Genetic correlations between live yearling bull and steer carcass traits adjusted to different slaughter end points. 2. Carcass fat partitioning[1,2]

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ABSTRACT: Partial carcass dissection data from 1,031 finished crossbred beef steers were used to calculate heritabilities and genetic correlations among subcutaneous, intermuscular, and body cavity fat percentage and marbling score adjusted to slaughter age-, HCW-, fat depth-, and marbling score-constant endpoints. Genetic correlations were also calculated among these fat partitions with live growth and ultrasound traits evaluated in yearling beef bulls (n = 2,172) and steer carcass measurements. Heritabilities of the different fat partitions ranged from 0.22 (marbling score-constant body cavity fat) to 0.46 (HCW-constant marbling score). Genetic correlations between subcutaneous fat and intermuscular fat (r_g = 0.16 to 0.32) and between intermuscular fat and body cavity fat (r_g = 0.38 to 0.50) were more highly associated than subcutaneous fat and body cavity fat (r_g = –0.08 to 0.05), indicating that fat depots are not under identical genetic control. Adjusting fat depots to different end points affected the magnitude but usually not the sign of the genetic correlations. Bull postweaning gain was associated with intermuscular (–0.24 to –0.35), body cavity (–0.24 to –0.29), and marbling fat (–0.24 to –0.39) in steers. Bull hip height was associated with body cavity (–0.20 to –0.29) and marbling fat (–0.20 to –0.47) in steers. Bull ultrasound fat depth was associated with subcutaneous (0.11 to 0.29), intermuscular (0.05 to 0.36), body cavity (0.27 to 0.49), and marbling fat (0.27 to 0.73) in steers. Bull ultrasound intramuscular fat percentage was associated with subcutaneous (–0.22 to –0.44) and intermuscular fat (–0.06 to 0.31) in steers. Bull ultrasound LM area was associated with body cavity (–0.25 to –0.31) and marbling fat (–0.25 to –0.30) in steers. Ultrasound LM width measurements were negatively correlated with subcutaneous fat (r_g = –0.09 to –0.18), intermuscular fat (r_g = –0.53 to –0.61), body cavity fat (r_g = –0.63 to –0.69), and marbling score (r_g = –0.75 to –0.87) at slaughter age-, HCW-, and fat depth-constant endpoints; correlations were generally lower at a marbling score-constant end point (r_g = 0.07 to –0.49). Ultrasound indicator traits measured in seedstock may be useful in altering fat partitioning in commercial beef carcasses.

Key words: cattle, fat partitioning, genetic parameters, selection, ultrasound

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INTRODUCTION

Ultrasound fat depth and LM size traits measured in seedstock cattle are heritable and genetically correlated to steer carcass lean percentage (Reverter et al., 2000; Crews and Kemp, 2001; Bergen et al., 2006). Although current ultrasound measurements use only subcutaneous fat depth as an indicator of overall carcass lean content, fat stored in intermuscular, body cavity, and intramuscular depots also influence carcass lean content.

Little is known about the genetic control of carcass fat partitioning despite its potential importance in beef cattle breeding programs. If genetic relationships among the different fat depots are not strongly positive, selection for increased carcass lean content based exclusively on decreased subcutaneous fat depth may not yield the desired reduction in the intermuscular or body

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cavity fat depots. Reducing intermuscular fat is important because it cannot be removed without damaging some retail cuts (Kempster, 1980).

The objective of this research was to evaluate the genetic relationships among the subcutaneous, intermuscular, body cavity, and intramuscular depots of finished feedlot steer carcasses adjusted to slaughter age-, HCW-, fat depth-, and marbling score-constant endpoints. A second objective was to quantify genetic relationships among live age-constant growth and ultrasound traits measured in yearling beef bulls and carcass measurements collected in steers with fat partitioning in steers adjusted to different slaughter end points.

MATERIALS AND METHODS

Details regarding the data, experimental procedures, and analytical models used in this study have been presented in a previous report (Bergen et al., 2006). In brief, growth and ultrasound data from yearling beef bulls (n = 2,172) and carcass data from finished crossbred feedlot steers (n = 1,031) were used. Exact breed composition was known for all animals. A 21-cm rib section (corresponding approximately to the 10th–11th–12th ribs) from each steer was dissected into lean, bone, subcutaneous, intermuscular, and body cavity fat depots following procedures originally developed by Hankins and Howe (1946). Previous results indicated that fat partitioning in this cut is related to fat partitioning of the wholesale rib and whole carcass side (Bergen, 2005). Dissected lean and fat weights were expressed as a percentage of total 10th–11th–12th rib weight. Marbling score was used as a substitute for chemical intramuscular fat percentage; previous research has shown that these traits have a high genetic correlation ($r_g = 0.94$; Fernandes et al., 2002).

Pairwise analyses among all bull and steer traits with carcass fat partitioning traits were performed in ASREML (Gilmour et al., 2000) to estimate (co)variance components and effects of covariates, contemporary group, feedlot regimen, breed, and expected heterozygosity using a pedigree file containing 10,068 animals. After accounting for the fixed breed effect in the animal model, homogeneous genetic, herd of origin, and residual (co)variance was assumed across all breeds, and all unknown sires and dams were assumed to originate from the same noninbred base population regardless of breed.

For summary purposes, heterosis and breed effects as well as phenotypic, additive genetic, and preweaning bull contemporary group variances were calculated as the average solution from the pairwise analyses performed for each trait. Breed effects were expressed relative to the Charolais breed, which was constrained to zero. Scan age was used as a covariate for yearling bull traits in all animal models. In contrast, steer carcass traits were adjusted to slaughter age-, HCW-, carcass fat depth-, or carcass marbling score-constant endpoints by regressing the appropriate slaughter end point covariate within feedlot regimen (i.e., high grain from weaning to slaughter vs. backgrounding before high grain finishing). Breed effects were estimated by regressing the dependent variable on the percentage of total breed composition contributed by each breed. Experimental procedures were approved by the University of Guelph's Animal Care Committee and followed guidelines established by the Canadian Council on Animal Care (1993).

RESULTS AND DISCUSSION

Feedlot Regimen, Heterosis, and Breed Solutions for Fat Partitioning Adjusted to Alternative Slaughter End points

All postweaning bull and steer contemporary groups were well connected by genetic ties (Bergen et al., 2006). Summary statistics indicate that backgrounded steers had numerically heavier carcasses with less total dissectible fat content than steers fed high grain from weaning until slaughter; other differences in 10th–11th–12th rib composition were negligible (Table 1). Data from Kempster et al. (1976) indicate that steers finished on grain diets were younger, lighter, and had more subcutaneous fat than forage-fed steers finished on cereal grains. Vaage et al. (1998) compared high-grain finishing from weaning to slaughter with prolonged backgrounding (174 d) before high-grain finishing and found that backgrounding led to increased carcass and wholesale rib weights without any significant change in fat percentage among the subcutaneous, intermuscular, or body cavity fat depots in the wholesale rib. Block et al. (2001) compared 70- and 126-d backgrounding periods before high grain finishing and found that although total and subcutaneous fat percentages in the wholesale rib did not differ among groups, steers backgrounded for 70 d had less body cavity and more intermuscular fat than steers backgrounded for 126 d.

When 10th–11th–12th rib composition data from the current study were adjusted to a common slaughter age, high-grain steers deposited subcutaneous fat and marbling more rapidly ($P < 0.05$) than did backgrounded steers, but rates of intermuscular and body cavity fat deposition were similar among the 2 feedlot regimes (Table 2). At a constant HCW, subcutaneous and body cavity fat deposition rates were similar among the feedlot regimens, but backgrounded cattle deposited intermuscular fat more rapidly ($P < 0.05$) and marbling less rapidly ($P < 0.05$) than high-grain steers (Table 2). When adjusted to a constant carcass fat depth, rates of subcutaneous, intermuscular, body cavity, and marbling fat deposition did not differ ($P > 0.10$) among backgrounded and high-grain steers. Finally, when adjusted to a constant marbling score, high grain steers displayed greater rates of fat deposition than backgrounded steers in all 3 depots (Table 2).

The objective of backgrounding is to delay physiological maturity so that cattle are heavier and older when

Table 1. Summary statistics for carcass and 10th–11th–12th rib weights and composition of finished crossbred feedlot steers

Feedlot regimen	Trait	Mean	SD	Minimum	Maximum
Grain finished (n = 495)	HCW, kg	337.0	51.5	234.0	583.0
	10th–11th–12th rib weight, kg	4.97	0.91	2.70	7.66
	Lean,[1] %	55.69	3.90	32.69	65.23
	Bone,[1] %	18.95	1.84	12.28	29.49
	Total fat,[1] %	25.36	4.14	15.34	38.53
	Subcutaneous fat,[1] %	10.17	1.73	5.02	15.93
	Intermuscular fat,[1] %	12.32	3.13	5.46	20.14
	Body cavity fat,[1] %	2.87	0.98	0.78	6.43
	Marbling score,[2] units	5.03	0.68	3.00	7.00
Backgrounded (n = 530)	HCW, kg	361.3	62.2	207.0	561.0
	10th–11th–12th rib weight, kg	4.98	0.99	2.82	7.74
	Lean,[1] %	56.41	3.72	37.79	66.22
	Bone,[1] %	19.43	2.19	13.69	32.00
	Total fat,[1] %	24.16	3.98	12.50	35.83
	Subcutaneous fat,[1] %	10.04	1.68	5.73	15.11
	Intermuscular fat,[1] %	11.85	3.00	4.69	22.19
	Body cavity fat,[1] %	2.93	1.04	0.74	7.01
	Marbling score,[2] units	5.12	0.70	3.00	7.50

[1] Percentage of 10th–11th–12th rib weight.

[2] $\leq$3.0 = devoid, 3.1 to 4.0 = traces, 4.1 to 5.9 = slight, 6.0 to 7.0 = small to moderate, and >7.0 = slightly abundant to abundant.

finished (Vaage et al., 1998). As discussed in Bergen et al. (2006), backgrounded steers were older and heavier than steers fed a high-grain diet from weaning to slaughter. The differences in subcutaneous and intermuscular fat deposition rates shown in Table 2 indicate that the backgrounded steers might have been less physiologically mature at slaughter.

Heterosis estimates (expressed as a percentage of the phenotypic mean) did not differ from zero ($P > 0.10$) for any fat depots at any slaughter end point (Table 2). Heterosis estimates for the subcutaneous, intermuscular, and body cavity depots were negative (except for slaughter age-constant body cavity fat content), indicating that crossbred animals tend to have proportionally less waste fat than their purebred parents. In contrast, crossbred steers should have more marbling than their purebred parents (Table 2). Johnston et al. (1992) reported a heterosis estimate of 5.8% for kidney knob and channel fat in crosses among Hereford and Devon cattle, and Marshall (1994) reported that published age-constant heterosis estimates averaged 4.9% for kidney fat and 3.8% for marbling score.

Breed solutions indicated that Hereford had the highest subcutaneous fat content at most end points, Charolais and Blonde d'Aquitaine had the least, and Angus, Gelbvieh, Simmental, and Limousin were intermediate (Table 2). Intermuscular fat content was generally highest for Hereford and Angus; intermediate for Charolais, Simmental, and Blonde d'Aquitaine; and lowest for Limousin and Gelbvieh. Gelbvieh had the most body cavity fat; Angus, Hereford, Charolais, and Blonde d'Aquitaine were intermediate; and Simmental and Limousin had the least body cavity fat (Table 2). Marbling was highest for Angus; intermediate for Hereford, Simmental, Blonde d' Aquitaine, Gelbvieh, and Charolais; and lowest for Limousin (Table 2). Breed rankings for each depot were similar regardless of end point.

Most studies have examined changes in the various fat depots relative to total carcass fat. These studies indicate that as fattening proceeds, the rate of subcutaneous fat deposition increases, and the rate of intermuscular fat deposition declines (Johnson et al., 1972; Berg and Butterfield, 1976; Kempster et al., 1976; Robelin, 1986; Perry and Arthur, 2000). This is reflected in broad differences among early and late-maturing beef breeds (Berg and Butterfield, 1976). If slaughtered at the same chronological age or at the same weight, early maturing cattle are expected to have a greater proportion of subcutaneous fat and a lower proportion of intermuscular fat than late-maturing breeds. If slaughtered at the same degree of physiological maturity, cattle of different beef breeds will have similar proportions of fat in each depot. Development patters of internal (body cavity and kidney and channel) fat are less clear (Kempster, 1980). Some references indicate that this depot matures early (Johnson et al., 1972), some indicate late (Berg and Butterfield, 1976; Robelin, 1986; Perry and Arthur, 2000), and some suggest that it grows at the same rate as overall fatness (Kempster et al., 1976; Jones et al., 1980). Dairy breeds tend to deposit fat internally, and beef breeds preferentially deposit external fat (Berg and Butterfield, 1976; Kempster et al., 1976). Intramuscular (marbling) fat content is often greater in early maturing than in late-maturing breeds (Gregory et al., 1994; Wheeler et al., 1996; Wheeler et al., 2004).

The objective of the current study was to evaluate genetic correlations among the different carcass fat depots. Evaluating the fat depots as a proportion of total 10th–11th–12th rib fat would have necessarily caused

Table 2. End point covariate, heterosis, and breed solutions for 10th–11th–12th rib subcutaneous, intermuscular, and body cavity fat content and carcass marbling score of finished feedlot steers adjusted to alternate end points

		Feedlot regimen[1]			Breed[2]					
Fat depot	End point	HG	BG	Heterosis, %	Angus	Hereford	Simmental	Limousin	Blonde d' Aquitaine	Gelbvieh
Subcutaneous, %	Slaughter age, d	0.010 ± 0.002^{b}	0.004 ± 0.002^{a}	–1.0 ± 3.6	1.85	4.43	1.41	1.74	0.43	2.02
	HCW, kg	0.005 ± 0.002	0.007 ± 0.002	–2.4 ± 3.5	1.99	4.65	1.53	1.78	0.52	2.16
	Fat depth, mm	0.315 ± 0.033	0.320 ± 0.034	–1.0 ± 3.3	1.26	3.66	1.23	1.38	0.45	1.69
	Marbling score,[3] units	0.485 ± 0.110^{b}	0.204 ± 0.106^{a}	–3.2 ± 3.6	1.14	4.07	1.10	1.55	0.27	1.54
Intermuscular, %	Slaughter age, d	0.012 ± 0.003	0.013 ± 0.003	–0.3 ± 4.5	1.92	3.19	–0.38	–1.39	–0.68	–1.30
	HCW, kg	0.002 ± 0.002^{b}	0.010 ± 0.003^{a}	–1.8 ± 4.5	1.82	3.21	–0.37	–1.51	–0.39	–1.40
	Fat depth, mm	0.465 ± 0.046	0.458 ± 0.051	–0.1 ± 4.2	1.00	2.03	–0.67	–1.90	–0.66	–1.78
	Marbling score,[3] units	1.184 ± 0.158^{b}	0.856 ± 0.153^{a}	–4.8 ± 4.4	0.25	2.57	–1.14	–1.73	–1.23	–2.07
Body cavity, %	Slaughter age, d	0.004 ± 0.001	0.004 ± 0.001	0.6 ± 5.8	–0.08	0.11	–0.59	–0.84	–0.24	0.71
	HCW, kg	0.002 ± 0.001	0.002 ± 0.001	–1.8 ± 5.8	–0.12	0.09	–0.59	–0.85	–0.21	0.68
	Fat depth, mm	0.022 ± 0.018	0.051 ± 0.018	–1.2 ± 5.8	–0.31	–0.13	–0.68	–0.95	–0.19	0.51
	Marbling score,[3] units	0.143 ± 0.054	0.100 ± 0.052	–3.0 ± 5.8	–0.42	–0.10	–0.74	–0.94	–0.27	0.50
Marbling,[3] units	Slaughter age, d	0.006 ± 0.001^{b}	0.004 ± 0.001^{a}	2.0 ± 1.4	0.65	–0.10	0.13	–0.16	0.21	–0.09
	HCW, kg	0.004 ± 0.001^{b}	0.002 ± 0.001^{a}	1.4 ± 1.4	0.74	0.04	0.21	–0.13	0.33	0.00
	Fat depth, mm	0.054 ± 0.014	0.060 ± 0.014	1.6 ± 1.4	0.36	–0.41	0.02	–0.28	0.24	–0.30

[a,b] Values in the same row with different superscripts differ ($P \leq 0.10$).

[1] HG = steers fed a high-grain diet from weaning to slaughter; BG = steers backgrounded before high-grain finishing.

[2] Mean ± SE for breed effects were similar across end points and ranged from 0.52 to 1.17% (subcutaneous fat), 0.71 to 1.71% (intermuscular fat), 0.23 to 0.52% (body cavity fat), and 0.20 to 0.45 units (marbling score).

[3] ≤ 3.0 = devoid, 3.1 to 4.0 = traces, 4.1 to 5.9 = slight, 6.0 to 7.0 = small to moderate, ≥ 7.0 = slightly abundant to abundant.

negative genetic correlations among some pairs of fat depots. Consequently, fat depots were expressed as a proportion of total 10th–11th–12th rib weight. Two recent studies have reported fat partitioning in the wholesale rib of steers slaughtered at fat-constant end points. Vaage et al. (1998) divided crossbred steers into 2 weight groups corresponding to differences in the degree of Continental breeding. After recalculating fat partitioning data as a proportion of wholesale rib weight, "light" steers had more subcutaneous fat (7.9 vs. 7.2%), less intermuscular fat (14.3 vs. 15.3%), and greater marbling scores (2.0 vs. 1.6) than "heavy" steers, but body cavity fat content was similar between the 2 groups (3.6%; Vaage et al., 1998). Average breed solutions obtained from the current study indicated that British steers also had numerically more subcutaneous, intermuscular, and marbling fat than Continental steers (Table 2). Block et al. (2001) reported that Hereford-cross steers had numerically more subcutaneous fat (9.8 vs. 8.6%), less intermuscular fat (15.7 vs. 16.7%), and lower marbling scores (1.4 vs. 2.0) than Charolais-cross steers but similar levels of body cavity fat (3.9 vs. 3.8%). Similar results were obtained for subcutaneous and marbling fat in the current study (Table 2). Compared with Charolais-cross steers, Angus- and Hereford-cross steers had numerically more subcutaneous fat (10.4, 10.9, and 10.0% for Angus-, Hereford-, and Charolais-cross steers, respectively) and less intermuscular fat (18.2, 18.1, and 18.6%, respectively), with similar levels of body cavity fat (4.0%). Angus- and Charolais-cross steers had greater marbling scores than Hereford-cross steers (2.0, 2.1 and 1.6, respectively; Block et al., 2001). Similar results were obtained for subcutaneous fat in the current study (Table 2). However, numerical discrepancies were observed between the results of the current study (Table 2) and those of Vaage et al. (1998) and Block et al. (2001) for body cavity fat and with results of Block et al. (2001) for intermuscular fat. The current study accounted for both within- and between-breed variation; Vaage et al. (1998) and Block et al. (2001) did not consider relationships among animals. Confirmation or clarification of breed influences on fat partitioning observed in the current study awaits additional data from other studies, preferably involving whole-side dissection.

Heritabilities and Genetic and Phenotypic Correlations Among Fat Depots Adjusted to Alternative Slaughter End Points

As shown in Table 3, heritabilities of the 4 fat depots ranged from 0.22 (body cavity fat content adjusted to a constant marbling score) to 0.44 (intermuscular fat content adjusted to a constant marbling score). Fat partitioning should respond to selection if it can be assessed economically and accurately on a routine basis. Crews and Kemp (2001) reported greater age-constant heritabilities for intermuscular fat percentage (0.64) and marbling score (0.55). In contrast, Anderson et al. (1974) found low heritabilities for subcutaneous fat (0.01 ± 0.21) and intermuscular fat (0.19 ± 0.23) percentages, although numbers of observations were somewhat limited (49 sires averaging 4.4 offspring).

Genetic correlations among the fat depots were low to moderate (Table 3) and appeared to follow an anatomical gradient; subcutaneous fat content was more strongly related to intermuscular fat content ($r_g = 0.16$ to 0.32) than to body cavity fat content ($r_g = -0.08$ to 0.05). The genetic correlation between intermuscular and body cavity fat contents were similar at all endpoints ($r_g = 0.38$ to 0.50). Marbling score was more highly associated with body cavity fat content ($r_g = 0.18$ to 0.28) than with intermuscular fat content ($r_g = 0.01$ to 0.12) and had a weak negative relationship with subcutaneous fat content at all end points ($r_g = -0.01$ to –0.11). The low genetic correlation between subcutaneous and body cavity fat depots may help explain the differences in fat partitioning among beef and dairy breeds reported in other studies (Berg and Butterfield, 1976; Kempster et al., 1976; Kempster, 1980). Fat partitioning among the different carcass depots are generally positive. However, the low to moderate magnitude of the genetic correlations indicate that different genetic mechanisms control fat partitioning among the subcutaneous, intermuscular, and body cavity depots. In support of these findings, Schenkel et al. (2005) reported that several single nucleotide polymorphisms in the leptin gene influenced dissectible fat yield but were unrelated to intramuscular fat percentage or quality grade.

Genetic Correlations Between Live Bull and Steer Carcass Traits with Steer Carcass Fat Partitioning Adjusted to Alternate Slaughter End Points

Genetic correlations between indicator traits with fat partitioning traits are shown in Table 4. Genetic correlations between yearling bull growth and ultrasound traits with carcass fat partitioning traits were generally no larger than their SE (Table 4). This may mean that the population genetic correlations do not differ from zero, or it may reflect the relatively low number of tested bulls with progeny in the partial carcass dissection data set. Provided the genetic correlations are representative of the population, the SE should decline with the addition of more data. This is assumed in the following discussion. Selection for increased postweaning gain in bulls should lead to decreased subcutaneous ($r_g = -0.10$ to –0.18), intermuscular ($r_g = -0.24$ to –0.35), body cavity ($r_g = -0.24$ to 0.29), and marbling ($r_g = -0.34$ to –0.39) fat content in steers (Table 4). Similar results were observed for hip height (Table 4), suggesting that selection for growth rate and size in bulls may influence steer carcass fat partitioning. Crews and Kemp (2001) reported that yearling weight in bulls and heifers was negatively associated with age-constant intermuscular

Table 3. Estimates of phenotypic variance, heritability (diagonal, indicated in bold), and genetic and phenotypic correlations (above and below diagonal, respectively) among fat content in the subcutaneous, intermuscular, body cavity, and marbling depots in the 10th–11th–12th rib section of finished feedlot steers adjusted to different slaughter end points (±SE)

		Carcass fat depot heritability and correlation			
Fat depot	Phenotypic variance[1]	Subcutaneous	Intermuscular	Body cavity	Marbling
Slaughter age end point					
Subcutaneous	2.39 ± 0.12%^{2}	**0.42 ± 0.09**	0.32 ± 0.16	0.05 ± 0.21	–0.01 ± 0.18
Intermuscular	5.25 ± 0.27%^{2}	0.30 ± 0.03	**0.40 ± 0.10**	0.50 ± 0.18	0.12 ± 0.18
Body cavity	0.55 ± 0.03%^{2}	0.10 ± 0.04	0.15 ± 0.03	**0.26 ± 0.08**	0.28 ± 0.20
Marbling	0.34 ± 0.02 score^2	0.11 ± 0.04	0.28 ± 0.03	0.10 ± 0.04	**0.43 ± 0.09**
HCW end point					
Subcutaneous	2.39 ± 0.12%^{2}	**0.40 ± 0.09**	0.30 ± 0.17	0.00 ± 0.22	–0.05 ± 0.18
Intermuscular	5.28 ± 0.27%^{2}	0.30 ± 0.03	**0.37 ± 0.09**	0.48 ± 0.20	0.11 ± 0.18
Body cavity	0.56 ± 0.03%^{2}	0.11 ± 0.04	0.16 ± 0.03	**0.23 ± 0.08**	0.23 ± 0.21
Marbling	0.35 ± 0.02 score^2	0.11 ± 0.04	0.29 ± 0.03	0.12 ± 0.04	**0.46 ± 0.10**
Grade fat end point					
Subcutaneous	2.04 ± 0.10%^{2}	**0.38 ± 0.09**	0.16 ± 0.18	–0.08 ± 0.22	–0.16 ± 0.19
Intermuscular	4.55 ± 0.24%^{2}	0.18 ± 0.04	**0.39 ± 0.09**	0.38 ± 0.20	0.01 ± 0.19
Body cavity	0.56 ± 0.03%^{2}	0.09 ± 0.04	0.14 ± 0.03	**0.23 ± 0.08**	0.18 ± 0.22
Marbling	0.35 ± 0.02 score^2	0.07 ± 0.04	0.26 ± 0.03	0.12 ± 0.04	**0.37 ± 0.09**
Marbling score end point					
Subcutaneous	2.39 ± 0.12%^{2}	**0.41 ± 0.09**	0.32 ± 0.16	–0.01 ± 0.22	
Intermuscular	5.00 ± 0.27%^{2}	0.29 ± 0.03	**0.44 ± 0.10**	0.41 ± 0.20	
Body cavity	0.56 ± 0.03%^{2}	0.10 ± 0.04	0.15 ± 0.03	**0.22 ± 0.08**	

[1] Measured as a percentage for fat contents and as a unit score for marbling. The phenotypic variance values are all squared terms.

fat content (r_g = –0.33) and essentially independent of marbling score (r_g = –0.03) in steers. In contrast, Thompson et al. (1987) found that divergent selection for weaning weight had little effect on fat partitioning in mature Merino sheep, suggesting a low genetic correlation between these traits. Perry and Arthur (2000) studied carcass composition and fat partitioning in Angus steers produced by 3.5 generations of divergent selection for yearling weight and found no differences in carcass composition or fat partitioning in steers slaughtered at 44 to 47 mo of age. Morris et al. (1993) compared Angus bulls from control and selected lines for 17 calf crops for yearling weight. Despite a 17.6% increase in HCW, fat partitioning among subcutaneous, intermuscular, and kidney and channel fat depots did not differ significantly between selected and control lines (Morris et al., 1993). Morris et al. (1993) and Perry and Arthur (2000) compared selected and control lines in animals that were 4 and 2 yr old, respectively. However, the absence of strain differences in physiologically mature animals in these studies does not imply that the strains reached physiological maturity at the same age. If comparisons had been conducted in typical market (i.e., physiologically immature) animals at a constant weight or fat depth, differences in fat partitioning might have been more apparent.

Selection for reduced 12th-13th rib ultrasound fat depth in bulls is expected to result in decreased fat content in the subcutaneous (r_g = 0.11 to 0.29), intermuscular (r_g = 0.01 to 0.36), body cavity (r_g = 0.27 to 0.49), and marbling (r_g = 0.39 to 0.73) depots (Table 4). Crews and Kemp (2001) also reported positive correlations between yearling bull and heifer ultrasound fat depths with intermuscular fat content of steers (r_g = 0.18 and 0.75, respectively), but negative correlations with marbling score (r_g = –0.27 and –0.15, respectively). Adjusting 10th–11th–12th rib fat content data to a grade fat or marbling score-constant end point reduced the magnitude of the correlations between yearling bull ultrasound fat depth and dissected carcass fat percentage. For example, genetic correlations between yearling bull ultrasound fat depth with carcass intermuscular fat decreased from 0.36 (slaughter age constant) and 0.26 (HCW constant) to 0.05 (carcass fat depth constant) and 0.01 (marbling score constant; Table 4). Results of Bergen et al. (2006) indicated that yearling bull ultrasound 12th-13th rib fat depth also had stronger genetic correlations with dissected steer lean meat yield adjusted to slaughter age and HCW-constant end points (r_g = –0.34 and –0.25, respectively) than at carcass fat depth or marbling score-constant end points (r_g = –0.02 and –0.03, respectively). The sign of the genetic correlation between yearling bull ultrasound intramuscular fat content with steer carcass fat varied among depots. Genetic correlations were generally positive with body cavity and intermuscular fat content and negative with subcutaneous fat content. Selection for increased ultrasound intramuscular fat percentage in yearling bulls may lead to undesired correlated increases in body cavity and intermuscular fat content in steers, supporting concerns expressed by Kempster (1980). This may be a concern if selection for carcass traits is based almost exclusively on seedstock ultrasound measurements.

Table 4. Genetic correlations among yearling bull growth and ultrasound traits, and steer carcass measurements with fat content in the subcutaneous, intermuscular, body cavity, and marbling depots in the 10th–11th–12th rib section, of finished feedlot steers, adjusted to different slaughter end points

	Slaughter end point adjustment[1]														
	Slaughter age				HCW				Fat depth				Marbling score		
Item	SC[2]	IM[3]	BC[4]	MS[5]	SC	IM	BC	MS	SC	IM	BC	MS	SC	IM	BC
Bull weight and height traits															
Yearling weight	0.01	–0.29	–0.23	**–0.58**	–0.06	–0.35	–0.29	**–0.63**	–0.02	–0.36	–0.23	**–0.59**	0.09	–0.12	–0.17
Post-weaning gain	–0.14	–0.30	–0.24	–0.34	–0.18	–0.35	–0.29	–0.39	–0.12	–0.30	–0.25	–0.36	–0.10	–0.24	–0.24
Hip height	0.02	–0.10	–0.21	**–0.42**	–0.06	–0.19	–0.29	**–0.47**	–0.05	–0.19	–0.27	**–0.46**	0.05	0.05	–0.20
12th–13th rib ultrasound fat traits															
Rib fat depth	0.29	0.36	0.49	**0.73**	0.29	0.26	0.39	0.55	0.11	0.05	0.31	0.39	0.13	0.01	0.27
Intramuscular fat percentage	–0.22	0.31	0.16	NC[6]	–0.23	0.26	0.12	NC	–0.44	0.12	0.05	NC	–0.41	–0.06	–0.05
12th–13th rib ultrasound LM size traits															
Area	0.00	–0.10	–0.29	–0.30	–0.01	–0.11	–0.31	–0.30	0.05	–0.05	–0.30	–0.26	0.08	0.02	–0.25
Method 1 depth	0.06	–0.10	–0.18	–0.30	0.08	–0.09	–0.20	–0.24	0.20	0.03	–0.19	–0.23	0.14	0.02	–0.15
Method 1 width	–0.09	–0.53	–0.63	**–0.84**	–0.18	–0.61	–0.69	**–0.87**	–0.14	–0.57	–0.63	**–0.75**	0.07	–0.19	–0.49
Method 2 depth	0.04	0.13	0.05	–0.06	0.08	0.17	0.06	0.01	0.19	0.29	0.07	0.04	0.07	0.11	0.04
Method 2 width	–0.55	NC	NC	NC	–0.63	NC	NC	NC	–0.44	**–0.91**	–0.99	**–0.98**	–0.37	–0.71	–0.90
Steer carcass traits[7]															
HCW	0.11	–0.20	0.12	–0.26					–0.07	**–0.39**	–0.02	**–0.44**	0.08	–0.16	0.06
Fat depth	**0.50**	**0.42**	0.37	0.13	**0.45**	**0.48**	0.33	0.18					**0.46**	**0.40**	0.31
LM area	–0.29	**–0.38**	–0.18	**–0.49**	**–0.39**	–0.26	–0.23	–0.15	–0.29	**–0.37**	–0.23	**–0.56**	–0.27	–0.29	–0.19
Ruler lean meat yield[8]	**–0.49**	**–0.57**	–0.25	–0.24	**–0.46**	**–0.49**	–0.20	–0.10	–0.20	–0.73	0.13	–0.86	**–0.46**	**–0.54**	–0.18
Blue Tag lean meat yield[9]	**–0.51**	**–0.42**	–0.33	–0.26	**–0.49**	**–0.40**	–0.30	–0.21	–0.30	–0.19	–0.24	–0.25	**–0.49**	**–0.37**	–0.31
Dissected lean meat yield[10]	**–0.69**	**–0.80**	**–0.52**	–0.21	**–0.67**	**–0.78**	**–0.49**	–0.14	**–0.58**	**–0.73**	–0.45	–0.06	**–0.68**	**–0.79**	**–0.44**

[1] SE values were similar across fat depots and end points and ranged from 0.20 to 0.30 (correlations with yearling weight, postweaning gain, and hip height), 0.29 to 0.38 (correlations with ultrasound fat depth and intramuscular fat percentage), 0.30 to 0.54 (correlations with ultrasound LM size traits), 0.16 to 0.27 (carcass weight, fat depth, and LM area), 0.20 to 0.68 (correlations with ruler lean meat yield), 0.14 to 0.22 (correlations with Blue Tag lean meat yield), and 0.07 to 0.20 (correlations with dissected lean meat yield). Significant ($P \leq 0.05$) correlations (*t*-test) are shown in bold.

[2] SC = subcutaneous fat (percentage of total 10th–11th–12th rib weight).

[3] IM = intermuscular fat (percentage of total 10th–11th–12th rib weight).

[4] BC = body cavity fat (percentage of total 10th–11th–12th rib weight).

[5] MS = carcass marbling score.

[6] NC = bivariate model did not converge.

[7] In each column, carcass traits and the corresponding fat partitioning trait are adjusted to the same end point.

[8] Carcass lean meat yield predicted from HCW, fat depth, and LM area.

[9] Carcass lean meat yield predicted from carcass fat depth and LM depth and width using the Canadian beef grading ruler.

[10] Dissected 10th–11th–12th rib lean meat yield.

Yearling bull ultrasound LM area had low or negative genetic correlations with fat content in all 4 depots at all end points. Crews and Kemp (2001) found that age-constant steer intermuscular fat content was negatively correlated with ultrasound LM area in yearling bulls (r_g = –0.66) and heifers (r_g = –0.12). Those researchers also reported that age-constant steer carcass marbling score was positively associated with ultrasound LM area in bulls (r_g = 0.31) but not heifers (r_g = –0.01). Linear LM depth and width measurements have not been studied as extensively as LM area. In the current study, Method 1 depth and width measurements also tended to be negatively associated with fat content in the 4 depots (Table 4). Notably, Method 1 width had relatively strong negative correlations with intermuscular (r_g = –0.53 to –0.61), body cavity fat (r_g = –0.63 to –0.69), and marbling score (r_g = –0.75 to –0.87) at slaughter age-, HCW-, and fat depth-constant end points. This raises the possibility that yearling bull ultrasound LM Method 1 width may be a useful indicator trait for reducing intermuscular and body cavity fat, which are likely difficult to measure ultrasonically. Bivariate models involving Method 2 width failed to converge with intermuscular, body cavity, and marbling fat depots at constant slaughter age and HCW end points. Method 2 width also failed to converge with carcass marbling score and 10th–11th–12th rib dissected lean percentage in earlier studies (Bergen et al., 2005b, 2006). These convergence problems may be related to the low heritability of Method 2 width (h^2 = 0.13; Bergen et al., 2005b). A larger ultrasound and carcass data set might have produced more conclusive results. In contrast, Method 2 depth measurements tended to be positively correlated with fat content in all 4 depots (except for slaughter age-constant marbling score). Bergen et al. (2005b) reported that Method 2 LM depth was negatively related to dissected carcass lean meat yield at all slaughter end point adjustments. Although no biological explanation presents itself for the relationship between LM shape and fat partitioning, results suggest that muscle shape might have important relationships with carcass fat partitioning as well as lean percentage.

Hot carcass weight tended to have a low, positive correlation with subcutaneous and body cavity fat content and a stronger, negative correlation with intermuscular fat content and marbling score. Carcass fat depth was positively correlated with fat content in all 4 depots at all end points and had a numerically stronger relationship with intermuscular and subcutaneous fat content than with body cavity fat content. Carcass LM area was negatively correlated with fat content in all depots at all end points and tended to have a stronger association with subcutaneous and intermuscular depots than with body cavity fat. As expected, lean meat yield estimates had moderate to strong negative correlations with all fat depots at all end points. The one exception was ruler lean meat yield, which had a positive relationship with body cavity fat content at the fat depth-constant end point.

The importance of fat partitioning is further underscored in Table 4. Dissected lean meat yield had stronger genetic correlations with intermuscular fat than with subcutaneous fat content at slaughter age (–0.80 vs. –0.69), HCW (–0.78 vs. –0.67), fat depth (–0.73 vs. –0.58), and marbling score (0.79 vs. –0.68) end points. Results shown in Bergen et al. (2006) indicated that yearling bull ultrasound fat depth was related to dissected lean meat yield in steers, particularly at slaughter age (r_g = –0.34) and HCW (r_g = –0.25) end points. Selection based on yearling bull ultrasound fat depth will reduce steer carcass fat content in both the subcutaneous (r_g = 0.29) and intermuscular (r_g = 0.26 to 0.36) fat depots at slaughter age- and HCW-constant end points (Table 4). However, the low genetic correlations between subcutaneous and intermuscular fat content at slaughter age- (r_g = 0.30) and HCW-constant (0.32) endpoints suggest that selection aimed solely at reducing subcutaneous fat content will have limited impact on intermuscular fat content. Consequently, identification of additional indicator traits more strongly related to intermuscular fat content may be beneficial. Method 1 LM width appears to have potential in this regard (r_g = –0.53 and –0.61 at slaughter age-constant and HCW-constant end points, respectively). Analysis of additional data sets is warranted to confirm or dismiss the potential value of alternative LM size measurements as indicator traits for fat partitioning in commercial beef carcasses. Additional ultrasound measurements such as body wall depth (Greiner et al., 2003; Bergen et al., 2005a) that may provide a more direct measurement of intermuscular fat content also warrant further investigation in this regard.

IMPLICATIONS

Genetic correlations less than unity indicate that the subcutaneous, intermuscular, body cavity, and marbling fat depots are not under identical genetic control. Although selection against subcutaneous fat depth (based on either ultrasound or carcass measurements) will likely lead to decreases in overall fat content, it may not yield the desired reduction in the intermuscular or body cavity fat depots. Inclusion of longissimus muscle shape measurements, such as depth or width, may allow more specific selection against intermuscular fat content.

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