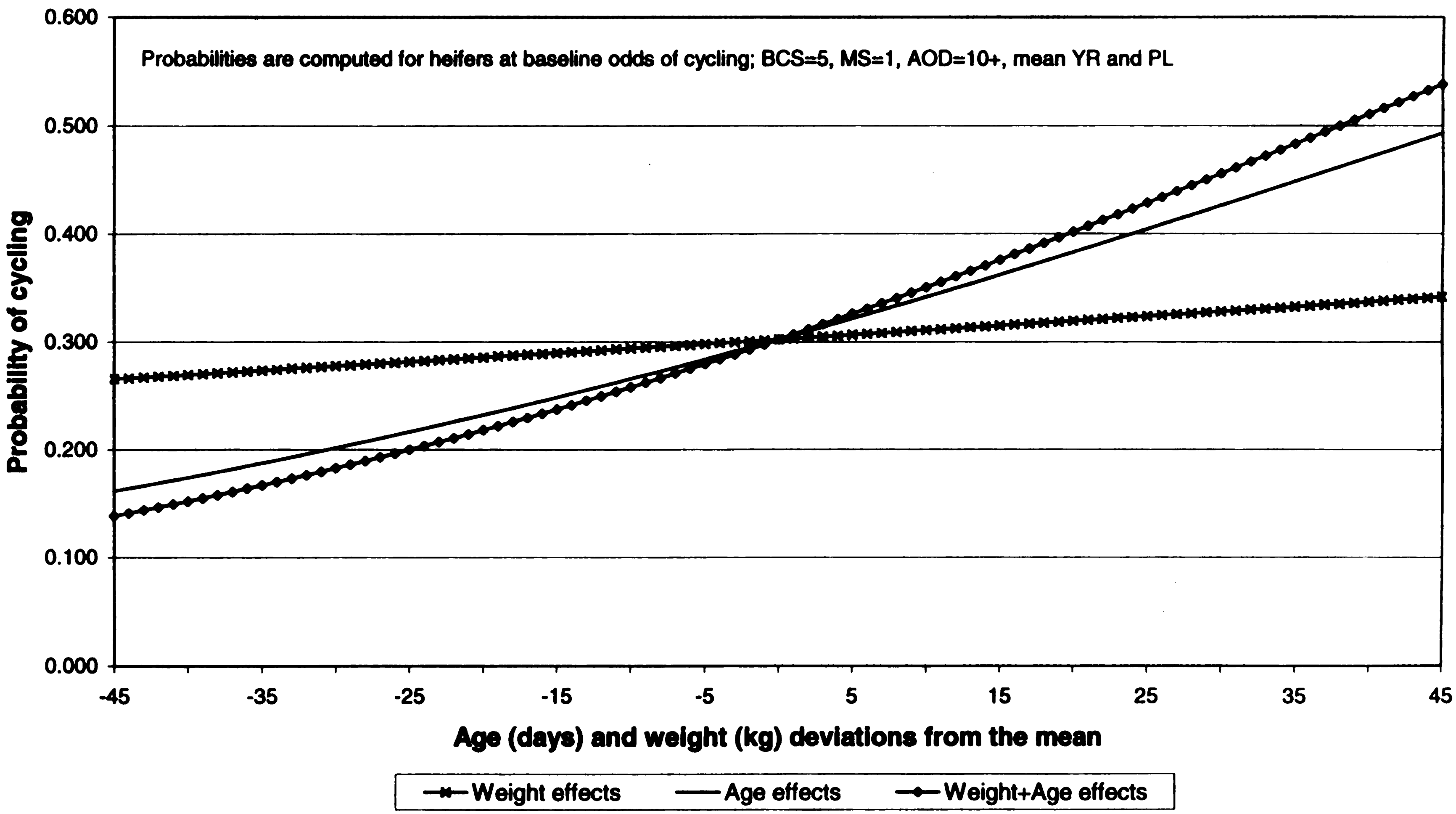


Figure 3.2. Probability of cycling for body condition score 6 heifers with muscle and age differences

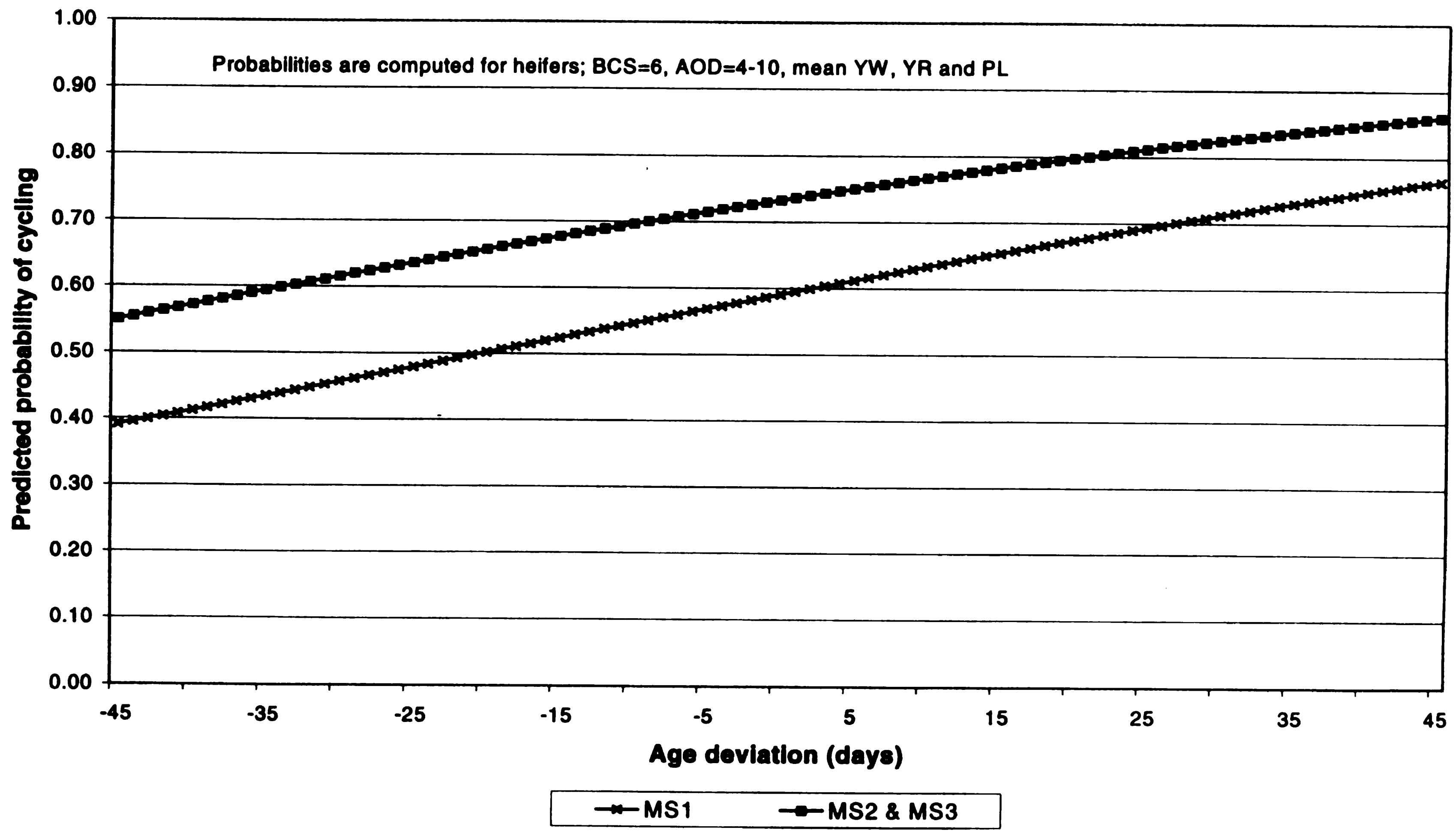


Figure 3.3. Probability of cycling for average muscled heifers with body condition and age differences

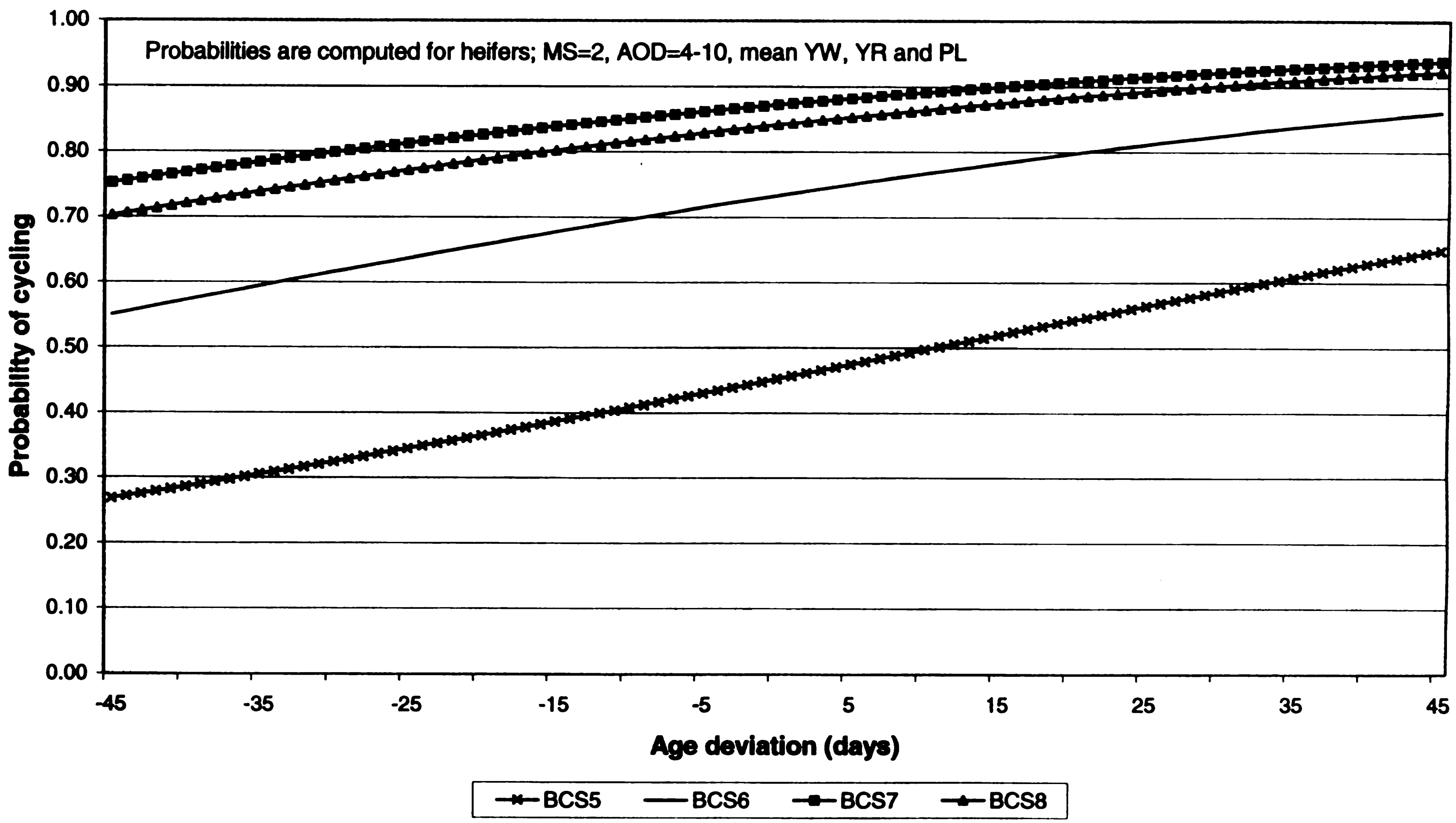


Figure 3.4. Probability of cycling for heifers with composition and age differences

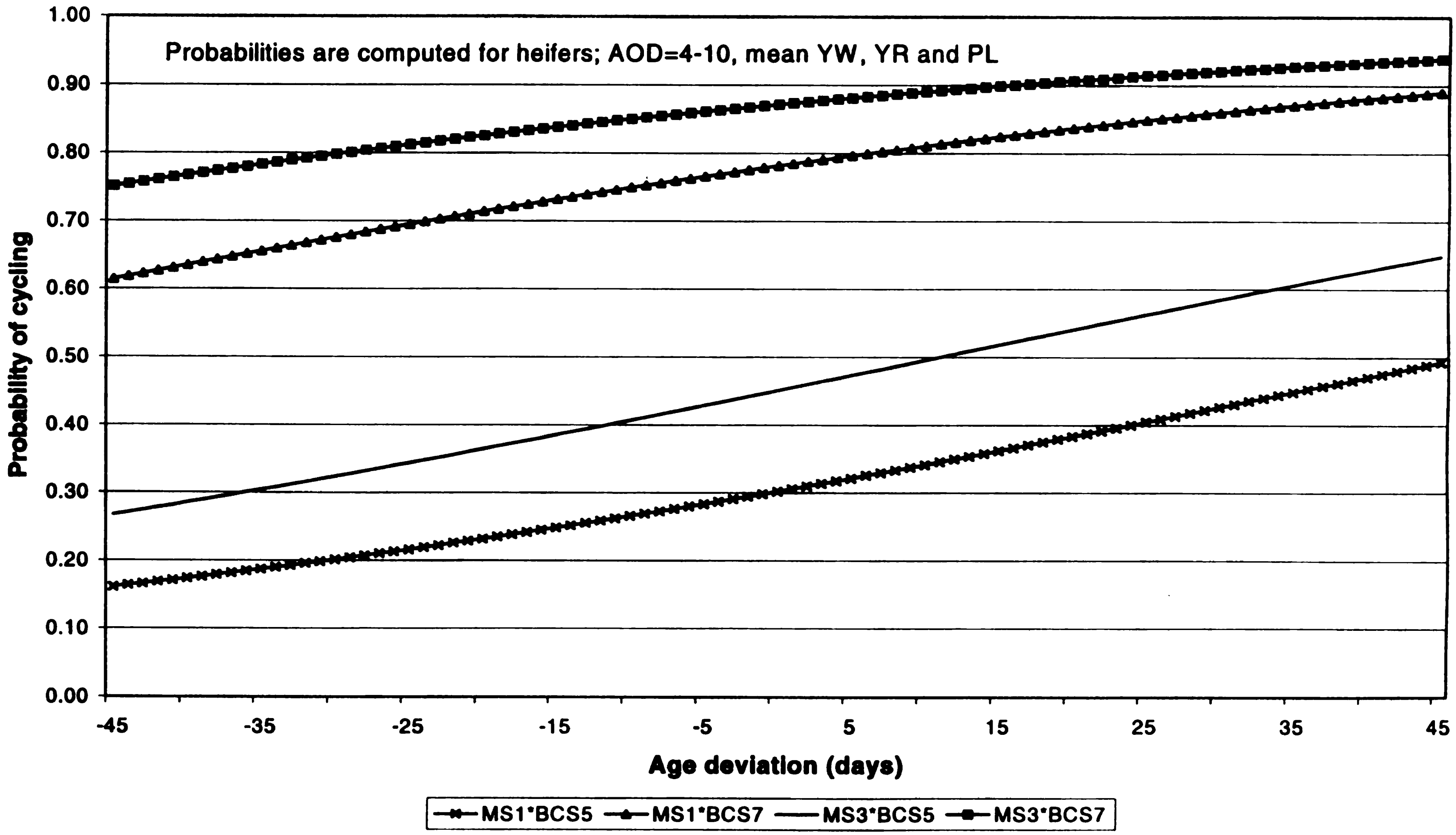
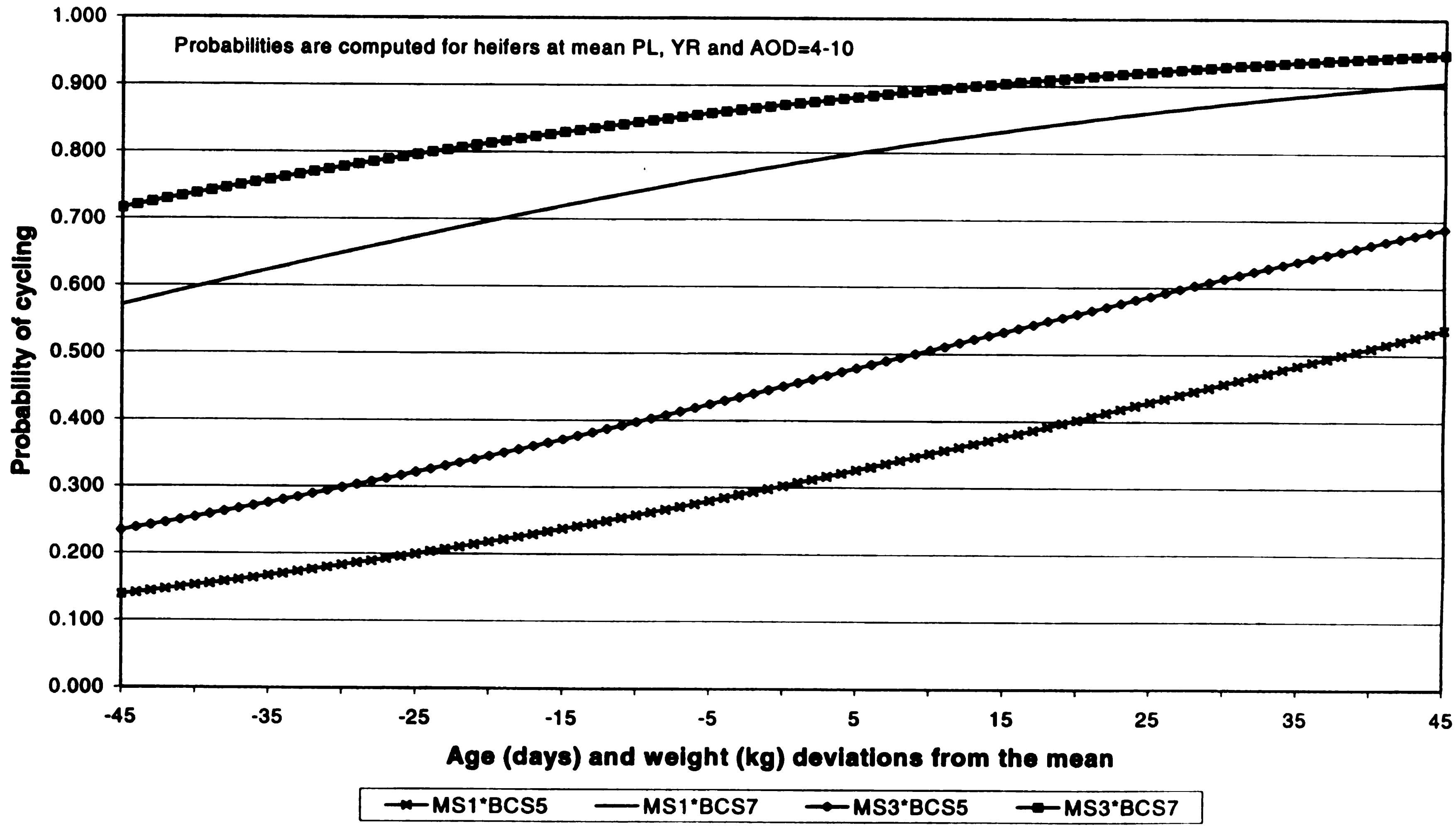


Figure 3.5. Probability of cycling for heifers with composition differences as both age and weight are increased.



Scrotal Circumference.

Parameter estimates for fixed factor effects on yearling scrotal circumference are given in table 3.5. The mean scrotal circumference was 31.9 cm., which is close to Limousin breed recommendations for yearling bulls (Directions, Limousin Breeders Symposium, 1990). Both weight and age were significant sources of variation in scrotal circumference ($p<.05$). As expected, scrotal circumference increased with increasing age and weight. Regression coefficients for WT and AGE were .0224, cm/kg and .0075, cm/day respectively. AOD effects were important for sons of first calf heifers and consistent with estimates and adjustment factors reported in literature. Sons of 3-year old and mature dams did not have significantly different scrotal circumferences, but parameter estimates tended to follow literature estimates.

Composition effects on scrotal circumference. Somewhat contrary to estimates of heifer fertility, fatter and lighter muscled bulls had larger scrotal circumferences (Figure 3.6). Excluding BCS 4 (n=4), bulls with higher BCS values had larger yearling SC. Solutions for SC on BCS increased .6 cm for a BCS increase from 5 to 6 and 1.2 cm for an increase from 5 to 7 ($p<.05$). Heavier muscled bulls had significantly smaller scrotal measurements than average and light muscled bulls ($p<.05$). Solutions of SC for light and average muscled bulls were $.808 \pm .338$ and $.479 \pm .136$, cm. Additionally, there was a weight by muscle score interaction which contributed to the negative effect of increased muscularity on scrotal circumference (figure 3.7). Coefficients for SC on WT by MS were $.018 \pm .005$ and $.007 \pm .003$, cm/kg for MS 1 and 2, respectively.

Table 3.5. Parameter estimates for yearling scrotal circumference.

Variable		Parameter Estimate	SE	T	Pr < |T|
Intercept		31.928	.485	65.84	.000
Weight[a] (kg)		.021	.002	8.75	.000
Age[a] (days)		.015	.004	3.71	.000
Muscle Score[b]					
	1	.783	.335	2.33	.019
	2	.485	.135	3.58	.000
	3	-	-	-	-
Wt*MS[c]					
	1	.018	.005	3.27	.001
	2	.007	.003	2.33	.020
	3	-	-	-	-
Body Condition Score[d]					
	4	-.816	1.155	-.71	.480
	5	-1.252	.430	-2.91	.004
	6	-.621	.394	-1.58	.116
	7	-	-	-	-
Age of Dam					
	2	-.569	.275	-2.07	.039
	3	-.161	.256	-.63	.529
	4-10	.225	.223	1.01	.314
	>10	-	-	-	-

[a] Expressed as deviations from the mean.
[b] MS; 1 = light muscled, 2 = average muscled, 3 = heavy muscled
[c] Interaction between weight and muscle score class.
[d] BCS; 4 = Thin, 5 = Moderate, 6 = High Moderate, 7 = Good.

Figure 3.6. Age adjusted composition effects on predicted scrotal circumference

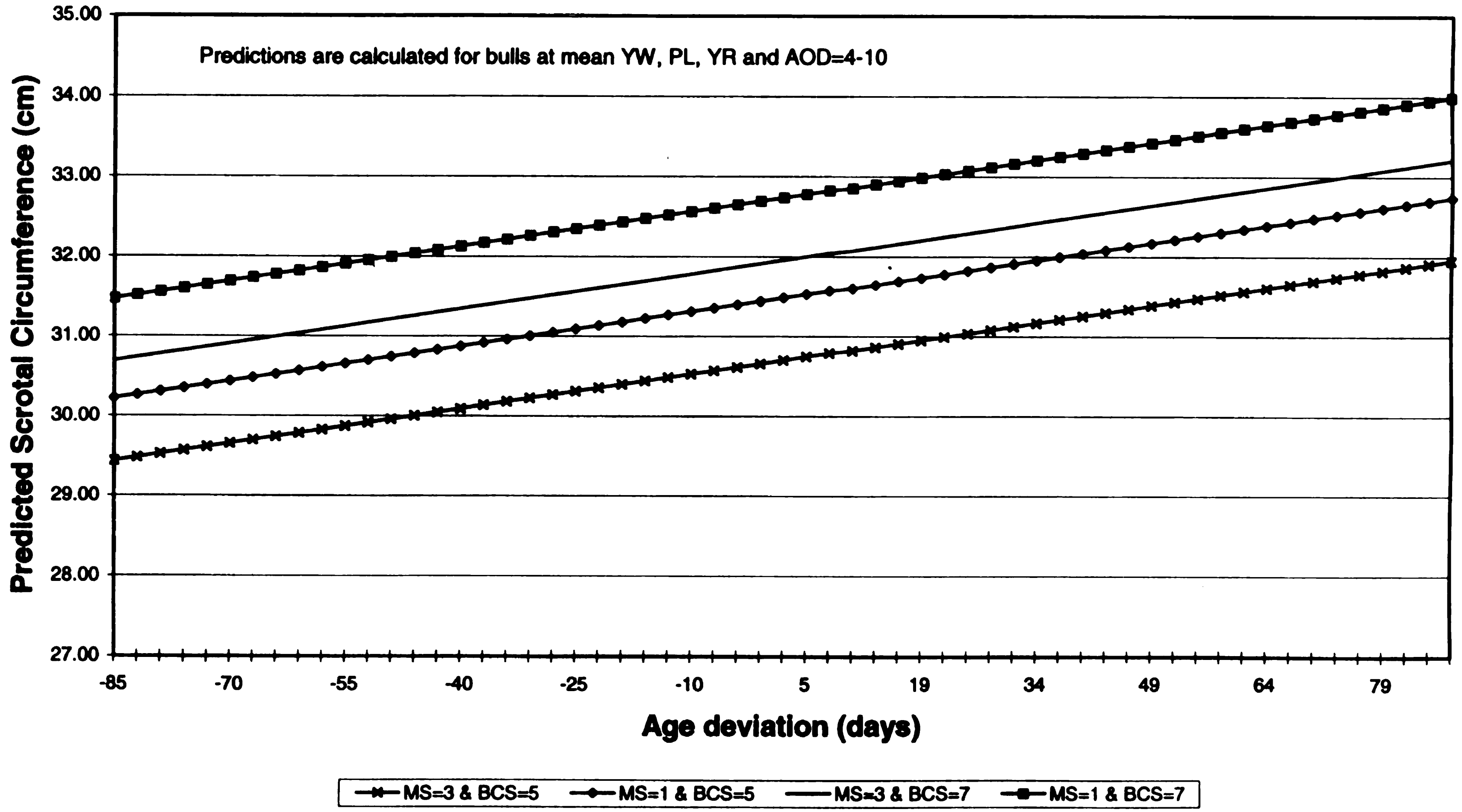
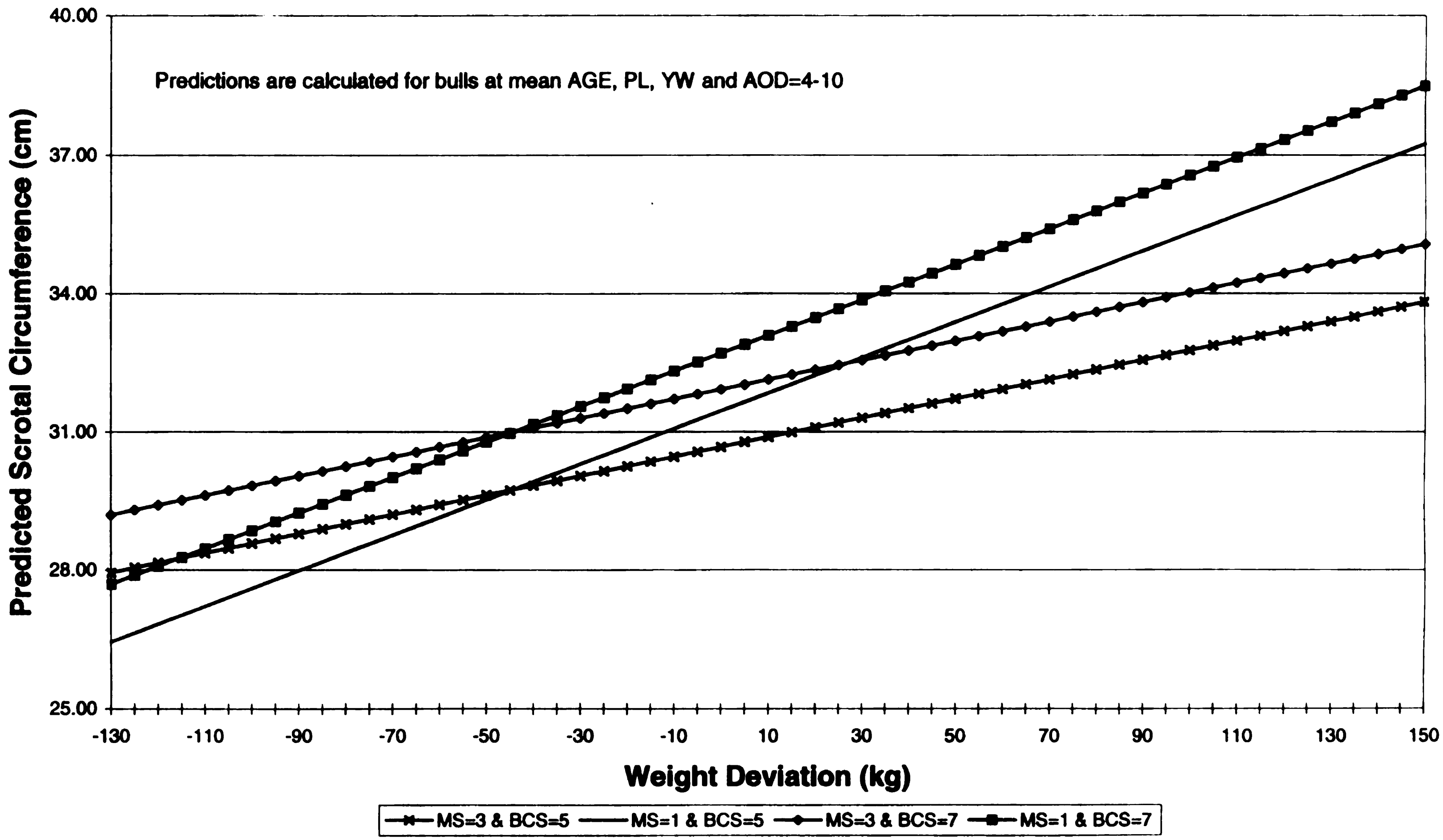


Figure 3.7. Weight adjusted composition effects on scrotal circumference



Discussion

The relationships between composition and indicators of reproductive fitness in yearling cattle presented here challenge the perspective of many involved with beef cattle breeding. It is commonly acknowledged that reproductive fitness traits of Limousin cattle generally require improvement, yet the amount of progress required to meet industry demands is debatable. Heifers cycling at a year of age will undergo at least three heat cycles before being bred to calve at 24 months. Certainly, favorable relationships have been well established between reduced age at puberty and lifetime fertility and productivity of a cow. However, the role of the Limousin breed in the beef industry mandates genetic advancement of fertility traits be conducted in the context of maintaining breed strengths. The data indicate Limousin breeders appear to have that opportunity.

Commonly accepted philosophy dictates maternal ability, including fertility and milk genetics, is of primary importance in replacement heifer selection and that muscularity can be ignored in the female and addressed through sire selection. However, if greater muscling is not detrimental to reproductive fitness in yearling Limousin heifers, given adequate weight, body condition, and a comparable environment, then breeders should retain heavier muscled females. Doing so allows Limousin breeders to accomplish two important goals. First, breed muscle advantages will be maintained without reliance upon utilization of the heaviest muscled bulls in the breed. At the same time, intense sire selection pressure can be directed towards fertility trait improvement and other breed weaknesses. Therefore, corrective mating schemes can be implemented in the manner that will produce the most rapid genetic improvement, through sire selection. The implications of this are substantial for Limousin seedstock producers wishing to supply the beef industry with muscular terminal sires and retain or merchandise female siblings as replacements.

The cause of the sex effects of muscularity on reproductive fitness traits is disconcerting and unknown at this time. Conceivably, composition traits that appear positively correlated with phenotypic expression of fertility may in fact have negative, underlying genetic relationships expressed differently in males and females. Perhaps the discrepancy is a function of the differing maturing rates for bulls and heifers. One might theorize that composition differences have varying effects depending upon the point on the growth curve at which they are measured. Perhaps herd management is the essential element distinguishing between bulls and heifers. Heifers at Running Creek Ranch must breed to calve as two-year-olds to maximize production efficiency. Therefore, heifers are fed so that as many as possible can achieve cycling status prior to the breeding season. Two-year-old virgin bulls, however, are in sufficient demand that there is not as much pressure placed on reproductive maturation rate in the male population.

Many will contend the scrotal circumference results justify a belief that heavy muscled bulls, specifically muscular Limousin bulls, are useful solely as terminal sires. These convictions appear well founded as documentation states that daughters of sires with smaller yearling scrotal circumferences are older at puberty and less reproductively efficient throughout their lifetimes. My belief is the results suggest against attempting to utilize extremes, i.e. compensating for light muscled heifers by utilizing the heaviest muscled bulls.

Implications

Limousin breeders have the opportunity to retain heavy muscled replacement females with confidence in their reproductive ability, provided heifers possess the genetic potential required and receive management levels sufficient to achieve adequate weight and body condition prior to breeding. Moreover, selection efforts directed towards fertility trait improvement through sire selection, in which maximum genetic response is expected, without sacrificing breed advantages in muscularity is possible. A paradigm shift may be required as Limousin seedstock producers look to females in their attempt to maintain muscularity and rebalance fertility trait and composition trait emphasis among potential sires.

Chapter 4

Genetic and composition effects on reproductive fitness traits in yearling Limousin cattle.

D. D. Faidley[1], B. D. Banks[1], R. J. Tempelman[1], H. D. Ritchie[1], K. J. Andersen[2], and D. G. LeFever[3]

[1]Michigan State University, E. Lansing, [2]North American Limousin Foundation, Englewood, CO, [3]Colorado State University, Fort Collins.

Abstract

Genetic and composition effects on indicators of fertility were evaluated from Limousin field data as part of ongoing research at Running Creek Ranch, Elizabeth, CO. Yearling reproductive tract score (RTS) of 1,578 heifers and scrotal circumference (SC) of 1,248 bulls were used in the analysis. Traits measured included yearling weight (WT, kg), RTS of heifers, SC of bulls, body condition score (BCS), and muscle score (MS). Dam age (AOD) was categorized for dams 2, 3, 4 to 9, and ≥10 yr. Percent Limousin (PL) was classified ≤75, 76-87, 88-93 and >93%. Yearling MS were grouped as light (MS<2), average (MS 2) or heavy muscled (MS>2). Heifer BCS ranged between 5 and 8, while all bulls had BCS between 4 and 7. Reproductive tract ordinal scores of heifers ranged from 1 to 5. Higher RTS scores indicate greater reproductive tract maturity. For RTS analyses, heifers were either grouped as cycling (n=1134, RTS≥4) or non-cycling (n=444, RTS≤3). Univariate and bivariate analyses were conducted to model RTS and SC as functions of main effects: animal age (AGE, days), WT, AOD, PL, year (YR), MS, BCS and random sire effect. Reduced models in which the covariates AGE or WT were removed were also tested. All fixed effects except PL were important ($p<.05$) in at least one model. In general, increases in WT, AGE and BCS favorably affected both the probability of cycling and SC. Average and heavy muscled heifers were favorable to light muscled heifers for RTS, while their heavy muscled bull mates had the smallest SC estimates. Heritability estimates ranged from .04 to .13 for RTS and .23 to .37 for SC. Surprisingly, genetic correlation coefficients between the response variables ranged between –.2 and .02.

Introduction and Objectives

Breeders of Limousin cattle have targeted reproductive fitness traits for improvement without sacrificing inherent breed muscle advantages. Relationships between fertility and composition traits are not well defined, but constitute important breeding stock selection considerations.

The binary nature of many fertility traits (e.g. cycling vs. non-cycling, pregnant vs. non-pregnant) does not facilitate distinction of the subtle differences in inherent fertility that exist between females. Furthermore, poor accuracy of breeding values for fertility traits coupled with lower selection intensity in female populations restrict progress through dam selection. Consequently, sire selection for fertility traits, such as scrotal circumference, is considered the most rapid method for improving inherent fertility in beef cattle.

Others have speculated age at puberty in heifers is essentially the same trait as scrotal circumference in yearling bulls due to strong, favorable genetic correlations (Brinks et al., 1978; King et al., 1983). Correlations among breed means (Lunstra, 1982; Gregory et al, 1991; Gregory et al, 1992; Cundiff, et al., 1993) have supported this conclusion. These studies also suggest phenotypic levels of performance of Limousin cattle for scrotal circumference, age at puberty and other fertility traits are lower than those of other breeds. Moreover, both female age at puberty and scrotal circumference are favorably related to growth, reproduction and maternal performance. (Laster et al., 1979; Werre, 1980; Bourdon and Brinks, 1985; Werre and Brinks, 1986; Smith et al., 1989)

Gregory et al. (1995) reported small, but favorable genetic and phenotypic correlations for body condition score with scrotal circumference in yearling bulls and age at puberty in yearling females. Limousin heifers were shown to be the leanest of nine breed groups in the Germ Plasm Evaluation Project at the Meat Animal Research Center, Clay Center, NE, and among the latest for age at puberty (Gregory, et al. 1991). Subjective muscle scores (1 = extremely light muscled to 9 = extremely heavy muscled) were assigned to yearling bulls in the GPE project (Gregory et al., 1995) and shown to have a negative genetic relationship ($-.17 \pm .07$) with scrotal circumference, but no phenotypic relationship. Moser et al. (1996), reported no difference in composition among yearling crossbred progeny of Limousin sires with high and low adjusted yearling scrotal circumferences (difference=8 cm). However, sires with average SC expected progeny differences (EPD) had progeny with significantly larger weaning ultrasonic ribeye area measurements than those of low SC EPD sires.

Therefore, the objectives of this study were to:

1) Account for composition differences in a genetic analysis of reproductive trait indicators in yearling cattle,
2) Estimate a genetic correlation between scrotal circumference and cycling status in half-sibs.

Materials and Methods

Heifer Population.

Data. Field data collection was initiated in 1990 on 2179 yearling Limousin heifers as part of ongoing research at Running Creek Ranch, Elizabeth, CO. Traits measured included yearling weight (WT, kg), body condition score (BCS) as described by Ritchie et al. (1992), reproductive tract score (RTS as described by Andersen et al. (1991), and muscle score (MS) which will be described later. All data collection was performed by one, trained technician. Herdbook information for Running Creek Ranch was provided by the North American Limousin Foundation (NALF), Englewood, CO. Heifer age (AGE, days), age of dam (AOD, years), percent Limousin (PL) and sire information was obtained from the NALF herd file.

Heifer Management. The heifers included in this analysis were recorded in mid-May at approximately 13 months of age. Calves were not creep fed. Following weaning, heifers were wintered in a single contemporary group under dry-lot conditions. No healthy heifers were culled or removed from the replacement heifer group until after they had been measured as yearlings. Heifers were fed a silage-based ration adequate for maintenance and approximately .8 kg/day gain. The herd objective is to retain or sell as many replacement females as possible. Subsequently, the feeding objective was to maximize the number of heifers cycling at the time of measurement. Therefore, heifers were grown at a rate sufficient to ensure that adequate weight and body condition levels for cycling were reached. Cycling heifers were implanted with Syncro-Mate B® at the time of recording to synchronize estrus at the start of the breeding season. Non-cycling heifers were culled.

Reproductive Tract Scoring System. Several researchers have studied age of puberty (AP) in beef heifers when defined as the age at first behavioral estrus. However, because AP is difficult and labor-intensive to measure, direct selection for age at puberty in females is seldom practiced. Andersen et al. (1991) described the reproductive tract scoring (RTS) system developed at Colorado State University which estimates pubertal status via rectal palpation of the uterine horns and ovaries. Each heifer is assigned a score of 1 (infantile) through 5 (palpable corpus luteum) as described in Table 4.1.

A RTS of 1 is assigned to heifers with infantile tracts as indicated by small, toneless uterine horns and small ovaries devoid of significant structures. Heifers scored as 1 are likely the furthest from cycling at the time of examination. Heifers given a RTS of 2 are thought to be closer to cycling than those scoring 1 due primarily to the presence of small follicles and slightly larger uterine horns and ovaries. Those heifers assigned a RTS of 3 are thought to be on the verge of cycling based on slight uterine tone in addition to the presence of follicles. Heifers assigned a score of 4 are presumably cycling as indicated by good uterine tone, uterine size, and follicular growth. However, heifers with tract scores of 4 lack an easily distinguished corpus luteum due to the stage of the estrous cycle. Heifers with tract scores of 5 are similar to those scoring 4 except for the presence of a palpable corpus luteum.

Table 4.1. Description of reproductive tract scores[a]

		Ovaries (approx. size)			
Repro. tract scores	Uterine horns	Length (mm)	Height (mm)	Width (mm)	Ovarian structures
1	Immature < 20 mm diameter - no tone	15	10	8	No palpable follicles
2	20-25 mm diameter - no tone	18	12	10	8 mm follicles
3	25-30 mm diameter - slight tone	22	15	10	8-10 mm follicles
4	30 mm diameter - good tone	30	16	12	< 10 mm follicles corpus luteum possible
5	> 30 mm diameter - good tone, erect	>32	20	15	>10 mm follicles corpus luteum present

[a] Reproductive tract score was determined approximately 1 mo prior to breeding.

Muscle Score. Numerous studies have reported use of a scoring system to describe muscularity differences between cattle (Gregory et al., 1995; Koch et al., 1995; Wolfe et al., 1990). Subjective scores were assigned utilizing visual appraisal of an animal's topline, hip, quarter, and base width. For these analyses ordinal scores ranged between 1 and 3.5 with higher levels indicating greater muscularity as follows:

1.0) Extremely lacking in muscularity. Narrow loin, hip and stance and tapered through the rear quarter. Little visible muscle tissue.

1.5) More apparent muscling than in muscle score 1, but still flat quartered and narrow throughout.

2.0) Average muscling. Moderate visible muscle shape in topline and rear quarter.

2.5) Above average muscularity.

3.0) Heavily muscled. Wide stance, thick and expressive quarter and hip, broad loin with visible muscle shape throughout topline.

3.5) Very heavily muscled. Abundant visible muscular shape.

Data Editing. For these analyses heifers were either grouped as cycling (72%, RTS≥4) and coded as 1, or non-cycling (28%, RTS≤3) coded as 0. Thus, RTS was used simply to distinguish between pre-pubertal heifers and those who had achieved pubertal status. Yearling MS ranged from 1 to 3.5 and were grouped as light (MS<2), average (MS 2) or heavy muscled (MS>2). All heifers had BCS between 5 and 8. Percentage Limousin (PL) was included to account for potential heterosis effects. Initially, PL was grouped according to NALF specifications as: 37-50, 51-75, 76-87, 88-93, 94-100. However, due to the existence of predominantly high percentage cattle and resulting small class sizes in the lower percentage categories, PL was regrouped: ≤75, 76-87, 88-92 and >92%. Age of dam (AOD) was stratified for 2, 3, 4-9, and dams 10 years old and older. The mean age and actual weight at time of recording were subtracted from each age and weight record to minimize computer round off error. Heifers with missing data (n=601) were removed from the analysis. Only those females with a complete array of response and explanatory variables remained (n=1578, Table 4.2).

Table 4.2. Data description for Running Creek Ranch females-135 sires

Trait		Mean	N	Percent	S. D.	Range
Age (days)		398			22.81	317-455
Weight (WT, kg)		380			4.91	216-525
Percent Limousin (PL)						
	< 75%		115	7.3%		
	76-87%		59	3.7%		
	88-92%		113	7.2%		
	> 92%		1291	81.8%		
Age of dam (AOD)						
	2		283	17.9%		
	3		246	15.6%		
	4-10		911	57.7%		
	>10		138	8.8%		
Reproductive Tract Score (RTS)						
	Cycling (1)		1134	71.9%		
	Non-cycling (0)		444	28.1%		
Muscle Score (MS)		2.2				1-3.5
	Light (≤ 1.5)		127	8.1%		
	Average (= 2)		985	62.4%		
	Heavy (≥ 2.5)		466	29.5%		
Body Condition Score (BCS)		6.2				5-8
	5		85	5.4%		
	6		1098	69.6%		
	7		381	24.1%		
	8		14	.09%		

Bull Population.

Data. Data collection on 1,474 yearling Limousin bulls at Running Creek Ranch, Elizabeth, CO was also initiated in 1990. Traits measured were the same as those for the heifer analysis with the substitution of SC for RTS.

Bull Management. Bulls were reared under similar conditions as their heifer mates, though an unknown number were culled at weaning, presumably due to lack of performance. The important distinction is that after weaning, bulls were grown at proportionately slower rates relative to their gain potential than were females. Running Creek Ranch has a substantial number of repeat and potential customers who prefer 18-month old bulls for use in fall calving programs, and two-year old bulls they can expose to more cows. Cost of gain is a more important economic factor than maximum early growth to their bull production efforts. Consequently, there were no apparent average daily gain targets for the bulls. Therefore, bull development strategies utilized lower quality, more cost effective feeds. Bulls that met NALF recommendations for adjusted yearling scrotal circumferences (≥32 cm.) could be sold in the spring as yearlings or later. Bulls were culled that failed to meet Society of Theriogenology criteria for breeding soundness examinations at sale time (SC<30 cm.).

Data Editing. Procedures followed when grouping, AOD, PL, and MS for RTS analysis were replicated prior to modeling SC. All bulls had BCS between 4 and 7. Bulls with missing data (n=224) were removed from the analysis. Only those males with a complete array of response and explanatory variables remained (n=1248, Table 4.3).

Table 4.3. Data description for Running Creek Ranch males-127 sires

Trait		Mean	N	Percent	S.D.	Range
Age (days)		383				298-471
Weight (WT, kg)		429				368-567
Percent Limousin (PL)						
	≤ 75%		86	6.9%		
	76-87%		46	3.7%		
	87-92%		77	6.2%		
	≥ 93%		1039	83.2%		
Age of dam (AOD)						
	2		164	13.1%		
	3		203	16.3%		
	4-10		785	62.9%		
	>10		96	7.7%		
Scrotal Circumference (SC, cm)		32.07			2.64	24-42.25
	≥ 34			27.6%		
	≤ 30			25%		
Muscle Score (MS)		2.3				1-3.5
	Light (≤ 1.5)		102	8.2%		
	Average (= 2)		701	56.2%		
	Heavy (≥ 2.5)		445	36.6%		
Body Condition Score (BCS)		5.8				4-7
	4		9	.7%		
	5		339	27.2%		
	6		870	69.7%		
	7		30	2.4%		

Univariate Analysis

Reproductive Tract Score. A sire model was used to examine random genetic effects on cycling status. 135 sires were considered unrelated and fitted to the main effects model that included AGE, WT, PL, AOD, year (YR), MS and BCS. The resulting linear mixed model is generally described as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zu} + \mathbf{e}$$

where: **y** is a N x 1 vector of phenotypic observations,

b is a p x 1 vector of fixed effects associated with **y**,

u is a q x 1 vector of random effects associated with **y**,

X is a known incidence matrix of order N x p relating elements of **b** to elements of **y**,

Z is a known incidence matrix of order N x q relating elements of **u** to elements of **y**, and

e is a N x 1 vector of residual effects.

Additional attributes of the general form of mixed linear models include the expectations of the random variable which include:

$$E(\mathbf{y}) = \mathbf{Xb}$$

$$E(\mathbf{u}) = 0, \text{ and}$$

$$E(\mathbf{e}) = 0$$

Henderson (1953) developed the Best Linear Unbiased Prediction (BLUP) which is used to predict random effects, such as breeding values, utilizing the mixed model. BLUP is primarily used to identify individuals with maximum genetic merit in selection programs, monitor response to selection and has become the dominant methodology for estimating breeding values. The literature collection describing BLUP methodology is voluminous and extensive (Henderson, 1977a, 1984a, 1988a; Schaeffer, 1991; Kennedy, 1991, Searle et al., 1992; and Mrode, 1996)

Sire models are used to estimate breeding value of bulls from large arrays of descendants (Lynch and Walsh, 1998). In this model the additive genetic value of each offspring is expressed in terms of its sire's breeding values and the dam contribution is incorporated into the error term.

The final model for analysis of cycling status is as follows:

RTS = Cycling vs. non-cycling (1 or 0)

- a intercept
- YR year (1990, 1991, 1992, 1993, 1994, 1995, 1996)
- PL percent Limousin (< 75, 75-87, > 87)
- AOD age of dam (2, 3, 4-10, >10)
- MS muscle score (1, 2, 3)
- BCS body condition score (5, 6, 7, 8)
- AGE age at recording deviation from the mean
- WT actual weight at recording deviation from the mean
- SIRE random genetic effect of sire N~(0, $I\sigma^2_s$)
- e random error N~(0, $I\sigma^2_e$)

The author realizes the binary nature of RTS violates assumptions of a normally distributed error term. Methodology to correctly account for this limitation of mixed linear models will be discussed in a later section.

Scrotal Circumference. Mixed model analysis on the bull data was performed utilizing the same methodology as the RTS analysis described above, with the substitution of scrotal circumference as the response variable. The final model included main effects: year (YR), PL, AOD, AGE, WT, MS, BCS and the random effect of sire. Keeton et al. (1996), suggested either bull age or bull weight should be fit to a scrotal circumference model, as the traits were highly and favorably correlated (.91). In these data however, both bull AGE and WT proved to be significant sources of variation.

The final model for analysis of scrotal circumference is as follows:

SC = Scrotal Circumference

- a intercept
- YR year (1990, 1991, 1992, 1993, 1994, 1995, 1996)
- PL percent Limousin (< 76, 76-87, 88-93, >93)
- AOD age of dam (2, 3, 4-10, >10)
- MS muscle score (1, 2, 3)
- BCS body condition score (4, 5, 6, 7)
- AGE age at recording deviation from the mean
- WT actual weight at recording deviation from the mean
- SIRE random genetic effect of sire $N\sim(0, I\sigma^2_s)$
- e random error $N\sim(0, I\sigma^2_e)$

Sires. Data collection was performed on progeny of 152 sires. Sire identification was conducted in such a manner that a single number denoted each sire regardless of analysis method or model. However, not all sires had both male and female progeny records. For univariate analyses, 135 sires were used to model RTS, while 127 sires were represented in the bull population. As a matter of definition, "paired" sires are those 110 sires with both male and female progeny records. The bivariate analyses were performed separately on 110 paired sires, those sires with both male and female progeny records, as well as the full data set including all 152 sires. Paired data sets included 1491 females and 1225 males as described in Table 4.4 and 4.5.

Table 4.4. Paired data description for Running Creek Ranch females-110 paired sires

Trait		Mean	N	Percent	S. D.	Range
Age (days)		398			22.39	318-455
Weight (WT, kg)		380			4.19	216-525
Percent Limousin (PL)						
	< 75%		108	7.2%		
	76-87%		49	3.3%		
	88-92%		101	6.8%		
	> 92%		1233	82.7%		
Age of dam (AOD)						
	2		247	16.6%		
	3		235	15.8%		
	4-10		876	58.8%		
	>10		133	8.9%		
Reproductive Tract Score (RTS)						
	Cycling (1)		1087	72.9%		
	Non-cycling (0)		404	27.1%		
Muscle Score (MS)		2.2				1-3.5
	Light (≤ 1.5)		117	7.9%		
	Average (= 2)		929	62.3%		
	Heavy (≥ 2.5)		445	29.8%		
Body Condition Score (BCS)		6.2				5-8
	5		69	4.6%		
	6		1040	69.8%		
	7		369	24.8%		
	8		13	.09%		

Table 4.5. Paired data description for Running Creek Ranch males-110 paired sires

Trait		Mean	N	Percent	S.D.	Range
Age (days)		383				298-453
Weight (WT, kg)		429				368-513
Percent Limousin (PL)						
	≤ 75%		84	7.9%		
	76-87%		46	4.7%		
	87-92%		77	6.3%		
	≥ 93%		1018	83.1%		
Age of dam (AOD)						
	2		163	13.3%		
	3		198	16.2%		
	4-10		770	63.8%		
	>10		94	8.7%		
Scrotal Circumference (SC, cm)		32.06			2.64	24-42.25
	≥ 34		≅25%			
	≤ 30		≅25%			
Muscle Score (MS)		2.3				1-3.5
	Light (≤ 1.5)		101	8.2%		
	Average (= 2)		687	56.1%		
	Heavy (≥ 2.5)		437	36.7%		
Body Condition Score (BCS)		5.8				4-7
	4		9	.7%		
	5		333	27.2%		
	6		858	70%		
	7		25	2%		

Bivariate Analyses.

Janss and Foulley (1993) described a general bivariate analyses (BIVARB) which successfully accommodated unequal design matrices for a binary threshold and continuous variable. In their evaluation, birth weight was included in an analysis of calving ease scores due to its high genetic and residual correlation with calving difficulty (Philipsson, 1976; Meijering, 1985). Many have reported scrotal circumference in males and age at puberty in females are associated (Brinks et al., 1978; King et al., 1983). Thus, it seems appropriate that to predict of sire breeding values for a threshold trait such as RTS, scrotal circumference of male progeny should be included in a multiple trait analysis. Observations for the continuous trait, SC, follow the linear model:

$$\mathbf{SC} = \mathbf{X_1B_1} + \mathbf{Z_1u_1} + \mathbf{e_1}$$

where **X** and **B** are incidence matrices, relating scrotal circumference records to fixed effects (**B**) and to sire effects (**u**). The error variance is given as σ^2_{e1}. Observations for the threshold trait, RTS, are modeled as:

$$\mathbf{RTS} = \mathbf{X_2B_2} + \mathbf{Z_2u_2} + \mathbf{e_2}$$

where all terms are similar to those in the continuous trait model. The variance on the underlying scale is arbitrary (=1). The variance structure for the sire effects is given as:

$$\mathbf{V}\begin{bmatrix}\mathbf{u_1}\\ \mathbf{u_2}\end{bmatrix} = \mathbf{G} = \begin{bmatrix}\mathbf{G_{11}} & \mathbf{G_{12}}\\ \mathbf{G_{21}} & \mathbf{G_{22}}\end{bmatrix} = \begin{bmatrix}\mathbf{I}\sigma^2_{U11} & \mathbf{I}\sigma^2_{U12}\\ \mathbf{I}\sigma^2_{U21} & \mathbf{I}\sigma^2_{U22}\end{bmatrix} \ldots\mathbf{and}\ldots \mathbf{G}^{-1} = \begin{bmatrix}\mathbf{G}^{11} & \mathbf{G}^{12}\\ \mathbf{G}^{21} & \mathbf{G}^{22}\end{bmatrix}$$

As in the univariate analyses, sires were assumed unrelated in the bivariate model. Several attempts were made to fit the relationship matrix to the BIVARB model, but resulting (co)variance estimates were incalculable and convergence criterion was never met.

Bivariate Model Specification. Three different models and six separate data sets were used for these analyses. Differences between data sets are found in the number of sires analyzed and/or the number of covariates included. The full data set includes progeny records of 152 sires. The corresponding model fits the same seven fixed effects as the single trait model, including both AGE and WT as covariates. The reduced models included either AGE or WT in an attempt to remove collinearity from the model. As previously mentioned, the data were also paired by sire to include only those 110 sires with both male and female progeny records. A full description of each bivariate model used is given in table 4.6.

Age and Weight adjusted bivariate analyses were also conducted on unpaired and paired data sets using multiple-trait-restricted-maximum-likelihood (MTDFREML) for estimation of genetic variances and covariances (Boldman, et al., 1993).

Table 4.6. Models and data sets used for bivariate analyses modeling both SC and RTS as response variables.

	152 Sires - Unpaired			110 Sires - Paired		
Fixed Effect	Full	Age	Weight	Full	Age	Weight
YR	X	X	X	X	X	X
PL	X	X	X	X	X	X
AOD	X	X	X	X	X	X
MS	X	X	X	X	X	X
BCS	X	X	X	X	X	X
AGE	X	X		X	X	
WT	X		X	X		X

Results

Univariate Analysis

Fixed factor effects on reproductive tract score. Type 3 (SAS®) F-tests of fixed effects are given in Table 4.7. Parameter estimates for fixed effects are given in Table 4.8. The intercept cycling status value for heifers was .827. This value corresponds to a heifer of >92% Limousin, born 1996 to a ≥10 year old dam, of average age and weight, with body condition score 8 and muscle score 3. Heifer age was the most significant source of variation ($p<.001$), and had the largest F value. WT was also important ($p = .012$). Neither AOD ($p = .425$) or PL ($p = .707$) were significant explanatory variables as fixed effects.

Effects of composition on reproductive tract score. In general, heavier muscled and fatter heifers were more likely to be cycling than their lighter muscled and/or leaner counterparts. Cycling status was not different among average and heavy muscled heifers according to t-tests ($p = .951$), but both groups were advantageous to light muscled heifers regarding cycling status ($p < .05$).

Although muscle score effects were significant, body condition score was a more important factor affecting predicted probability of cycling. Increases in BCS had favorable affects on reproductive tract maturity. Obese heifers (BCS 8) were the exception, as their estimates for cycling were lower numerically than those heifers in good condition (BCS 7). However, t-tests for significant differences between body condition scores revealed BCS 8 heifers were not different than BCS 6 or BCS 7 ($p>.05$). All other body condition score classes were significantly different from each other ($p<.05$).

The combined effects of muscularity and body condition indicate the relative importance of each trait on cycling status. The combination of fatter and lighter muscled heifers is preferable to lean, heavy muscled heifers regarding reproductive tract maturity.

Some may be concerned about possible confounding of muscle score and body condition scores. Logic dictates muscle and fat accretion accompany increases in age and weight under conventional management practices. Subjectively assigned scores such as these are certainly more prone to bias than are objectively measured traits. Step-wise selection procedures were utilized in a prior analysis to test interactions between composition and continuous traits. As previously mentioned, no interactions explained significant variation above and beyond that described by the main effects model. Likewise, model statistics indicated the main effects model sufficiently described the relationships of age, weight, body condition and muscularity with reproductive fitness.

Fixed factor effects on scrotal circumference. Type 3 (SAS®) F-tests of fixed effects are given in Table 4.7. Parameter estimates for fixed effects are given in Table 4.8. The adjusted mean scrotal circumference was 32.6 cm., which is slightly higher than Limousin breed recommendations for yearling bulls (Directions, Limousin Breeder Symposium, 1990). This intercept value corresponds to bulls of >92% Limousin, measured in 1996 to a ≥10 year old dam, of average age and weight, with body condition score 7 and muscle score 3. Both weight and age were significant sources of variation in scrotal circumference ($p<.05$). As expected, scrotal circumference increased with increasing age and weight. Regression coefficients for SC on WT and AGE were .057, cm/kg and .016, cm/day respectively. Age of dam effects were important for sons of first calf heifers and mature dams and consistent with estimates and adjustment factors reported in literature. Sons of 3-year old, and cows ≥10 did not have significantly different scrotal circumferences, but parameter estimates tended to follow literature estimates.

Composition effects on scrotal circumference. As with estimates of heifer fertility, fatter bulls had larger scrotal circumferences, excluding BCS 4 (n=9), which was not significantly different than other BCS classes ($p>.05$). Solutions for SC on BCS increased .65 cm for a BCS increase from 5 to 6 and 1.23 cm for an increase from 5 to 7 ($p<.05$). Heavier muscled bulls had significantly smaller scrotal measurements than average muscled bulls ($p<.05$). Light muscled bulls were not different than average or heavy muscled bulls ($p>.05$). Contrary to the heifer analysis, however, SC solutions for light muscled bulls were numerically higher than those of heavy muscled bulls. Solutions of SC for light and average muscled bulls were $.144 \pm .251$ and $.480 \pm .131$, cm.

Summary of univariate fixed effect results. These data suggest that selection of heavier muscled replacement heifers, given adequate weight and body condition score, is not detrimental to reproductive fitness. Moreover, yearling scrotal circumference can be improved while muscling is maintained at average levels. Minimum body condition levels are required to achieve desirable phenotypic expression of fertility traits. Of note is the comparison between F-values for BCS and WT, which indicated a greater importance of BCS than WT for heifer cycling status.

Table 4.7. Type 3 (SAS®) Tests of Fixed Effects

Effect	Cycling Status				Scrotal Circumference			
	Num DF[a]	Den DF[b]	F Value	Pr > F	Num DF[a]	Den DF[b]	F Value	Pr > F
BCS	3	1424	11.69	<.001	3	1102	6.44	<.001
MS	2	1424	4.53	.011	2	1102	7.32	<.001
AOD	3	1424	.93	.425	3	1102	5.4	.001
PL	3	1424	.47	.707	3	1102	1.03	.380
Year	6	1424	3.46	.002	6	1102	23.66	<.001
Age	1	1424	26.52	<.001	1	1102	13.55	<.001
Weight	1	1424	6.26	.012	1	1102	24.99	<.001

[a] F-test numerator degrees of freedom.
[b] F-test denominator degrees of freedom.

Table 4.8. Univariate analysis parameter estimates

		Cycling Status		Scrotal Circumference	
Effect	Level	Estimate	Pr > |t|	Estimate	Pr > |t|
Intercept		.827 ± .120	<.001	32.638 ± .493	<.001
BCS[m]					
	4			-.034[f] ± 1.015	.973
	5	-.301[a] ± .126	.017	-1.233[g] ± .419	.003
	6	-.052[b] ± .112	.641	-.581[f] ± .384	.131
	7	.055[c] ± .112	.623	0[f]	.
	8	0[b,c]	.		
MS[n]					
	1	-.125[d] ± .046	.007	.144[h,i] ± .251	.567
	2	-.002[e] ± .025	.951	.480[i] ± .131	<.001
	3	0[e]	.	0[h]	.
AOD					
	2	-.038 ± .046	.412	-.651[j] ± .321	.043
	3	-.046 ± .044	.303	-.211[j,k] ± .260	.418
	4-9	-.061 ± .038	.108	.243[l] ± .217	.263
	10+	0	.	0[k,l]	.
PL					
	<75	-.042 ± .040	.291	-.147 ± .228	.519
	75-86	.001 ± .056	.990	.424 ± .314	.177
	87-92	-.024 ± .040	.551	-.188 ± .238	.429
	>92	0	.	0	.
Year[o]					
	1990	-.062 ± .041	.133	-1.066 ± .312	<.001
	1991	-.007 ± .038	.864	-.709 ± .302	.019
	1992	-.140 ± .048	.004	-1.752 ± 1.177	.137
	1993	.015 ± .040	.712	-.670 ± .269	.013
	1994	.074 ± .041	.070	1.315 ± .248	<.001
	1995	.040 ± .034	.242	-.095 ± .263	.719
	1996	0	.	0	.
Age[p]		.003 ± .001	<.001	.016 ± .004	<.001
Weight[p]		.009 ± .000	.012	.057 ± .004	<.001

[a-l]Variables with different superscripts are different ($p<.05$)

[m] BCS; 8 = Obese, 7 = Good, 6 = High Moderate, 5 = Moderate, 4 = Thin

[n] MS; 3 = heavy muscled, 2 = average muscled, 1 = light muscled.

[o] Year effects were not tested for differences

[p] Expressed as deviations from the mean.

Genetic effects on reproductive tract score. Reproductive tract score analysis variance parameter estimates are given in Table 4.9. Sire effects were not a significant source of variation in the univariate analysis. The heritability estimate of .04 is lower than those of RTS (Andersen, et al., 1991, Andersen, 1991) and many heritability estimates for heifer age at puberty (Smith et al., 1976, Werre and Brinks, 1986; MacNeil et al., 1984). McInerney (1977) and Smith et al. (1989a) reported heritability estimates for age at puberty of .07 ± .1 and .1 ± .09, respectively, which encompass the estimates calculated here.

Table 4.9. Variance parameter estimates – reproductive tract score

	Cycling Status		
Covariance Parameter	Estimate	Z Value	Pr Z
Sire	.002 ± .002	.85	.198
Residual	.165 ± .006	27.17	<.001
h^2	.039		

Genetic effects on scrotal circumference. Scrotal circumference variance parameter estimates are given in Table 4.1. Sire effects were a significant source of variation in the univariate analysis. The heritability estimate of .37 is lower than the average of scrotal circumference estimates found in the literature (≅.5) Literature heritability estimates range from .16 (Kriese et al., 1991) to .78 (Coulter and Foote, 1976).

Table 4.10. Variance parameter estimates – scrotal circumference

	Scrotal Circumference		
Covariance Parameter	Estimate	Z Value	Pr Z
Sire	.386 ± .128	3.02	.001
Residual	3.840 ± .162	23.76	<.001
h^2	.366		

Bivariate analysis fixed effect estimates.

Age and weight adjusted model. Age and weight adjusted fixed effect estimates and associated standard errors for unpaired and paired data are given in Table 4.11. Regression coefficients calculated in the bivariate analysis were in general agreement in both order and scale to estimates derived from univariate analyses. Regression coefficients for RTS or SC on either AGE or WT were positive. Increases in BCS had favorable effects on SC and RTS, except for the leanest bulls (n=9) and the fattest heifers (unpaired n=14, paired n=13). MS effects were consistent with single trait analysis estimates. AOD, PL, and YR effects mirrored results from univariate analysis. Differences between analyses of paired and unpaired data, occurred on some fixed effect factor levels that had relatively high standard errors (i.e. bull BCS 4).

Age adjusted model. Age adjusted fixed effect estimates and associated standard errors for unpaired and paired data are given in Table 4.12. As expected, regression coefficients for SC and RTS on age increased with WT removed from the model, particularly for SC. YR effects appear considerably different from the full model. Solutions of SC and RTS on BCS increased in absolute value, acknowledging a strong correlation between WT and BCS. Of note is the difference in MS effects on SC when WT is removed from the model. In the AGE and WT adjusted model MS 1 had a less detrimental effect on SC than MS 3. In this model, however, the effect of MS 1 on SC is negative, and the effect of MS 3 on SC is positive and comparable to regression coefficients for average muscled bulls. These results indicate MS is strongly correlated with WT, agreeing with earlier findings of a purely phenotypic analysis on the same data that required fitting a WT x MS interaction.

Weight adjusted model. Weight adjusted fixed effect estimates and associated standard errors for unpaired and paired data are given in Table 4.13. Regression coefficients for SC and RTS on weight increased with age removed from the model. Composition effects resembled those from the full model more closely than results from the model in which WT was removed. AOD, PL, and YR effects were similar to the full model as well.

Table 4.11. Age & weight adjusted bivariate analysis fixed effect estimates

Effect	Level	Cycling Status Estimates Unpaired[a]	Cycling Status Estimates Paired[b]	Scrotal Circumference Estimates Unpaired[a]	Scrotal Circumference Estimates Paired[b]
Mean		.499 ± .343	.485 ± .344	31.825 ± .380	31.945 ± .380
BCS					
	4			.408 ± .621	-.238 ± .709
	5	-.757 ± .101	-.756 ± .106	-.760 ± .144	-.652 ± .151
	6	-.006 ± .082	.022 ± .083	-.108 ± .143	.003 ± .150
	7	.471 ± .086	.507 ± .087	.460 ± .215	.887 ± .243
	8	.292 ± .209	.227 ± .214		
MS					
	1	-.267 ± .120	-.311 ± .121	-.062 ± .137	-.027 ± .137
	2	.120 ± .114	.142 ± .115	.274 ± .120	.248 ± .120
	3	.147 ± .116	.168 ± .117	-.212 ± .124	-.221 ± .124
AOD					
	2	-.002 ± .071	.018 ± .072	-.487 ± .102	-.476 ± .101
	3	-.044 ± .070	-.048 ± .070	-.052 ± .084	-.040 ± .084
	4-9	-.099 ± .066	-.100 ± .067	.391 ± .075	.380 ± .074
	10+	.144 ± .074	.130 ± .074	.148 ± .095	.136 ± .094
PL					
	<75	-.088 ± .076	-.120 ± .077	-.171 ± .102	-.204 ± .101
	75-86	.074 ± .084	.094 ± .088	.409 ± .127	.424 ± .124
	87-92	-.032 ± .076	-.005 ± .078	-.217 ± .105	-.223 ± .103
	>92	.046 ± .068	.031 ± .069	-.021 ± .079	.002 ± .078
YR					
	1990	-.160 ± .030	-.176 ± .031	-.639 ± .088	-.863 ± .096
	1991	-.016 ± .029	-.036 ± .029	-.302 ± .086	-.509 ± .095
	1992	-.361 ± .035	-.229 ± .040	-1.275 ± 1.121	-.066 ± 1.507
	1993	.043 ± .031	.027 ± .032	-.263 ± .075	-.417 ± .086
	1994	.309 ± .034	.276 ± .032	1.736 ± .069	1.526 ± .078
	1995	.166 ± .029	.156 ± .024	.326 ± .074	.117 ± .086
	1996	.018 ± .028	-.018 ± .022	.418 ± .088	.212 ± .098
Age[c]		.010 ± .000	.012 ± .000	.016 ± .000	.017 ± .000
WT[c]		.003 ± .000	.003 ± .000	.056 ± .000	.058 ± .000

[a] 152 sires

[b] 110 sires

[c] Expressed as deviations from the mean.

Table 4.12. Age adjusted bivariate analysis fixed effect estimates

		Cycling Status Estimates		Scrotal Circumference Estimates	
Effect	Level	Unpaired[a]	Paired[b]	Unpaired[a]	Paired[b]
Mean		.478 ± .343	.464 ± .345	31.743 ± .391	31.805 ± .391
BCS					
	4			-1.278 ± .719	-1.225 ± .839
	5	-.831 ± .100	-.835 ± .104	-.938 ± .161	-1.027 ± .168
	6	-.025 ± .082	.005 ± .084	.395 ± .158	.305 ± .168
	7	.501 ± .086	.538 ± .087	1.821 ± .236	1.947 ± .275
	8	.355 ± .211	.292 ± .216		
MS					
	1	-.323 ± .119	-.371 ± .120	-.514 ± .141	-.521 ± .141
	2	.123 ± .114	.145 ± .115	.269 ± .122	.260 ± .122
	3	.200 ± .116	.226 ± .116	.245 ± .126	.261 ± .126
AOD					
	2	-.021 ± .071	-.005 ± .072	-.775 ± .106	-.770 ± .106
	3	-.041 ± .069	-.045 ± .070	.052 ± .088	.065 ± .088
	4-9	-.077 ± .066	-.078 ± .067	.571 ± .077	.559 ± .076
	10+	.139 ± .074	.127 ± .074	.153 ± .101	.145 ± .100
PL					
	<75	-.074 ± .076	-.106 ± .077	-.249 ± .110	-.291 ± .109
	75-86	.076 ± .084	.098 ± .089	.519 ± .140	.542 ± .136
	87-92	-.050 ± .076	-.024 ± .078	-.174 ± .114	-.171 ± .111
	>92	.048 ± .068	.032 ± .069	-.096 ± .082	-.080 ± .081
YR					
	1990	-.137 ± .030	-.153 ± .030	-1.674 ± .094	-1.673 ± .107
	1991	-.036 ± .029	-.055 ± .029	-.933 ± .096	-.901 ± .108
	1992	-.385 ± .034	-.251 ± .040	1.288 ± 1.303	1.131 ± 1.801
	1993	-.010 ± .031	-.030 ± .031	-1.013 ± .082	-.926 ± .097
	1994	.333 ± .034	.300 ± .034	1.060 ± .075	1.071 ± .088
	1995	.196 ± .029	.187 ± .029	.623 ± .083	.628 ± .098
	1996	.038 ± .028	.001 ± .028	.650 ± .099	.670 ± .111
Age[c]		.012 ± .000	.013 ± .000	.039 ± .000	.042 ± .000

[a] 152 sires

[b] 110 sires

[c] Expressed as deviations from the mean

Table 4.13. Weight adjusted bivariate analysis fixed effect estimates

Effect	Level	Cycling Status Estimate		Scrotal Circumference Estimate	
		Unpaired[a]	Paired[b]	Unpaired[a]	Paired[b]
Mean		.502 ± .343	.498 ± .344	31.815 ± .381	31.932 ± .381
BCS	4			.474 ± .626	-.268 ± .715
	5	-.851 ± .101	-.848 ± .105	-.782 ± .145	-.632 ± .151
	6	-.020 ± .082	-.003 ± .083	-.115 ± .143	.039 ± .151
	7	.488 ± .085	.514 ± .087	.423 ± .216	.862 ± .245
	8	.383 ± .208	.337 ± .212		
MS	1	-.227 ± .120	-.256 ± .120	-.078 ± .137	-.039 ± .137
	2	.112 ± .114	.128 ± .115	.278 ± .120	.251 ± .120
	3	.115 ± .116	.127 ± .116	-.200 ± .124	-.212 ± .124
AOD	2	.087 ± .071	.125 ± .072	-.361 ± .102	-.326 ± .102
	3	-.039 ± .070	-.044 ± .070	-.049 ± .085	-.044 ± .085
	4-9	-.149 ± .066	-.159 ± .067	.325 ± .075	.307 ± .074
	10+	.101 ± .074	.078 ± .074	.084 ± .095	.063 ± .094
PL	<75	-.062 ± .076	-.093 ± .077	-.158 ± .102	-.187 ± .101
	75-86	.026 ± .084	.029 ± .088	.368 ± .127	.380 ± .125
	87-92	-.022 ± .076	.015 ± .078	-.199 ± .105	-.205 ± .103
	>92	.058 ± .068	.049 ± .069	-.010 ± .079	.011 ± .078
YR	1990	-.215 ± .031	-.235 ± .031	-.485 ± .088	-.730 ± .097
	1991	.009 ± .029	-.012 ± .029	-.198 ± .087	-.438 ± .097
	1992	-.487 ± .034	-.370 ± .039	-1.391 ± 1.133	.045 ± 1.524
	1993	.143 ± .031	.141 ± .031	-.237 ± .076	-.434 ± .087
	1994	.357 ± .034	.327 ± .034	1.739 ± .070	1.492 ± .079
	1995	.150 ± .029	.136 ± .029	.327 ± .075	.079 ± .087
	1996	.042 ± .028	.012 ± .028	.245 ± .087	-.015 ± .096
WT[c]		.005 ± .000	.005 ± .000	.061 ± .000	.063 ± .000

[a] 152 sires

[b] 110 sires

[c] Expressed as deviations from the mean.

Bivariate Analysis Random Effect Estimates

Genetic effects. Sire (co)variance parameter estimates for all bivariate models are given in Table 4.14. Sire variance estimates for SC and RTS were greatest in the WT adjusted models analyzed using BIVARB. With AGE effects added, sire variance decreased, and decreased further when WT was removed from the model. MTDFREML estimates of sire variance were the same as previously calculated in the single trait analyses. Genetic covariances calculated from all models including AGE as a covariate were negative. When AGE is removed from the model, the genetic covariances calculated from WT adjusted models are essentially zero.

Table 4.14. Sire (co)variances for scrotal circumference and cycling status in yearling Limousin cattle

Method	Model	SC[a]	RTS[a]	SC:RTS[b]
MTDFREML	Age & Weight Adjusted	.386	.002	-.005
MTDFREML	Paired Age & Weight Adjusted	.364	.002	-.004
BIVARB	Age & Weight Adjusted	.340	.025	-.019
BIVARB	Paired Age & Weight Adjusted	.341	.023	-.017
BIVARB	Age Adjusted	.309	.023	-.016
BIVARB	Paired Age Adjusted	.313	.023	-.012
BIVARB	Weight Adjusted	.407	.035	.003
BIVARB	Paired Weight Adjusted	.407	.032	-.002

[a]Genetic variance
[b]Genetic covariance

Environmental effects. Environmental variance estimates are given in Table 4.15. Bivariate MTDFREML analyses yielded the same genetic and environmental variance estimates as univariate analyses. Environmental variances for the continuous trait were smaller in models including the weight covariate than models in which weight was removed. Environmental covariance is set to zero as traits were not measured on the same animal.

Table 4.15. Environmental variances for scrotal circumference and cycling status in yearling Limousin cattle

Method	Model	SC[a]	RTS[a]
MTDFREML	Age & Weight Adjusted	3.837	.165
MTDFREML	Paired Age & Weight Adjusted	3.803	.163
BIVARB	Age & Weight Adjusted	4.243	1
BIVARB	Paired Age & Weight Adjusted	4.047	1
BIVARB	Age Adjusted	5.148	1
BIVARB	Paired Age Adjusted	4.919	1
BIVARB	Weight Adjusted	4.254	1
BIVARB	Paired Weight Adjusted	4.067	1

[a]Environmental variance

Heritability and genetic correlation estimates. Heritability and genetic correlation estimates are given in 4.16. Heritability for the discrete trait (RTS) in the full models increased from single trait, and MTDFREML analysis (.04) to the analysis performed using BIVARB (unpaired = .10, paired = .09). Thus, BIVARB analyses produced higher genetic variances and corresponding herititability estimates for the discrete trait than those calculated in MTDFREML. This is due to the fact that BIVARB models the discrete trait on the underlying scale, and thus accounts for liability for RTS more correctly. Heritability decreased for the continuous trait (SC) from the AGE and WT adjusted results (.30) to the AGE only model (unpaired = .23, paired = .25). Heritability increased for both traits from the AGE and WT adjusted results to the model in which AGE was removed. Heritability estimates for the continuous trait ranged from .23 in the unpaired AGE adjusted model to .36 (unpaired and paired MTDFREML; paired, WT adjusted BIVARB). Of note is the range of negative genetic correlations of –.16 to -.20 for models including AGE vs. the genetic correlations calculated when AGE is removed (unpaired = .02, paired = -.01).

Table 4.16. Heritabilities and genetic correlations for scrotal circumference and cycling status in yearling Limousin cattle

Method	Model	SC[a]	RTS[a]	SC:RTS[b]
Univariate	SC	.37	--	--
Univariate	RTS	--	.04	--
MTDFREML	Age & Weight Adjusted	.36	.04	-.19
MTDFREML	Paired Age & Weight Adjusted	.36	.04	-.16
BIVARB	Age & Weight Adjusted	.30	.10	-.20
BIVARB	Paired Age & Weight Adjusted	.31	.09	-.19
BIVARB	Age Adjusted	.23	.09	-.19
BIVARB	Paired Age Adjusted	.25	.09	-.15
BIVARB	Weight Adjusted	.35	.13	.02
BIVARB	Paired Weight Adjusted	.36	.12	-.01

[a] Heritability
[b] Genetic correlation

Discussion

It is widely accepted among beef cattle breeders that age at puberty and yearling scrotal circumference are influenced by a number of the same genes in the different sexes. The genetic correlation estimates reported here between scrotal circumference and reproductive tract score seem to contradict such assessments. However, although threshold-continuous bivariate analyses produced larger heritability estimates of RTS the environmental variance component remained large. Thus, it seems likely that herd management is an essential element creating expressed fertility trait differences between sons and daughters of a sire. Heifers at Running Creek Ranch must breed to calve as two-year-olds to maximize production efficiency. Therefore, heifers are fed so that as many as possible can achieve cycling status prior to the breeding season. Two-year-old virgin bulls, however, are in sufficient demand that there is less management emphasis on early growth and reproductive maturation rate in the male population. Additionally, Bourdon and Brinks (1986) reported genotype x environment, and genotype x genotype x environment interactions affected fertility traits, perhaps to a larger extent than environmental effects alone; findings which may be particularly applicable to these data.

Limousin breed recommendations for age adjusting scrotal circumference to 365 days require bulls be measured between 10 and 14 months, as scrotal circumferences increase at linear rates during that time (Directions, Limousin Breeders Symposium, 1991). Conversely, reproductive maturation rates in females of similar ages are most definitely not linear, but sigmoidal, or logistic in nature. The bivariate estimation method used in these analyses is designed to accommodate this discrepancy, but perhaps the time of reproductive tract score measurement was inappropriate. Heifers in these analyses were measured just prior to being mated, with the primary aim being to cull those females unlikely to respond to estrus synchronization or become pregnant within a fixed breeding season. The objective was not to determine when a heifer first cycled (age at puberty), but instead identify those heifers cycling at the time of measurement. Although, reproductive tract scores can serve as estimators of age at puberty, their usefulness in that regard is time dependent. Andersen (1991) theorized that, if the objective is to reduce age at puberty and select for superior fertility trait genetics, reproductive tract scores should be taken when no more than half the population is thought to be cycling. As previously mentioned, genetic improvement of fertility traits was not the objective at Running Creek

Ranch beyond the inherent economic benefits of removing from the breeding herd those females unlikely to conceive within a fixed mating season. Were reproductive tract scores taken earlier or possibly even grouped differently, the genetic relationship with scrotal circumference may have been more similar to literature estimates of comparable analyses. The reproductive tract scoring system may require modification for use in Limousin cattle. All literature heritability estimates for RTS were calculated from analysis on cattle of British origin rather than Continental breeds.

Summers et al. (1999) modeled Limousin heifer pregnancy data with the intent of developing EPD for pregnancy. A corresponding study indicated relationships between scrotal circumference and heifer pregnancy are similar to those reported here (Edwards, 1999, personal communication). Pregnancy status, like cycling status, is a binary trait, and was estimated using a maximum *a posteriori* probit (MAP) threshold model (Gianola and Foulley, 1983; Harville and Mee, 1984). The bivariate analysis described by Janss and Foulley (1993), used in this analysis is an extension of the MAP threshold model as it includes analysis of continuous traits. Therefore, the bivariate analysis method described utilized here, BIVARB, should be examined further. Heritability estimates for the binary trait were improved in these analyses utilizing BIVARB over univariate and MTDFREML estimation methods. More importantly, fertility traits are considerably more economically important (Melton, 1995) than other beef production measures and producers need information regarding genetic and management opportunities. The threshold nature of female age at puberty does create estimation difficulties, which is among the reasons literature heritability estimates for most fertility traits measured in beef females are typically low. Researchers need methods to analyze threshold traits in conjunction with other, related traits, such as birthweight and calving ease scores, if appropriate, and accurate information is to be supplied to producers.

Additionally, it is noteworthy that the bivariate programs utilized do not report standard errors for genetic covariance parameters. Consequently, the authors are unsure of the true strength of the genetic covariance/correlation estimate. Thus, although the true correlation could be moderately negative for these data, it could be essentially zero as well.

Theoretically, beef cattle producers can breed for improved expressed fertility by selecting for traits that are positively correlated with fertility traits, such as growth and body condition. Although genetic effects were not estimated for the composition traits described in this study, it seems reasonable that joint selection for growth and fleshing ability are likely to create favorable corresponding responses in yearling fertility trait indicators.

While it is obvious that age is the primary covariate that should be included in any such analysis, weight is also an important source of variation. Although age and weight are highly related in most feasible and practical production schemes, the critical point is that management prevails as perhaps the most essential component affecting expressed fertility. While age allows for a more direct comparison across herds, breeds and regions, weight is a trait which producers can manage for, and thus influence directly. Another such trait is body condition score, which along with muscle score, appears to be, as expected, highly correlated with weight. The importance of management is fortified when the effects of weight and body condition are jointly considered. While breeders are not advised by this author to select against growth, common sense indicates that retaining higher body condition score heifers with lower weights will reduce mature weights and maintenance costs.

Certain relationships between composition and indicators of reproductive fitness in yearling cattle presented here challenge the perspective of many involved with beef cattle breeding. It is commonly acknowledged reproductive fitness traits of Limousin cattle generally require improvement, yet the amount of progress required to meet industry demands is debatable. Heifers cycling at a year of age will undergo at least three heat cycles before being bred to calve at 24 months. Certainly, favorable relationships have been well established between reduced age at puberty and lifetime fertility and productivity of a cow. However, the role of the Limousin breed in the beef industry mandates genetic advancement of fertility traits be conducted in the context of maintaining breed strengths. The data indicate Limousin breeders appear to have that opportunity.

IMPLICATIONS

Commonly accepted philosophy dictates maternal ability, including fertility and milk genetics, is of primary importance in replacement heifer selection and that muscularity can be ignored in the female and addressed through sire selection. However, if greater muscling is not detrimental to reproductive fitness in yearling Limousin heifers, given adequate weight, body condition, and a comparable environment, then breeders should retain heavier muscled females. Doing so allows Limousin breeders to accomplish two important goals. First, breed muscle advantages will be maintained without reliance upon utilization of the heaviest muscled bulls in the breed. At the same time, intense sire selection pressure can be directed towards fertility trait improvement and other breed weaknesses. Therefore, corrective mating schemes can be implemented in the manner which will produce the most rapid genetic improvement, through sire selection. Breeders are cautioned, however, as a result of these analyses that improvement in yearling female fertility may not be maximized through use of sire scrotal circumference EPD in environments comparable to the one maintained at this ranch. Additional research is needed to delineate genotypic expression of reproductive fitness traits in a given environment. Perhaps different sire lines or mating systems may be identified for specific management practices.

SUMMARY and CONCLUSIONS

Composition effects are important sources of variation in measures of fertility indicators in yearling Limousin cattle. Except for obese heifers, heavier conditioned cattle appear to be more fertile. Muscularity effects cannot be explained as simply, as they appear to be affected by sex and correlations with weight. Lighter muscled heifers were not as fertile as heifers of average and even greater muscularity. Heavier muscled bulls, on the other hand, had the smallest scrotal circumferences. In early phenotypic analyses, phenotypic selection for larger scrotal circumference was equivalent to selection against muscularity and vice-versa. Fortunately, when genetic effects were considered, average muscled bulls had the largest adjusted scrotal measurements, indicating that optimums for scrotal circumference and muscularity exist.

Genetic analyses yielded unexpected results, as correlations between male and female fertility traits were either not important or negative. This phenomenon contradicts most literature estimates of genetic relationships between male scrotal circumference and fertility traits in either daughters or half-sib sisters. However, recent reports of relationships between pregnancy status and sire scrotal circumference EPD in Limousin cattle support the estimates calculated in this study (Edwards, 1999).

The bivariate program described by Janss and Foulley (1993) accomplished an important objective by producing larger heritability estimates for the discrete trait than those obtained through single trait analyses or MTDFREML. Heritability estimates for scrotal circumference and cycling status were low, but in the range of literature estimates.

A paradigm shift may be required as Limousin seedstock producers look to females in their attempt to maintain muscularity, balance fertility trait and composition trait emphasis among potential sires. Limousin breeders who adopt this philosophy have the opportunity to retain heavy muscled replacement females with confidence in their reproductive ability, provided heifers possess the genetic potential required and receive management levels sufficient to achieve adequate weight and body condition prior to breeding. The implications of this are substantial for Limousin seedstock producers wishing to supply the beef industry with heavy muscled terminal sires and retain or merchandise female siblings as replacements.

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