Genetic Variation in Growth and Body Dimensions of Jersey and Limousin Cross Cattle. 2. Post-Weaning Dry and Wet Season Performance

R. A. Afolayan*, W. S. Pitchford, A. W. Weatherly and C. D. K. Bottema
Livestock Systems Alliance, Adelaide University, Roseworthy, SA 5371, Australia

ABSTRACT : The importance of direct genetic, maternal, heterosis and epistatic effects were examined on post-weaning weight, height, length, girth, fat depth and muscle (ratio of stifle to hip width) with dry and wet season gains in these traits. The breeds used were two pure breeds (Jersey and Limousin), the Limousin×Jersey F_1, and two backcrosses (F_1×Jersey dams and F_1×Limousin dams). Direct genetic effects were large ($p<0.001$) for all traits except for length. Jersey maternal effects were large for weight, girth, fat depth and muscle in the post-weaning wet season gains which is an evidence of the impact of Jersey dam on progeny beyond weaning. There were large heterosis effects on fat depth and muscle relative to other traits. Epistatic effects were observed for post-weaning performance in weight, girth, fat depth and muscle. There are indications that there were different genetic effects for post-weaning compared to pre-weaning growth traits. Thus, it could be hypothesized from this study that different quantitative trait loci (QTL) affect early and late growth in Jersey and Limousin cross cattle breeds. The follow up work will examine the different chromosomal gene effects on pre- and post-weaning growth. ***(Asian-Aust. J. Anim. Sci. 2002. Vol 15, No. 10 : 1378-1385)***

Key Words : Genetic Effects, Weight, Height, Fat Depth, Muscle

INTRODUCTION

Some important growth traits (e.g. body weight) in beef cattle improvement programs is influenced by both direct and maternal effects (Pitchford et al., 1993). Most reports, however, limited the assessment of these effects to weight and changes in weights in the early life of calves. Recent evaluation of weight traits by some workers has indicated an under-estimation of these genetic effects without the inclusion of grand maternal genetic effects (Davies et al., 1998; Dondenhoff et al., 1998). Body composition measurements (bone, fat and muscle) are also required to sufficiently describe variation in saleable yield performance of beef cattle. However, there is no literature on post-weaning body composition traits in cattle breeds.

The genetic improvement realized from heterotic, direct and maternal effects might be enhanced by epistatic effects expressed in the pre- or post- weaning performance of calves. Apart from heterotic gain, crossbreeding involving backcrossing to parental breed offers non- additive genetic effects in recombinants, which could either maintain or improve productivity. Although the earlier report by Afolayan et al. (2002a) has indicated that there may be no epistatic effects during pre-weaning growth performance, ample evidence exists that genetic effects may not be the same in different production environments (Long et al., 1979; Barlow, 1981; Bolton et al., 1987a,b; Brown et al., 1993).

There have been few studies specifically designed to investigate the interaction of genetic effects with environmental changes (Barlow, 1981; Brown et al., 1993), but there is little or no information on the effect of seasonal changes in many additive and non-additive genetic effects on post-weaning growth traits. It is important, therefore, that these genetic effects on post-weaning growth traits of composite populations are investigated as age progresses in different seasons. The advantages of composite breeds as an alternative to continuous crossbreeding have been previously reported (Dickerson, 1973; Gregory and Cundiff, 1980). Breed differences, rather than intra-population selection, can generally be exploited to optimize performance levels more quickly in crosses or in composite populations (Cundiff et al., 1998). Therefore, the objective of this study was to evaluate four genetic effects on growth and development of Jersey and Limousin progeny in different seasons and stages of growth.

MATERIALS AND METHODS

General procedures

In 1993, 280 purebred Jersey and Limousin dams were procured as part of the Davis Mapping herd. These dams were mated to purebred Jersey and Limousin sires to produce purebred Jersey (JJ), purebred Limousin (LL) or F_1 (LJ) calves born in 1994 and 1995. Mating F_1 bulls to parental breed cows (Jersey and Limousin) began in 1995 and backcross progeny [3/4 Jersey (XJ), 3/4 Limousin (XL)] were produced from 1996 until 1998. In the design, which involved two phases, year and breed were partially confounded. However, some purebred JJ calves were produced in 1996 to help link the two phases. Sires and dams were commonly used across years.

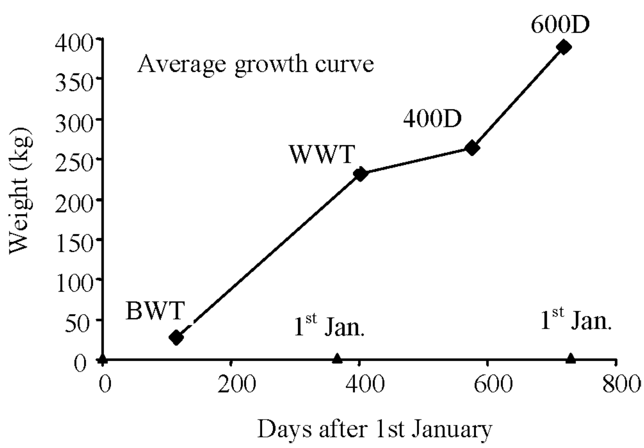
* Corresponding Author: R. A. Afolayan. Tel: +61-8-83037643, Fax: +61-8-83037972, E-mail: Raphael.afolayan@student.adelaide.edu.au
Received January 28, 2002; Accepted May 13, 2002

Calving occurred each year in autumn from early March through mid-May. Calves stayed with their dams on pasture until weaning (at an average age of 250 days). After weaning, calves grazed pasture and/or hay supplemented for 430-500 days. The animals' post-weaning weight (WT), height (HT), length (LH), girth (GH), fat depth at P8 site (FD)(Afolayan et al., 2002a) and muscularity (MUS, measured by stifle width as a proportion of hip width expressed as percent) were obtained at two ages. These ages were approximately 400 days and 600 days after birth, i.e. during winter after the dry season and summer after the wet season, respectively. Growth rates were calculated between weaning and 400 days (dry season gain=January to June) and between 400 and 600 days (wet season gain=July to December). Thus, season was confounded with age.

The environment is classified "Mediterranean" with hot dry (34% annual rainfall) summers and cool wet (66% annual rainfall) winters as outlined previously (Afolayan et al., 2002a). Pasture availability and quality in spring during and following the winter months (April-September) is far superior to autumn during and after the summer months (October to March). This study examines dry season (39% annual rainfall) and wet season (61% annual rainfall) growth rates. The pre- and post- weaning growth pattern of calves in different seasons is presented (Figure 1). The methods used for collection of weights and body dimension traits have also been described (Afolayan et al., 2002a). The degree of muscularity was not taken at weaning for calves born in 1994 and at 400 days of age for the 1996 drop. Also, there were no 600 day measurement of height, length and girth for heifers born in 1994.

Statistical analysis

Fixed effects of year of birth (YOB: 1994-1998), day of birth (DOB: 5 classes with each comprising 20% of calves



BWT=birth weight, WWT=weaning weight
400D=400 day weight, 600D=600 day weight

Figure 1. Pre- and post-weaning growth pattern of calves in different seasons.

born in succession), sex of calf (heifer or steer), breed of calf (JJ, XJ, LJ, XL, LL) and year×sex interaction in a model with sire and dam fitted as random effects were tested on twenty four traits (Table 1) (Proc Mixed, SAS 1992). Since there were no values for weaning muscle in 1994 and 400 day muscle in 1996, the model for the dry season muscle gain included fixed effect of phase, year nested within phase and of breed nested within phase. However, the 400 day muscle included only phase and year nested within phase because of the missing 1996-drop data that included some purebred Jerseys (to aid linkage across years). Genetic effects were defined in terms of direct additive, maternal additive, heterosis and epistatic effects. Estimation of these effects was as reported previously (Afolayan et al., 2001a). Significance was defined as $p<0.05$.

RESULTS

Non- genetic effects

400 and 600 day performance : The weight and height at 400 day postpartum were influenced by all the fixed effects (Table 1). However, the year of birth by sex interaction was only significant for 400 day weight, height and muscle score and not for length, girth and fat depth. While steers born in 1994 were better than heifers in weight (14%) and muscle score (6%), it was the 1995 born steers, on the average, that were 5% taller than heifers born in the same year. Day of birth effect was significant for all the 400 day traits with the exception of the muscle score. The pattern was similar to the weaning weight, height, length and girth. However, for fat depth, the first of 80% of calves born were the same (2.0 mm), while the last 20% were leaner (1.3 mm).

At 600 day postpartum, effects due to the year of birth by sex interaction were significant ($p<0.01$) for all traits (Table 1). The steers born in 1995 were bigger than heifers of the same year in weight (7%), height (12%), length (11%) and girth (21%), respectively. Steers were also fatter (167%) and more muscular (20%) than heifers. It was, however, observed that the steers were only fatter than heifers in the first phase of the experiment (1994-1995), but the reverse was the case in the second phase (1996-1998). This was because phase 1 steers were measured for growth and body dimensions at an older age than heifers but male and female calves were always measured at the same time in the second phase (1996-98) of the experiment. Regardless of the year, the heifers were consistently less muscular than the steers. Also, the significant effect due to day of birth was the same as observed for 400 day postpartum traits with the exception of length.

Dry and wet season gains : All fixed effects significantly influenced the weight gain in both seasons except the day of birth (Table 1). However, the result for

Table 1. Analysis of variance and tests of significance for post-weaning traits

Trait	Effect							
	YOB[a]	DOB[a]	Sex[a]	Breed[a]	YOBxSex[a]	Sire[b]	Dam[b]	Residual[b]
400 days								
Weight (kg)	59.9***	16.6***	96.6***	51.6***	3.3**	38.2	173.4	552.0
Height (cm)	22.9***	4.0**	101.8***	44.8***	5.2***	2.2	2.5	15.9
Length (cm)	14.7***	4.1**	21.7***	2.8*	0.2	1.1	3.6	44.6
Girth (cm)	40.7***	10.6***	82.3***	28.1***	1.9	0.8	5.7	31.0
Fat depth (mm)	211.1***	2.5*	10.0**	8.6***	0.4	0	0	0.7
Muscle (%)	42.0***	0.8	8.3**	210.9***	6.6***	0.5	3.2	24.3
600 days								
Weight (kg)	30.4***	6.4***	637.7***	62.2***	176.2***	119.9	265.6	949.3
Height (cm)	11.8***	4.5**	471.4***	54.5***	29.1	3.1	3.5	14.1
Length (cm)	5.8***	1.2	96.4***	12.6***	33.4***	1.2	6.4	27.1
Girth (cm)	5.8***	5.4***	428.9***	29.4***	144.0***	2.4	5.2	38.7
Fat depth (mm)	35.7***	2.4*	9.3**	7.2***	53.0***	0.2	0.8	3.6
Muscle (%)	67.9***	0.6	84.5***	44.2***	22.6***	0	0.4	63.5
ADG1								
Weight (g/d)	114.2***	1.9	10.1**	4.1**	8.3***	0	824.7	10,225.9
Height (mm/d)	94.0***	2.8*	19.4***	2.5*	6.7***	1.4	21.9	613.7
Length (mm/d)	23.6***	0.3	12.2***	0.5	0.2	57.2	100.1	2,937.7
Girth (mm/d)	247.8***	2.1	24.1***	0.3	1.8	26.8	153.3	1,273.9
Fat depth (um/d)	174.0***	2.8*	1.1	8.4***	0.2	0.9	1.7	59.0
Muscle (%/dx10^{-3})	0.7	1.5	7.4**	4.3**	10.1***	0	81.9	2,588.2
ADG2								
Weight (g/d)	175.3***	1.4	1,958.5***	27.6***	1,221.0***	1,120.6	1,809.4	24,181.8
Height (mm/d)	44.5***	0.2	339.0***	4.0**	110.5	10.3	2.5	633.8
Length (mm/d)	20.8***	1.8	93.2***	6.6***	101.0***	14.9	66.2	1,807.6
Girth (mm/d)	88.8***	1.8	889.2***	7.3***	766.0***	13.5	0	1,456.3
Fat depth (um/d)	81.3***	1.6	105.4***	8.8***	152.2***	4.9	26.2	170.3
Muscle (%/dx10^{-3})	95.3***	1.0	62.3***	40.9	58.8***	16.9	0	6,059.8

[a] Fixed effects type III mean squares, [b] Random effect variances.
* $p<0.05$, ** $p<0.01$, *** $p<0.001$.
ADG1=Dry season average daily gain. ADG2=Wet season average daily gain, YOB=Year of birth, DOB=Day of birth.

gain in height, length, girth, fat depth and muscle score were not consistent in both seasons. For the dry season post weaning gain, there was a significant (p<0.01) year by sex interaction in weight, girth and muscle. While the steers born 1994 were 5% heavier than heifers of the same year, the 1995 born steers were bigger than heifers in girth and muscle. However, the observed significant (p<0.01) year by sex interaction in wet season post-weaning gain for all the traits were consistent except for gain in length. Steers born in 1995 grew faster than the heifers in weight (23%), height (7%), girth (18%), fat depth (64%) and muscle (3%). With regard to length for this season, the best gain was obtained in 1996 and the heifers were generally longer than steers in all the years.

Breed and genetic effects

400 and 600 day performance : Breed effects were highly significant (p<0.01) for all the traits measured at 400 and 600 days postpartum except for height, which had a lower significance (p<0.05) at 400 days of age (Table 1). The variation due to sire and dam were generally small compared to that of the residual variation.

Breed rankings for 400 day postpartum weight, height, girth and muscle were the same as at weaning (Afolayan et al., 2001a). Size increased as the proportion of Limousin genes increased (Table 2). In length, however, LL and XL were the same but higher than LJ=XJ and JJ respectively. At 400 days, crossbred calves (XJ, LJ and XL) were similar in fat depth and higher than the two purebreds (JJ or LL). The direct Jersey effect resulted in calves significantly (p<0.01) lower in weight, height, girth and muscle but this effect was not significant for length or fat depth. However, the Jersey maternal effects resulted in increased weight, muscle (p<0.01) and height (p<0.05) but not for length, girth or fat depth. Large and positive heterotic effects were observed for fat depth (p<0.01). Negative heterosis was observed for weight and muscle (p<0.01) but not for height, length and girth (p>0.05). At 400 days, no epistatic effects were observed for the traits (Table 3).

The effect due to breed differences was highly significant (p<0.01) for all the traits at 600 day postpartum. The pattern was similar to that obtained at 400 day postpartum and the ranking of the breeds were consistent for many of the measured traits. Breed means shows that the purebred Limousin was the heaviest (weight) and

Table 2. Least square means for the fixed effect of breed for post-weaning traits

Trait	Breed				
	Jersey (JJ)	LJ×JJ (XJ)	LL×JJ (LJ)	LJ×LL (XL)	Limousin (LL)
400 day					
Weight (kg)	220.2±5.7	254.2±5.0	258.4±7.0	281.2±5.1	304.8±6.7
Height (cm)	110.1±1.2	115.9±1.0	117.9±1.4	120.5±1.0	123.8±1.3
Length (cm)	122.2±1.2	125.3±1.1	125.4±1.6	126.7±1.1	126.3±1.5
Girth (cm)	150.2±1.1	154.6±1.0	156.4±1.4	159.0±1.0	162.6±1.3
Fat depth (mm)	1.3±0.1	1.7±0.1	1.8±0.2	1.6±0.1	1.0±0.2
Muscle (%)	72.8±1.0	70.1±0.6	82.8±0.9	79.0±0.7	98.3±0.8
600 day					
Weight (kg)	328.7±9.1	358.1±7.8	400.7±10.6	407.2±7.9	458.3±10.3
Height (cm)	117.7±1.4	124.8±1.1	126.2±1.6	130.8±1.2	132.2±1.5
Length (cm)	129.0±1.2	130.9±1.0	131.9±1.6	134.2±1.0	136.9±1.5
Girth (cm)	170.4±1.5	172.1±1.2	181.2±1.9	177.4±1.2	187.8±1.8
Fat depth (mm)	2.4±0.4	3.2±0.4	5.5±0.5	3.1±0.4	4.4±0.5
Muscle (%)	73.1±1.1	80.2±1.1	75.4±1.7	89.3±1.1	80.3±1.6
ADG1					
Weight (g/d)	138.9±14.6	195.9±13.9	163.7±21.4	208.8±14.0	196.3±20.0
Height (mm/d)	41.1±3.7	50.2±3.5	53.4±5.3	48.6±3.5	54.0±5.0
Length (mm/d)	68.3±9.3	73.0±8.5	79.7±12.5	69.8±8.5	68.1±11.9
Girth (mm/d)	312.1±6.5	312.2±5.9	312.5±8.6	308.3±6.0	310.3±8.2
Fat depth (um/d)	1.0±1.3	2.3±1.2	-4.3±1.7	0.3±1.2	2.9±1.2
Muscle ($\%/d\times10^{-3}$)	-2.9±1.0	-4.7±0.4	-4.7±0.9	-4.8±0.5	-7.2±0.8
ADG2					
Weight (g/d)	725.9±32.7	732.4±29.0	970.0±41.4	842.8±29.0	1186.6±39.9
Height (mm/d)	46.6±4.4	56.5±3.6	44.3±6.4	62.4±3.6	57.5±6.0
Length (mm/d)	49.3±7.2	44.6±5.7	38.0±10.7	53.5±5.8	77.9±9.9
Girth (mm/d)	140.2±6.4	118.1±5.2	165.7±9.5	122.4±5.2	181.5±8.8
Fat depth (um/d)	10.9±2.5	13.1±2.2	31.7±3.3	13.2±2.3	28.9±3.1
Muscle ($\%/d\times10^{-3}$)	12.4±1.2	-0.6±0.6	6.4±1.2	-0.8±0.8	-4.1±1.0

ADG1, ADG2 same as Table 1.

biggest (height, length and girth) with the purebred Jersey at the other extreme. There was a gradual increase in weight, height, length and girth as the proportion of Limousin genes increased (Table 2). In contrast to observation for muscle at 400 day, XL calves were more muscular than XJ=LL and LJ=JJ, respectively. At this age, the F_1 (LJ) calves were still fatter than any other genotypes.

At 600 days postpartum, Jersey direct genetic effect was highly significant ($p<0.01$) for all the traits with the exception of muscle (Table 3). The direct effects resulted in calves with less weight, height, length, girth and fat depth. Large Jersey maternal effects were also observed on girth, fat depth and muscle with a smaller effect on weight. In contrast to the direct effects, however, maternal effects due to Jersey genes produced slightly heavy ($p<0.05$) but fatter ($p<0.01$) calves with large girth ($p<0.01$) and far less muscle ($p<0.01$). No significant maternal effects were observed on height or length at 600 days. Heterotic effects were significant but lower for fat depth ($p<0.05$) and positively higher ($p<0.01$) for muscle at this age as compared to 400 day postpartum. At 600 day postpartum, the negative heterotic effects on weight was no longer significant but there was significant and positive heterosis on muscle. Also, a strong and positive epistatic effect was observed on muscle at this age.

Dry and wet season gains : As expected, breed differences in daily gain were significant for most traits in the dry season (weaning to 400 day). XL calves had the highest gain in weight, followed by XJ=LL, LJ and JJ (Table 2). The ranking order for height was similar to pre-weaning (Afolayan et al., 2002a). Muscle also followed the same trend (Figure 2). However, there was a significant fat depth loss in F_1 (LJ), and the XJ and XL gained less fat than the purebred mean (Figure 2). The direct Jersey effects resulted in increased muscle gain but reduced weight and fat depth gain. There was a positive but low Jersey maternal effect on height and fat depth, and a negative and low maternal effect on muscle. Heterotic and epistatic effects were the same as for pre-weaning (Afolayan et al., 2001a).

In the wet season (400 day to 600 day), the gains in all the traits were faster than the dry season for all the genotypes. The ranking was similar to the dry season performance. However, the amount of fat depth and muscle lost in the dry season by genotypes affected the level of the wet season gain (Figure 3). The direct Jersey effects in the wet- and dry season were similar for gain in weight, fat

Table 3. Genetic effects and tests of significance (difference from zero) for post-weaning traits

Trait	Genetic effect			
	Jersey direct	Jersey maternal	Heterosis	Epistasis
400 day				
Weight (kg)	-57.6±8.3***	15.3±4.8**	-19.3±5.3***	29.7±15.9
Height (cm)	-9.1±1.8***	2.2±1.0*	-1.2±0.9	3.7±3.1
Length (cm)	-2.8±1.8	0.7±1.1	0.5±1.4	3.0±3.8
Girth (cm)	-8.1±1.6***	1.9±1.0	-1.8±1.2	2.5±3.3
Fat depth (mm)	0.1±0.2	0.0±0.1	0.6±0.2***	0.4±0.4
Muscle (%)	-16.5±1.4***	3.8±0.9***	-6.5±1.1***	-
600 day				
Weight (kg)	-80.5±13.2***	15.7±7.3*	-8.6±7.1	-13.1±23.7
Height (cm)	-8.5±2.0***	1.3±1.1	0.0±0.9	5.8±3.4
Length (cm)	-4.5±1.7**	0.6±1.0	-1.6±1.3	0.8±3.4
Girth (cm)	-12.1±2.2***	3.3±1.3**	-1.3±1.5	-7.4±4.2
Fat depth (mm)	-2.1±0.6***	1.1±0.4**	1.0±0.4*	-1.5±1.2
Muscle (%)	1.9±1.7	-5.5±1.1***	4.2±1.7**	12.0±4.0**
ADG1				
Weight (g/d)	-44.6±22.3*	15.9±14.7	-19.7±21.5	89.3±52.1
Height (mm/d)	-14.5±5.5**	8.0±3.6*	-2.2±5.2	5.9±12.9
Length (mm/d)	-3.1±14.0	3.1±8.7	8.4±11.4	-1.9±29.9
Girth (mm/d)	-2.2±9.5	3.1±5.9	3.1±9.5	-1.8±7.7
Fat depth (um/d)	-3.9±1.9*	3.0±1.2*	-9.2±1.6***	7.9±4.2
Muscle (%/d×10^{-3})	43.0±13.9**	-21.2±8.8*	24.8±13.2	-
ADG2				
Weight (g/d)	-282.4±48.8***	86.0±28.6**	-38.5±34.2	230.8±95.5*
Height (mm/d)	-5.0±6.7	-0.5±4.1	-7.3±5.7	22.1±13.8
Length (mm/d)	-19.7±10.9	5.4±6.7	-31.0±9.6***	1.9±23.0
Girth (mm/d)	-37.0±9.7***	16.4±6.0**	-11.5±8.6	-69.7±20.7***
Fat depth (um/d)	-17.9±3.7***	8.9±2.3***	2.9±2.9	-16.4±7.7*
Muscle (%/d×10^{-3})	16.2±1.8***	-8.0±1.2***	10.3±1.7***	-

* p<0.05, ** p<0.01, *** p<0.001, ADG1, ADG2 same as in Table 1.

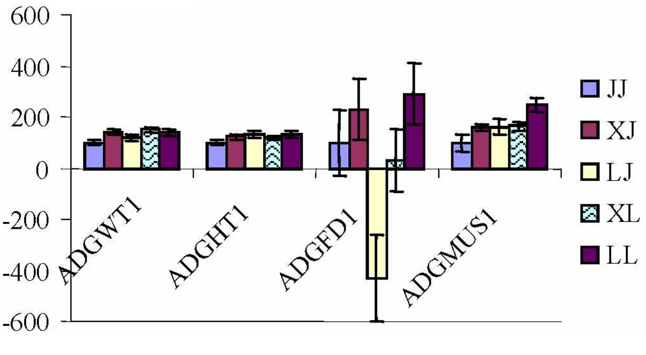
depth and muscle (Table 4). However, the wet season as compared to the dry season led to greater breed effects on weight, fat depth and muscle. Also, the significant direct effect on dry season height was no longer apparent in the wet season, while the direct effect on girth which was not apparent in dry became highly significant (p<0.01) in the wet season. The Jersey maternal effect on weight and girth was significant and was higher in significance for fat depth and muscle in the wet season compared to dry season. However, the maternal effect apparent on height in dry season was no longer significant in the wet season. The Jersey maternal effect resulted in calves with increased weight, additional fat depth and less muscle gain. The heterotic effect was significant and positive for muscle with calves gaining more muscle. However, the significant negative heterosis on fat depth gain in the dry season was not evident in the wet season. Although no epistatic effects were observed for any of the dry season traits, there was a positive epistatic effect for weight and negative epistatic effects for girth and fat depth during the following wet season.

DISCUSSION

Non-genetic effects

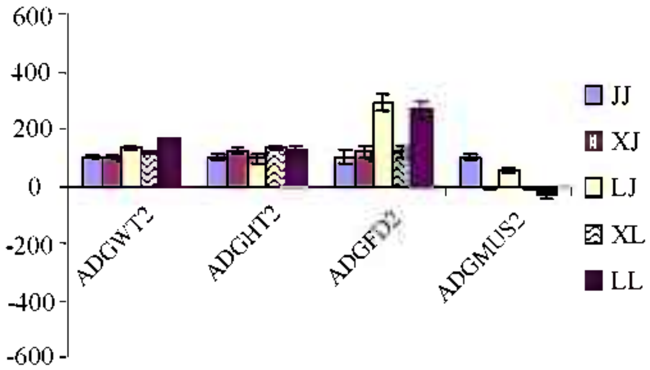
The gene composition, pre- and post-natal environment and even age generally influence the performance of animals in traits of economic importance. Seasonal pasture productivity induced by climatic environment was an evidence of pasture availability (Wheeler and Freer, 1986), with pasture quality and quantity being better in the higher rainfall months than in the drier months. Evidence of the impact of the quality and quantity of pasture available for grazing on the magnitude and direction of post-weaning growth of weight and body dimension traits of pure and crossbred calves were observed in this study. Comparable results were obtained previously with post weaning growth of steer (Arthur et al., 1994) and heifer (Hearnshaw et al., 1994) calves from Hereford, Brahman and their crosses.

A limitation of this study is the confounding between age of calves and season of growth. However, higher growth performance was observed in older growing calves, a period which was during the wet season, compared to when calves were younger in the dry season. The findings



Standard errors. ADG WT1, HT1, FD1, MUS1=Dry season gains in weight, height, fat depth and muscle. JJ=Jersey, XJ=Jersey backcross, LJ=JJ×LL, XL=Limousin backcross, LL=Limousin.

Figure 2. Breed means as a percentage of pure Jersey mean for dry season gain.



Standard errors. ADG WT2, HT2, FD2, MUS2= Wet season gains in weight, height, fat depth and muscle. JJ, XJ, LJ, XL, LL same as in Table 2.

Figure 3. Breed means as a percentage of pure Jersey mean for wet season gain.

indicated that weight gain was almost five times greater in the wet season (i.e. older age) than the dry season (i.e. younger age). The expectation would have been for the older animal to grow slower. Thus, the seasonal effect rather than age was assumed to be the primary cause of the differences in growth performance of the growing calves within the two phases of growth in this study.

Breed and genetic effects

Breed effect : In general, the better performance of Limousin and 3/4 Limousin as compared to other genotypes in weight and many of the body dimension traits was expected. This was largely due to the positive Limousin direct effect in contrast to the negative Jersey direct effect on these traits. In a crossbreeding experiment involving Brahman and Hereford, there was a similar increase in wither height as the amount of Brahman genes increased (Long et al., 1979; Stewart et al., 1980; Bolton et al., 1987; Comerford et al., 1988; Hearnshaw et al., 1994).

Direct effects : The direct effects on weight, height and girth traits as observed at weaning (Afolayan et al., 2002a) were still more important at 400 and 600 day postpartum compared to other genetic effects. This indicates that the individual breed genetic effects influence the performance of animals at any age since this effect was consistent across ages for these traits. However, the results were not consistent for length, fat depth and muscle. The positive impact of Jersey genes on fat depth at weaning (Afolayan et al., 2002a) was lost at 400 days and negative at 600 days (Table 3). In contrast, there was a large significant negative impact of Jersey genes on muscularity at weaning and 400 days, which disappeared by 600 days presumably because of compensatory growth. A Jersey breed effect on length was not noticed at weaning but became pronounced at 600 days after birth.

The genetic effects on growth were smaller in the dry season compared to the wet season due to improved nutrition. Arthur et al. (1994b) acknowledged the significance of the influence of post-weaning environment on the magnitude and direction of the genetic effect on a trait. Jersey direct effects were consistent in both seasons for weight, height, girth and fat depth but not for muscle. For example, the Jersey direct effect led to low weight, height, girth and fat depth gain but higher post-weaning muscle gain. This is in agreement with Koch et al. (1994) suggesting that the post-weaning muscle score might be influenced primarily by direct effect. The positive direct effect on muscle gain at older ages was unexpected, since the effect was negative at weaning (-21%, Afolayan et al., 2002a) and even at 400 days (-16%). This may be due to faster physiological maturation of Jersey relative to Limousin at these ages.

Maternal effects : The positive Jersey maternal effects for weight, height, girth, fat depth and muscle at 400 or 600 days of age is an indication of the importance of the carry-over effects of pre and post-natal nutrition from Jersey cows relative to Limousin cows. The Jersey is a dairy breed and has a high milk supply. The maternal effect over-rided the direct effect on these traits due to the large milk supply from the Jersey dams. However, the decrease in the level of its significance for weight and height, as well as the significant but negative effect for muscle as age progresses, suggested that the influence of the dam on post-weaning performance of progeny is minimal relative to pre-weaning performance. Also, the initial positive Jersey maternal effects on muscle at 400 days but positive Limousin maternal effects at 600 days may suggest an attribute of compensatory growth exhibited by calves born and nursed by Limousin dams. In addition, maternal effects for growth may vary with nutrition, which was confounded with age in this study.

The positive Jersey maternal effects on most daily gain traits were due to large milk production of this breed and had a large effect on progeny even at older ages when exposed to a good post-weaning environment. However, there was a negative effect on post-weaning muscle gain. Again, this may be due to compensatory growth in calves with Limousin dams relative to Jersey dams. This is further demonstrated in the genotype by seasonal re-ranking in weight (Dry: JJ<LJ<XJ=LL<XL vs Wet: JJ<XJ<XL<LJ<LL) and height (Dry: JJ<XL<XJ<LJ<LL vs Wet: LJ<JJ<XJ<LL<XL). However, the result of this study contradicts the lack of significant maternal additive effect for post-weaning average daily gain and live-weight observed by Arthur et al. (1994b).

Heterosis effects : The large fat differences of the F_1 (LJ) calves compared to other genotypes at all ages was predominantly due to heterotic effects but was also partly due to the maternal effect. The F_1 progeny were clearly fatter with less muscle than expected. However, the negative heterosis on dry season gain (Table 3; Figure 2) is just an indication of the loss of the pre-weaning effect. The significant negative heterosis on weight is contrary to earlier reports. Koch et al. (1985) obtained a greater than expected retained heterosis for post-weaning gain and final weight. Also, Pitchford et al. (1993) found that heterosis effects were 1-21% for mature weight and 0-4% for mature height depending on the environment. In male and female lines of three composite populations (MARC I, II and III), heterosis was important for average daily gain from weaning to 368 day, 368 day weight, and 368 day condition score (Gregory et al., 1991). The observed deviation of negative heterosis on weight at 400 days and no effect on post weaning weight gains might partly be due to the limited number of sires per breed (2-3) in this study. However, while sires were poorly represented, there were large numbers of dams from wide range of sources. Also, the phenotypic difference between the breeds (Limousin and Jersey), especially for carcass traits, is larger than for most other studies. The highly significant heterotic effect on muscle at both ages herein was in contrast to the previous findings of no significance heterotic effects on this trait (Gregory et al., 1991).

The impact from crossbreeding of this type, due to heterotic and maternal effects (Afolayan et al., 2002a), is further strengthened by the possibility of post- weaning compensatory growth for the pre-weaning disadvantaged calves. Those calves that were lacking in growth pre-weaning, probably due to the short milk supply from Limousin dam, were compensated when exposed to good post-weaning environment.

Epistatic effects : At weaning, there was no epistatic effect on any of the traits (Afolayan et al., 2002a). However, the positive epistatic effects on some post-weaning traits (weight and muscle) and negative effects on others (girth and fat depth) herein indicate that epistatic effects are important in older ages of growing calves. Thus, non-additive genetic attributes hidden in the recombinants at pre-weaning growing phase are revealed at post-weaning growing phase probably because of the change in nutrition or post-weaning environment. A study in mice has shown that there are different quantitative trait loci (QTL) affecting early and late growth (Vaughn et al., 1999). In that study, QTLs were mapped to separate chromosome locations. The breed re-ranking in the current study was a function of non-additive (heterosis and epistasis) genetic effects.

In conclusion, there were different significant genetic effects for post-weaning compared to pre-weaning growth of growing calves (Afolayan et al., 2002a). The non-additive genetic effects of epistasis (apart from maternal and heterotic effects) could probably be exploited in this type of crossbreeding program in older calves that are heavily dependent on forage rather than milk. This finding may support the hypothesis that different QTL are affecting growth at younger and older ages as reported in mice (Vaughn et al., 1999) The project from which this study emanated was originally designed for mapping QTL of various economic traits, including growth traits. Thus, the aspects of different QTL effects for growth at pre- and post-weaning ages will be examined to improve beef cattle breeding programs.

ACKNOWLEDGEMENTS

The J. S. Davies Bequest to the University of Adelaide and Adelaide University Research Scholarship awards to R.A. Afolayan primarily funded this study. The authors would also like to acknowledge the inputs of Judith Pitchford for data processing.

REFERENCES

Afolayan, R. A., W. S. Pitchford, A. W. Weatherly and C. D. K. Bottema. 2002a. Genetic variation in growth and body dimension of Jersey and Limousin cross cattle. 1. Pre-weaning performance. Asian-Aust. J. Anim. Sci. 15(10):1371-1377

Arthur, P.F., H. Hearnshaw, P. F. Kohun and R. Barlow. 1994a. Evaluation of Bos indicus and Bos taurus Straightbreds and crosses. I. Post-weaning growth of steers in Different Environments. Aust. J. Agric. Res. 45:783-794.

Arthur, P. F., H. Hearnshaw, P. F. Kohun and R. Barlow. 1994b. Evaluation of Bos indicus and Bos taurus Straightbreds and crosses. III. Direct and maternal Genetic Effects on growth Traits. Aust. J. Agric. Res. 45:807-818.

Barlow, R. 1980. Experimental evidence for interaction between heterosis and environment in animals. Anim. Breed. Abstr. 49:715-737.

Bolton, R. C., R. R. Frahm, J. W. Castree and S. W. Coleman. 1987a. Genotype × environment interactions involving proportion of Brahaman breeding and season of birth. I. Calf growth to weaning. J. Anim. Sci. 65:42.

Bolton, R. C., R. R. Frahm, J. W. Castree and S. W. Coleman. 1987b. Genotype × environment interactions involving proportion of Brahman breeding and season of birth. II. Post-weaning growth, sexual development and reproductive performance of heifers. J. Anim. Sci. 65:48-55.

Brown, M. A., A. H. Brown, Jr., W. G. Jackson and J. R. Miesner. 1993. Genotype × Environment interactions in Post-weaning Performance of Yearling in Angus, Brahman, and Reciprocal-Cross calves. J. Anim. Sci. 71:3273-3279.

Burns, W. C., M. Koger, W. T. Butts, O. F. Pahnish and R. L. Blackwell. 1979. Genotype by environment interaction in Hereford cattle. II. Birth and weaning traits. J. Anim. Sci. 49:403.

Comerford, J. W., L. L. Benyshek, J. K. Bertrand and M. H. Johnson. 1988. Evaluation of performance characteristics in a diallel among Simenmental, Limousin, polled Hereford and Brahman Beef cattle. I. Growth, hip height and pelvic size. J. Anim. Sci. 66:293.

Cundiff, L. V., K. E. Gregory and R. M. Koch. 1998. Germplasm Evaluation in Beef Cattle-Cycle IV: Birth and Weaning Traits. J. Anim. Sci. 76:2528-2335.

Davis, K. C., D. D. Kress, D. E. Doornbos and D. C. Anderson. 1998. Heterosis and breed additive effects for Hereford, Tarentaise, and the Reciprocal crosses for calf Traits. J. Anim. Sci. 76:701-705.

Dickerson, G. E. 1973. Inbreeding and heterosis in animals. In: proc. Of the Animal Breeding and Genetics Symp. In Honor of Dr Jay L. Lush. Am. Soc. Anim. Sci., champaign, IL. pp. 54-77.

Dondenhof, J., L. D. Van Vleck, S. D. Kachman and R. M. Koch. 1998. Parameter Estimates for Direct, maternal and grand maternal Genetic Effects for Birth Weight and Weaning Weight in Hereford Cattle. J. Anim. Sci. 76:2521-2527.

Gregory, K. E. and L. V. Cundiff. 1980. Crossbreeding in beef cattle. Evaluation of systems. J. Anim. Sci. 51:1224.

Gregory, K. E., L. V. Cundiff and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for growth traits in both sexes of beef cattle. J. Anim. Sci. 69:3202-3212.

Hearnshaw, H., P. F. Arthur, R. Barlow, P. J. Kohun and R. E. Darnell. 1994. Evaluation of Bos indicus and Bos taurus Straightbreds and crosses. II. Post-weaning Growth, Puberty, and Pelvic Size of Heifers. Aust. J. Agric. Res. 45:795-805.

Holloway, J. W., B. G. Warrington, F. M. Jr. Rouquette, C. R. Long, M. K. Owens and J. F. Baker. 1992. Forage availability ×heifer phenotype interactions for Brahman-Hereford F1 yearling heifers grazing humid pasture and semi arid rangeland. J. Anim. Sci. 70:2658.

Koch, R. M., G. E. Dickerson, L. V. Cundiff and K. E. Gregory. 1985. Heterosis retained in advanced generations of crosses among Angus and Hereford cattle. J. Anim. Sci. 60:1117.

Koch, R. M., L. V. Cundiff and K. E. Gregory. 1994. Cumulative Selection and Genetic change for Weaning or Yearling Weight or for Yearling Weight plus muscle Score in Hereford cattle. J. Anim. Sci. 72:864-885.

Koger, M., F. M. Peacock, W. G. Kirk and J. R. Crockett. 1975. Heterosis effects on weaning performance of Brahman-Shorthorn calves. J. Anim. Sci. 40:826.

Koger, M., W. C. Burns, O. F. Pahnish and W. T. Butts. 1979. Genotype by environment interactions in Hereford cattle. I. Reproductive traits. J. Anim. Sci. 49:396.

Long, C. R., T. S. Stewart, T. C. Cartwright and J. F. Baker. 1979a. Characterization of cattle of a five-breed diallel. II. Measures of size, condition and growth in heifers. J. Anim. Sci. 49:432.

Long, C. R., T. S. Stewart, T. C. Cartwright and J. F. Baker. 1979b. Characterization of cattle of a five-breed diallel. I. Measures of size, condition and growth in bulls. J. Anim. Sci. 49:418.

Long, C. R. 1980. Crossbreeding for beef production. Experimental results. J. Anim. Sci. 51:1197.

Pitchford, W. S., R. Barlow and H. Hearnshaw. 1993. Growth and calving performance of cows from crosses between the Brahaman and Hereford. Livestock Prod. Sci. 33:141-150.

Stewart, T. S., C. R. Long and T. C. Cartwright. 1980. Characterization of cattle of a five-breed diallel. III. Puberty in bulls and heifers. J. Anim. Sci. 50:808-820.

Vaughn, T. T., L. S. Pletscher, A. Peripato, K. King-ellison, E. Adams, C. Erilson and J. M. Cheverud. 1999. Mapping quantitative trait loci for murine growth: a close look at genetic architecture. Genet. Res., Camb. 74:313-322.

Wheeler, J. L. and M. Freer. 1986. Pasture and forage: The feed base for pastoral industries. In: 'The Pastoral Industries of Australia' (Ed. G. Alexander and O. B. Williams). Revised edition. Sydney University Press: Sydney, Australia. pp. 165-182.