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Breed variation and genetic parameters for growth and body development in diverse beef cattle genotypes

R. A. Afolayan[1†], W. S. Pitchford[1], M. P. B. Deland[2] and W. A. McKiernan[3]

[1]*Livestock Systems Alliance, The University of Adelaide, Roseworthy campus, Roseworthy SA 5371, Australia;* [2]*Struan Research Centre, South Australian Research and Development Institute (SARDI), Naracoorte, SA 5271, Australia;* [3]*NSW Department of Primary Industries, Orange Agricultural Institute, Forest Road, Orange, NSW 2800, Australia*

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Conformation scores can account for more than 20% of cattle price variation at Australian livestock sales. However, there are limited available references which define genetic factors relating objective live developmental traits to carcass composition. Weaning and post-weaning weight, height, length, girth, muscle (ratio of stifle to hip width) and fat depth of 1202 progeny from mature Hereford cows (637) mated to seven sire breeds (Jersey, Wagyu, Angus, Hereford, South Devon, Limousin and Belgian Blue) were examined for growth and development across ages. Crossbred Wagyu and Jersey were both lighter in weight and smaller in size (height, length and girth) than purebred Hereford and crossbred Angus, South Devon, Limousin and Belgian Blue. Within the five larger crossbreds, there were significant changes in relative weight from weaning to 600 days. Sire breeds differed in fat depth, with Angus being the fattest (9% on average fatter than Hereford and Wagyu), and Jersey 5% less fat than Hereford, followed by South Devon and Limousin (19% lower than Hereford) and Belgian Blue (39% lower than Hereford). Direct heritability ranged from 19 to 42% and was higher than the proportion of total phenotypic variance accounted for by maternal effects (which ranged from 0 to 17%) for most body measurement traits except for weight (38 v. 18%) and girth (36 v. 9%) traits at weaning, an indication of maternal effect on some body conformation traits at early ages. Muscularity (19 to 44%) and fat depth (26 to 43%) were moderately to highly heritable across ages. There were large differences for growth and the objective measures of body development between crossbreds with a degree of overlap among the progeny of the seven sire breeds. The variation between genetic (positive) and environmental (negative) correlations for dry versus wet season average daily gains in weight and fat, suggested the potential use of live-animal conformation traits for within breed selection of genetically superior animal in these traits across seasons.

Keywords: beef cattle, fat thickness, muscle weight, seasonal growth, skeletal development

Introduction

Cattle conformation scores reported in Australian national market reports can account for more than 20% of price per kilogram. Evaluation of growth based on weight and weight gains abound in the scientific literature (Jenkins *et al*., 1991; Meyer *et al*., 1993; Plasse *et al*., 2002). However, there are limited available references to genetic factors affecting live developmental traits that define body composition which would assist beef producers to breed cattle that consistently achieve market targets and hence reward them with increased carcass values.

Selection for improvement of carcass value based on growth and body composition could rapidly increase the rate of genetic gain in carcass quality traits of beef breeding herds. Accurate prediction of carcass value or quality based on body composition would enable early selection of efficient animals by beef producers as well as seed-stock breeders. A subset of the data from this study was used to describe the effectiveness of objective live measurements equations for the prediction of carcass traits (Afolayan *et al*., 2002a), as opposed to the combination of objective and subjective measurements used in other studies (Perry *et al*., 1993a and b; Herring *et al*., 1994). Objective live animal measurements involved simple adoptable techniques that would reduce production costs and allow wider application by the producers.

Recent feedlot trials with crossbred cattle (D.L. Rutley unpublished) have shown that in addition to weight, other traits such as height, fat depth and visual muscle score (as defined by McKiernan, 1990; Perry *et al*., 1993a and b)

Present address: NSW Department of Primary Industries, Orange Agricultural Institute, Forest Road ORANGE NSW 2800, Australia.
[†]E-mail: raphael.afolayan@dpi.nsw.gov.au

can assist prediction of feedlot performance of most economically important traits (average daily gain, carcass weight, carcass fat depth and saleable beef yield). Gilbert *et al.* (1993) also proposed the use of body dimensions or linear measurements either to supplement body weight as a measure of productivity or as predictors of some less visible characteristics. The aim of this study was to estimate the genetic variances for growth and objectively measured development (e.g. measure of muscularity and fatness) traits in progeny of seven sire breeds crossed with Hereford dams. The sire breeds represented the major beef breeds used in South Australia to meet the range of market specifications. The opportunities for selection between and within breeds across seasons and stages of growth are discussed.

Material and methods

Animal and management

The animals used in the study were 1202 calves born over a 4-year period (1994–1997) of the Australian Southern Crossbreeding Project (Rutley *et al.*, 1995). Not all animals were recorded for all traits as outlined in Table 1. Ninety-seven sires from seven breeds (Jersey, Wagyu, Angus, Hereford, South Devon, Limousin and Belgian Blue) were mated to mature Hereford cows (637) in a top-cross design. All cows had at least one previous calf and were aged 3 to 11 years at the time of calving. There were 12 to 15 progeny per sire (average of 13) and 12 to 16 sires per breed (average of 14). Sires were generally used in 1 year with only a few exceptions, whereas dams were commonly used for more than one year (the average of calves born per dam was two, including calves that did not survive to weaning).

Calves were born in autumn of every year between March and April (average birth date of April 3), about 3 weeks before the 'break of season' typical to 'Mediterranean' environments characterised by cool, wet winters and hot, dry summers on two South Australian properties (Struan and Wandilo) in three management herds. All calves were weaned in the summer (December-early January) at an average age of 250 days and were raised on pasture. After weaning, Wandilo born calves were transported to Struan where they were mixed with Struan born calves and randomly allocated to three post-weaning management groups per year. Calves were grown until 12 to 18 months of age and then transported to a commercial feedlot. In the feedlot, they were fed a minimum of 60% grain (various but primarily barley) with approximately 12 MJ/kgDM metabolisable energy and 130 g/kg of crude protein for 70 to 90 (heifers) or 150 to 180 days (steers). The steers born in 1997 were an exception because they were able to attain marketable weights without requiring grain finishing after a good pasture season in spring 1998. A detailed description of management of animals from birth to slaughter is given by Pitchford *et al.* (2002).

Measurements

Calves were tagged, weighed and bull calves castrated, within 3 days of birth. Calves were weighed at weaning without having been fasted and at two other post-weaning ages. These ages were approximately 400 days and 600 days after birth, that is, during winter after the dry season

Table 1 *Number of calves for each cohort and trait*

	Heifers				Steers				
Trait	1994	1995	1996	1997	1994	1995	1996	1997	Total
Weaning									
Weight	147	152	146	139	165	175	155	124	1202
Height	146	151	121	140	164	176	129	124	1151
Length	146	151	146	140	164	176	155	124	1202
Girth	146	151	146	140	164	176	155	124	1202
Muscle	–	–	146	140	–	–	155	124	565
Fat depth	146	151	146	140	164	176	155	124	1202
400-day									
Weight	147	151	146	139	165	176	155	123	1202
Height	147	152	–	140	165	176	155	–	935
Length	147	152	145	139	165	176	155	–	1079
Girth	147	152	145	140	165	176	155	–	1080
Muscle	–	152	145	140	–	175	155	–	767
Fat depth	147	152	146	140	165	176	–	123	1049
600-day									
Weight	147	–	–	–	165	176	155	–	643
Height	–	–	–	–	165	–	155	–	320
Length	–	–	–	–	165	–	155	–	320
Girth	–	–	–	–	165	–	155	–	320
Muscle	–	–	–	–	–	176	155	–	331
Fat depth	147	–	–	–	165	176	155	–	768

and during summer after the wet season. Height was measured as the difference between the distance from the top of the crush down to the top of the hips and the distance to the ground. The length was measured as the distance between the first sacral bone on the shoulder and the pin bone. Girth was measured as the circumference immediately posterior to the front legs. Other measurements at weaning and post-weaning were fat depth scanned at the P8 site on the rump using Ezi-scan® sonic device (AMAC Pty, Ltd) plus hip width (bone) and stifle width (muscle) measured using callipers. Stifle width as a percentage (%) of hip width was used as an indication of the muscularity (MUS) as reported previously (Afolayan *et al.*, 2002a and b). In general, weaning and post-weaning traits were measured at close, but different, ages in different years. In particular, at 600-days of age, there were less animals measured for weight and fat depth (Table 1). This was partly due to the design (many heifers had to be slaughtered at an average of 16 months of age when the majority of the carcasses were >200 kg) and partly due to accidental omissions. Growth rate (per day) was calculated between ages for each of the traits measured. Dry season gain was defined as the gain from 250 to 400 days (January to June) and wet season gain was defined as the gain from 400 to 600 days of age (approximately June-December). Thus, one of the limitations of this trial is that seasons were confounded with age.

Statistical analysis

Data were analysed using ASREML (Gilmour *et al.*, 2000). All traits were analysed using a univariate animal model containing fixed effects of cohort (eight categories of year and sex: 1994-drop heifers to 1997-drop steers), management group (a function of both pre- and post-weaning groups where there were four to six groups (paddocks utilised) per cohort, the total number of levels was 30), birth month (March or April), and sire breed (seven levels). The random effects of animal and dam (genetic and common environment) were also included in the model. Two-way interactions were generally not significant and were not included. Sire was nested within sire breed, so the significance of sire breed was effectively tested against sire as outlined by Gilmour *et al.* (2000). Bi-variate animal models with the same fixed effects and only animal random effect were used for estimating phenotypic, genetic and environmental correlations. Significance was defined as $P < 0.05$.

Results

Estimates of non-genetic effects

There was considerable variation across ages in weights, body dimensions and composition (Table 2). Also, the weaning and post-weaning variability differed between groups of traits, with fat having the highest variation (CV = 51%) at weaning, followed by weight, muscle and skeletal dimensional (height, length and girth) in that order (CV = 4–15%). The large coefficient of variation for fat depth was probably a function of the threshold nature of this trait with the mean (5.1 mm) being a small number and close to the minimum measurement (1 mm).

The differences between birth months at weaning were small for body dimensions and muscularity (not presented). However, there were highly significant differences for weight and fat depth, with March born calves being 4% heavier and 10% fatter than the April born calves. As expected, these differences diminished with age.

Cohort differences were large for most of the weaning traits due to differences in pasture availability between years (e.g. 1995-drop calves at weaning were 11% heavier, 3% taller, 5% longer and 1% bigger in girth than 1994-drop calves). There were also large cohort effects for muscularity and P8 fat depth at weaning with 1997-drop calves being on average more muscular (7%) and fatter (47%) than 1996-drop calves. The difference between cohorts for post-weaning traits was primarily due to post-weaning management differences between sexes (mostly at 600-day), which was confounded with age of entry into feedlot. Cohort effects were mainly significant between sexes for weight and fat depth with steer calves on average being heavier (517 kg) but leaner (9 mm) compared with the smaller (442 kg) but fatter heifer (11 mm) calves.

Within and between breed genetic variation

At weaning and subsequent ages, height was the most highly heritable trait (42 to 60%, Table 2). Weight, length and girth were low to moderately heritable (9 to 33%) across the ages. Heritability of muscularity measurements (19 to 44%) and fatness (26 to 43%) were similar or slightly more highly heritable than weight. Maternal permanent environmental effects were significantly greater than direct heritability estimates for weight (38% *v.* 18%) and girth (36% *v.* 14%) at weaning but the differences were not significant for traits measured later in life (Table 2). In general, low heritability estimates were obtained for gains in weight, muscle and fat depth across seasons (DSG and WSG) with gains in height, length or girth near zero.

At weaning, sire breed effects were important (Table 3) for all traits ($P < 0.01$). Breed ranking as a percentage of purebred Hereford (the only purebred) indicated four larger breeds (Angus, South Devon, Limousin and Belgian Blue) that averaged 2% heavier, 2% taller and 1% bigger in girth than Herefords. Most of the larger breeds were similar to Hereford in length with the exception of Limousin (1% shorter). However, the Wagyu and Jersey were lighter in weight (11% and 12%) and smaller in height, length, and girth (2% and 2%) than the purebred Hereford. Belgian Blue, Limousin South Devon and Angus were 3 to 4% more muscular than the Hereford and Wagyu. Not surprisingly, Jersey crosses were 4% less muscular than Hereford. Among the seven sire breeds, Angus had by far the greatest P8 fat depth at weaning (9% more than Hereford and Wagyu on average), with Jersey being 5% lower

Table 2 *Summary statistics and heritability estimates of traits at different ages*†

Traits	Mean	CV (%)	Minimum	Maximum	Dir. Herit. $h^2 \pm$ s.e. (%)	Mat. Env.‡ $c^2 \pm$ s.e.(%)
Weaning						
Weight (kg)	276.1	15	148.0	423.0	18 ± 6	38 ± 4
Height (mm)	1126	4	985	1260	42 ± 10	9 ± 4
Length (mm)	1202	5	1000	1410	25 ± 8	17 ± 4
Girth (mm)	1537	5	1220	1810	9 ± 5	36 ± 4
Muscle (%)	87.1	8	68.0	109.0	19 ± 9	0 ± 0
Fat depth (mm)	5.1	51	1.0	19.0	33 ± 9	13 ± 4
400-day						
Weight (kg)	349.2	12	219.0	496.0	33 ± 8	27 ± 4
Height (mm)	1223	7	1050	1500	60 ± 13	5 ± 6
Length (mm)	1305	4	1120	1500	24 ± 8	10 ± 4
Girth (mm)	1677	5	1370	1920	24 ± 8	27 ± 4
Muscle (%)	85.1	8	64.0	108.0	44 ± 10	0 ± 0
Fat depth (mm)	5.2	59	1.0	25.0	43 ± 8	0 ± 0
600-day						
Weight (kg)	498.4	16	304.0	740.0	32 ± 13	6 ± 7
Height (mm)	1385	5	1200	1580	54 ± 24	4 ± 16
Length (mm)	1422	5	1240	1650	19 ± 17	20 ± 16
Girth (mm)	1910	4	1630	2110	32 ± 19	14 ± 17
Muscle (%)	87.9	10	68.0	114.0	22 ± 16	0 ± 0
Fat depth (mm)	9.5	57	1.0	32.0	26 ± 8	0 ± 0
DSG						
Weight (g/day)	433.8	44	−287.0	1074.0	13 ± 6	5 ± 4
Height (μm/day)	562	82	−620	2129	2 ± 7	5 ± 5
Length (μm/day)	605	60	−775	2617	1 ± 6	0 ± 0
Girth (μm/day)	849	65	−930	3101	4 ± 5	8 ± 4
Muscle (%/day $\times 10^{-3}$)	−11.7	482	−165.6	198.6	8 ± 11	0 ± 0
Fat depth (μm/day)	−1.3	1388	−77.5	80.5	19 ± 6	0 ± 0
WSG						
Weight (g/day)	1263.0	53	−461.0	3163.0	33 ± 10	0 ± 0
Height (μm/day)	737	67	40	2609	0 ± 0	4 ± 15
Length (μm/day)	761	74	−543	2717	5 ± 14	1 ± 17
Girth (μm/day)	1690	56	−478	4022	0 ± 0	0 ± 0
Muscle (%/day $\times 10^{-3}$)	16.4	222	−98.7	127.8	21 ± 16	1 ± 14
Fat depth (μm/day)	51.9	104	−41.5	270.8	31 ± 10	0 ± 0

† Abbreviations are: DSG = dry season gains, WSG = wet season gains, CV = coefficient of variation, Dir. Herit. = direct heritability, Mat. Env. = maternal permanent environmental effect.
‡ Includes maternal direct and common environmental effect (c^2).

than Hereford, then South Devon and Limousin (19% lower than Hereford) and Belgian Blue the lowest (39% lower than Hereford).

The significant breed differences at weaning in weight, body dimensions (height, length and girth), muscularity and P8 fat depth were still observed at 400 and 600 days *post partum* (Table 3). At 400 days of age, the four heavy breeds (Angus, South Devon, Limousin and Belgian Blue) were greater than Hereford for weight, height, and girth ($P < 0.01$) but not for length ($P > 0.05$). Purebred Hereford were 1% greater than Limousin for length, similar to Angus and Belgian Blue (both 1309 mm) but 1% lower than South Devon at 400 days of age ($P < 0.01$). Muscularity of Wagyu (lighter breed) at the same age was close to Hereford. The Jersey continued to be 7% less muscular than the purebred Hereford. While Angus and South Devon was only 1% higher in muscularity than Hereford as compared with 3% differences at weaning, Belgian Blue and Limousin were 3% higher than Hereford at 400 days compared with 4% at weaning. The ranking for P8 fat depth at 400 days of age was similar to that at weaning except that the differences between the groups were more pronounced at weaning than later ages probably due to periods of slower growth and loss of fat (Table 2). Similar trends for breed ranking at 400 days of age were observed for all traits at 600 days of age (Table 3) except for height where Jersey (smaller breed) was close to Angus (1327 mm *v.* 1328 mm).

Correlations between traits

Estimates of genetic correlations between weight and body dimensional traits at 400 days of age (Table 4) were very high (0.66 to 0.91) with low standard errors (0.02 to 0.07).

Table 3 *Least-squares means (± s.e.) of sire breed for weaning- and post-weaning traits*

Traits	Sire breed						
	Jersey	Wagyu	Angus	Hereford	South Devon	Limousin	Belgian Blue
Weaning							
Weight	253.4 ± 2.6	256.2 ± 2.3	283.9 ± 2.6	282.6 ± 2.9	291.0 ± 2.4	283.3 ± 2.4	289.8 ± 2.4
Height	1106 ± 4	1108 ± 4	1122 ± 5	1116 ± 5	1136 ± 4	1142 ± 4	1130 ± 4
Length	1196 ± 5	1183 ± 5	1208 ± 5	1212 ± 6	1216 ± 5	1203 ± 5	1209 ± 5
Girth	1508 ± 5	1516 ± 5	1558 ± 5	1545 ± 6	1555 ± 5	1550 ± 5	1564 ± 5
Muscle	83.4 ± 0.7	86.8 ± 0.6	88.2 ± 0.8	86.3 ± 0.9	88.8 ± 0.7	90.2 ± 0.7	89.6 ± 0.7
Fat depth	5.4 ± 0.2	6.1 ± 0.2	6.4 ± 0.2	5.7 ± 0.3	4.6 ± 0.2	4.7 ± 0.2	3.5 ± 0.2
400-day							
Weight	319.8 ± 3.3	320.0 ± 2.9	360.5 ± 3.4	352.7 ± 3.7	364.7 ± 3.1	355.7 ± 3.0	365.5 ± 3.1
Height	1194 ± 5	1193 ± 5	1210 ± 5	1205 ± 6	1228 ± 5	1237 ± 5	1219 ± 5
Length	1292 ± 5	1284 ± 5	1309 ± 5	1312 ± 6	1319 ± 5	1303 ± 5	1309 ± 5
Girth	1639 ± 6	1645 ± 6	1708 ± 6	1678 ± 7	1691 ± 6	1679 ± 6	1700 ± 6
Muscle	78.8 ± 0.8	83.8 ± 0.7	86.4 ± 0.8	84.8 ± 0.9	85.7 ± 0.8	90.2 ± 0.7	92.0 ± 0.7
Fat depth	5.6 ± 0.3	5.8 ± 0.2	7.1 ± 0.3	5.8 ± 0.3	4.9 ± 0.3	4.4 ± 0.2	3.2 ± 0.2
600-day							
Weight	435.0 ± 6.3	420.6 ± 6.2	486.2 ± 6.7	468.4 ± 7.2	502.2 ± 6.7	485.1 ± 6.4	496.5 ± 6.4
Height	1327 ± 8	1318 ± 7	1328 ± 8	1331 ± 9	1356 ± 8	1363 ± 8	1341 ± 8
Length	1407 ± 12	1392 ± 11	1432 ± 12	1431 ± 13	1449 ± 12	1449 ± 12	1429 ± 12
Girth	1892 ± 13	1870 ± 12	1953 ± 14	1916 ± 15	1940 ± 13	1937 ± 14	1959 ± 13
Muscle	76.3 ± 1.2	83.0 ± 1.2	86.8 ± 1.2	83.0 ± 1.4	87.7 ± 1.3	94.8 ± 1.2	94.8 ± 1.3
Fat depth	10.1 ± 0.5	10.9 ± 0.4	13.2 ± 0.5	11.3 ± 0.5	9.1 ± 0.5	9.5 ± 0.5	7.8 ± 0.5

Within body dimensions, the genetic correlations were generally high (0.61 to 0.90) also at the same ages. The genetic correlations between weight and muscularity were moderate (0.35) and those between body dimensions and muscularity were low (0.08 to 0.24). Correlations between fat depth (P8) and weight or body dimensions were generally zero at 400 days. Also, there was near zero genetic correlation between fat depth and muscularity. Among the body dimensional traits, girth and length were more highly genetically correlated with weight than height at 400 days of age. At all ages, the genetic correlations between body dimensional traits (i.e. height, length and girth) and muscularity or fat were low.

The phenotypic correlations between weight and body dimensional traits were generally lower in absolute value at every stage of growth than the genetic correlations (Table 4). Weight had moderate to high phenotypic correlations with body dimensions (0.56 to 0.78), low with P8 fat depth (0.23), and surprisingly very low with muscularity (0.12) at 400 days. At the same age, the correlation between fat depth and muscle was very low (0.01). Among body dimensions, the phenotypic correlations were moderate (0.44 to 0.51). Many of the body dimensions (0.03 to 0.13) also had very low correlations with fat depth (except girth, 0.27) and the correlation of body dimensions with muscularity was near zero (Table 4).

Correlations (genetic and phenotypic) between most traits at weaning and 400 days were high and so were not tabulated but are reported by Afolayan (2003). The genetic (0.95) and phenotypic (0.73) correlations for weight traits were especially high. Surprisingly, correlations between skeletal measurements at different ages were lower than weight. Genetic correlations between weaning and 400 days ranged from 0.41 for girth to 0.82 for height. Muscle (0.50) and fat depth (0.66) were also reasonably highly genetically correlated between weaning and 400 days. Correlations between the traits at 400 and 600 days of age were similar to those between weaning and 400 days.

Genetic correlations between pre- or post-weaning gains in weight and body composition traits were tested with the age specific traits (not presented). Unfortunately, most genetic correlations between gains in body composition and

Table 4 *Genetic (below) and phenotypic (above diagonal) correlations among traits to 400 days*

Traits	Weight	Height	Length	Girth	Muscle	Fat depth
Weight		0.58 ± 0.02	0.56 ± 0.02	0.78 ± 0.01	0.12 ± 0.04	0.23 ± 0.03
Height	0.66 ± 0.07		0.49 ± 0.02	0.51 ± 0.02	−0.05 ± 0.04	0.03 ± 0.03
Length	0.89 ± 0.05	0.85 ± 0.07		0.44 ± 0.02	0.03 ± 0.03	0.13 ± 0.03
Girth	0.91 ± 0.02	0.61 ± 0.08	0.90 ± 0.06		0.06 ± 0.04	0.27 ± 0.03
Muscle	0.35 ± 0.14	0.09 ± 0.16	0.24 ± 0.19	0.08 ± 0.16		0.01 ± 0.04
Fat depth	0.17 ± 0.12	−0.32 ± 0.14	0.00 ± 0.20	0.19 ± 0.13	0.11 ± 0.17	

age specific traits were generally not estimable at much older ages (e.g. 600 days) because of missing data (Table 1) and large variation (Table 2). A few of the estimated values were outside the parameter space (< -1.0 or > 1.0), especially those correlations with gains in muscularity or fat depth. As expected, weight gains had very high correlations with weight traits at any age compared with height, length and girth traits. The genetic correlation between weight gains and muscle or fat depth were generally low and negative with high standard errors. Comparing post-weaning dry and wet season gains, weight and fat depth had positive moderate genetic correlations (0.66 and 0.38) but close to zero phenotypic correlations (Table 5). These were a function of negative environmental correlations (-0.34 and -0.23) between gains in the two periods (Table 5).

Discussion

Breed effect

For weight, there were clearly two small breeds (Jersey and Wagyu). The remaining breeds were all much larger, although there were significant differences between them, with Belgian Blue and South Devon being heavier than Hereford sired calves. Limousin and Angus were similar to Hereford at weaning, slightly heavier at 400 days, and significantly heavier at 600 days reflecting different growth pattern (curves). Neither caught up to the Belgian Blue and South Devon. South Devon sired calves grew faster than Belgian Blue from 400 to 600 days. Specifically, Pitchford *et al.* (2006) suggested that the Angus appeared to be an exceptional breed that 'bend the growth curve' since despite its smaller birth size (Angus sired calves were 5% lighter than purebred Hereford at birth), it was grouped among the three other breeds (South Devon, Limousin and Belgian Blue) as heaviest at slaughter (Angus sired calves were 5% heavier than purebred Hereford at slaughter) (Pitchford *et al.*, 2002). Clearly even based on a single trait (weight), breed choice will be determined by factors such as age of marketing since skeletal traits such as height or length were less clear than those for weight. However, Vargas *et al.* (2000) suggested that selection for optimum size could be realised by including both hip height and weight in a multiple-trait selection scheme in Brahman cattle.

Genetic effects

There was substantial variation in the objective measure of muscularity (ratio of stifle- to hip-width $\times$ 100) in this study, indicating the importance of within and between breed selection for maximising this economic trait in live animals. The heritability estimates of muscularity measures herein were comparable to average values of 40–47% for rib eye area (Koots *et al.*, 1994a) and of 42 to 47% for retail product yield (Shackelford *et al.*, 1994; Gregory *et al.*, 1995). Similar estimates have been reported also in Australian pure (53%) and crossbred (44%) cattle (Newman *et al.*, 2002) for actual retail beef yield. The moderate heritability estimates for post-weaning muscularity are an indication that reasonable genetic progress could be made by selecting for it and if the trait is genetically correlated with rib eye area or eye muscle area, that reflect more of actual meat yield, then it would be a cheap selection criterion in beef cattle industry. The ranges of heritability estimates for scanned P8 fat depth (26 to 43%) were close to those reported by Koots *et al.* (1994a) as weight constant backfat (44%).

In most previous studies, heritability and genetic correlations estimates for growth have been based on weight (Meyer, 1992; Koots *et al.*, 1994a and b; Dodenhoff *et al.*, 1998; Plasse *et al.*, 2002). Few studies included additional body measurements like hip height and body length mostly at post-weaning (Gilbert *et al.*, 1993; Vargas *et al.*, 2000). In this study, the direct heritability for weaning weight (18%, Table 2) was lower than both the unweighted (35% and 27%) and weighted (31% and 24%) mean estimates reviewed from over 170 papers (Koots *et al.*, 1994a). However, the direct yearling weight heritability estimate obtained for unweighted and weighted (35% and 33%) means by the same author on an age-constant basis was close to the 33% and 32% for 400- and 600-day weights herein. The differences in the estimates between these two studies may be a reflection of sampling variation. In a study that involved sires of Angus, Hereford, Shorthorn, Brahman, Belmont Red and Santa Gertrudis mated to Brahman dams, Newman *et al.* (2002) obtained high heritability estimates for 400-day weight (45 to 49%).

The heritability estimates reported herein for weaning height (42%) and 400-day height (60%) were very similar to those of Koots *et al.* (1994a) for weaning (43%) and yearling (54%) height, respectively. However, higher estimates were obtained for weaning height in the studies of Vargas *et al.* (2000) on a single breed (Brahman) measured at a much older age (18 months) and Gilbert *et al.* (1993) on Hereford and Angus breeds. Apart from the work of Gilbert *et al.* (1993) that provided heritability estimates for weaning and post-weaning length as an additional body dimensional trait, the mostly moderate estimates for body length (19 to 25%) and girth (9 to 32%) from weaning (250) day to 600-day of age herein represents the first Australian estimates for beef cattle breed types for genetic description of animal size. Gutierrez and Goyache (2002) were of the opinion that standard breed conformation described by skeletal and muscular development could be effectively used to evaluate the animal's productive ability.

Table 5 *Phenotypic, genetic and environmental correlations between dry and wet season gains in post weaning weight and fat depth*

Traits	Phenotypic	Genetic	Environmental
Weight[†]	-0.08 ± 0.04	0.66 ± 0.27	-0.34 ± 0.10
Fat depth[‡]	-0.12 ± 0.04	0.38 ± 0.29	-0.23 ± 0.09

[†] Correlations between dry season weight gain and wet season weight gain.
[‡] Correlations between dry season fat gain and wet season fat gain.

Correlations between traits

Subcutaneous fat depth, as measured herein, is positively correlated with both channel fat (Afolayan *et al.*, 2002c) and with intramuscular (IMF) fat content (Koots *et al.*, 1994b), which are determinants of carcass and meat quality. In this study, the moderate sized breeds (e.g. Angus) were of comparable level of muscularity with a larger breed (South Devon) but higher in fat depth than the highly marbled small size breeds (e.g. Wagyu or Jersey). In an earlier report using the same data set, Pitchford *et al.* (2002) indicated a moderate and positive genetic correlation between carcass P8 fat depth and intramuscular fat (0.36). This relationship may not be strong enough to jeopardise the possibility of within breed selection for low P8 fat depth to minimise wastage and for high IMF to maximise meat quality (Pitchford *et al.*, 2006).

Strong and positive genetic correlations between weight and many of the body dimensional traits indicated that selection for or against one trait would result in concomitant genetic changes in the other traits. The higher genetic correlation between weight and length (0.89) or girth (0.91) compared with height (0.66) at 400-days of age (Table 4) suggests that length and girth traits are genetically almost the same trait as weight but there is some genetic variation in height independent of weight. Because of the high genetic correlation (0.73) between weaning weight and height in Brahman cattle, Vargas *et al.* (2000) concluded that the same genes affect the two traits.

Compensatory growth is a well known phenomenon in developing animals (Ryan *et al.*, 1993a and b). The reduction in the magnitude of the phenotypic correlations between weight and body dimensional traits in post-weaning, compared with weaning, may indicate reduced variation due to compensatory growth. Calves with poor early growth in body composition traits, possibly due to poor pre-weaning environment tended to have higher post-weaning growth than calves in better pre-weaning condition. Vargas *et al.* (2000) similarly emphasised the importance of considering maternal effects for growth traits in general and for hip height, in particular, when developing selection strategies for Brahman cattle. Positive maternal effects on pre- and post-weaning weight, girth, muscle and fatness traits have been reported in composite crossbred calves due to large milk production from Jersey dams (Afolayan *et al.*, 2002a and b).

Many of the earlier studies have indicated also the importance of non-additive genetic effects (e.g. heterosis) on growth (mainly determined by weight and weight changes) in different cattle breeds (Pitchford *et al.*, 1993; Rodriguez-Almeida *et al.*, 1997; Davis *et al.*, 1998; Dodenhoff *et al.*, 1998). However, because of the single dam breed utilised in the study herein, the separation of direct breed from non-additive (e.g. heterosis) genetic effects was not possible.

The sign of the genetic correlations between dry and wet season gains (Table 5) herein indicated that regardless of the season, genetically superior animals would always be better than their inferior counterparts for weight and fat traits. Moreover, loss in performance during scarcity of feed (dry season) is proportionately compensated for in the following wet season when feed becomes abundant. As noted above, the results must be viewed with caution because of the confounding of age and season (i.e. dry season weaning to 400 days). However, Burrow (2001) also found higher genetic (0.19) than phenotypic (0.10) correlations between dry and wet season weight gain, also indicating low or negative environmental correlations between the periods. Post-weaning compensatory growth has also been reported for Brahman by Hereford cross steers (Arthur *et al.*, 1994) and heifers (Hearnshaw *et al.*, 1994).

The study has reported large breed differences in six growth traits and demonstrated that the traits are moderately to highly heritable at various ages post-weaning. Weight and skeletal traits including muscularity and fat traits were generally highly correlated. However, there were large differences between genetic (positive) and environmental (negative) correlations for dry and wet season weight and fat gains, suggesting the potential use of live-animal conformation traits for within breed selection across seasons.

Implications

The ability of the producer and livestock buyers to relate objective live animal characteristics, irrespective of breed, to carcass values is essential for optimum production and value based trading systems. There were large differences for growth and the objective measures of body development between crossbreds with a degree of overlap among the progeny of the seven sire breeds in this study. The measure of muscularity is likely to be genetically related to rib eye area or eye muscle area that reflect meat yield, whereas P8 fat depth is genetically related to intramuscular fat content, that reflects meat quality. Both these traits combined could be used to discriminate between breeds and serve as an easy and practical method to assist in selection within breeds in beef cattle production enterprises.

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