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Lipid characteristics of subcutaneous adipose tissue and *M. longissimus thoracis* of Angus and Wagyu steers fed to US and Japanese endpoints

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Abstract

We hypothesized that the concentrations of monounsaturated fatty acids (MUFA) and cholesterol of adipose tissue and *M. longissimus thoracis* would not differ between Angus and American Wagyu steers when fed to a typical US live weight, but would diverge when fed to a Japanese live weight. To test this, 8 steers of each breed type were assigned to a high-energy, corn-based diet, and another 8 steers of each breed type were fed coastal bermuda grass hay diet, supplemented with the corn-based diet to achieve a daily gain of 0.9 kg/d. Targeted final body weights were 525 kg for steers fed for 8 or 12 mo the corn- or hay-based diets, respectively, and were 650 kg for steers fed for 16 or 20 mo the corn- or hay-based diets. Digesta concentrations of stearic (18:0) and *trans*-vaccenic acid decreased, whereas linoleic acid (18:2n-6) increased between the US and Japanese endpoints (all $P \leqslant 0.03$). α-Linolenic acid (18:3n-3) increased in digesta only in the hay-fed steers during this time. Plasma concentrations of palmitic (16:0) and palmitoleic acid (16:1n-7), and the 16:1:18:0 ratio, were higher in Angus steers than in Wagyu steers. Also, the plasma 16:1:18:0 ratio was decreased by hay feeding in Angus steers, but increased in Wagyu steers, when fed to the Japanese endpoint. Concentrations of oleic (18:1n-9), linoleic, α-linolenic, and 18:2*trans*-10,*cis*-12 conjugated linoleic acid all were higher in Wagyu than in Angus subcutaneous (s.c.) adipose tissue, whereas myristic (14:0) and palmitic acid were higher in Angus s.c. adipose tissue ($P \leqslant 0.05$). All MUFA increased, and saturated fatty acids decreased, between the US and Japanese endpoints. Slip points of lipids in s.c. adipose tissue were over 10 °C lower ($P = 0.01$) in Japanese-endpoint steers than in US endpoint steers, consistent with the overall increase in MUFA with time on feed. The concentration of cholesterol in the *M. longissimus thoracis* increased with time, which may have been related to the increase in oleic acid. Because the breed × endpoint interaction was not significant for cholesterol or any of the adipose tissue fatty acids, we conclude that our original hypothesis was incorrect. Of the three factors tested (breed type, diet, and slaughter age endpoint), endpoint had the greatest effect on adipose tissue lipid composition.

Keywords: Bovine; Adipose tissue; Fatty acids; Melting point; Cholesterol

1. Introduction

Monounsaturated fatty acids (MUFA) in meat have been shown to influence beef palatability (Dryden & Marchello, 1970; Westerling & Hedrick, 1979) and fat softness (Perry, Nicholls, & Thompson, 1998; Smith, Yang, Larsen, & Tume, 1998). The balance between stearic acid (18:0) and oleic acid (18:1n-9) is primarily responsible for differences in fat softness (Smith et al., 1998), and the concentrations of these fatty acids in subcutaneous (s.c.) adipose tissue are affected by breed, sex, age, and nutrition (Clemens, Arthaud, Mandigo, & Woods, 1973; Eichhorn et al., 1986; Huerta-Leidenz et al., 1993; Mandell, Buchanan-Smith, & Campbell, 1998). Japanese Black cattle produce carcasses that have adipose tissues with higher percentages of

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MUFA than Holstein, Japanese Brown, Charolais, or Angus steers (Sturdivant, Lunt, Smith, & Smith, 1992; Oka et al., 2002; Zembayashi, Nishimura, Lunt, & Smith, 1995). Early studies from this laboratory were with American Wagyu cattle that had been derived from the two Japanese Black and two Japanese Brown bulls originally imported into the US (Lunt, Riley, & Smith, 1993). The Japanese bulls were crossed on Angus and Hereford × Angus cows, and subsequent generations were mated back to the imported bulls to produce a synthetic breed. As seen for purebred Japanese Black cattle, these American Wagyu steers produced carcasses higher in MUFA than Angus steers when fed high-roughage diets to a typical Japanese endpoint (650 kg; May, Sturdivant, Lunt, Miller, & Smith, 1993).

We hypothesized that adipose tissue MUFA concentrations in Angus steers would equal those of Wagyu steers if steers were fed a corn-based diet to a typical US carcass weight (525 kg). Therefore, this study was designed to document the interaction between diet (corn vs. a hay-based diet) and slaughter weight (525 or 650 kg) on fatty acid composition of digesta, plasma, and s.c. adipose tissue, and melting points (estimated by slip points) of s.c. adipose tissue lipids. We also measured cholesterol concentrations of lipids from *M. longissimus thoracis* from the same animals to document their relationship to intramuscular lipid and oleic acid concentrations in cattle raised to the Japanese endpoint.

2. Materials and methods

2.1. Animals and diets

Sixteen American Wagyu and 16 Angus steers were purchased as calves at weaning (approximately 8 mo of age). The American Wagyu steers were from the same foundation herd that provided steers for our earlier study (Lunt et al., 1993). Coastal bermuda grass hay containing 9.5% crude protein was fed free choice for 8 d after the steers were transported to the Texas A&M University Research Center, McGregor. Eight steers of each breed type were assigned to a high-energy, corn-based diet containing 48% ground corn, 20% ground sorghum, 15% cottonseed hulls, 7.5% molasses, 0.96% limestone, 0.56% trace mineral salt, and 0.08% vitamin premix. The diet was designed to achieve an average gain of 1.36 kg/d, and was fed free choice for 8 mo or 16 mo after weaning ($n = 4$ per breed type and time on feed). The remaining 8 steers of each breed type continued on the coastal bermuda grass hay diet, supplemented with the corn-based diet to achieve a targeted rate of gain of 0.9 kg/d. The hay-fed steers were fed for 12 or 20 mo after weaning ($n = 4$ per breed type and time on feed).

Production characteristics of these cattle were reported previously (Lunt, Choi, Chung, & Smith, 2005). The average initial weights for Wagyu and Angus steers were 169 and 211 kg, respectively. Targeted final body weights were 525 kg, considered as a US endpoint for steers fed the corn- or hay-based diets for 8 mo or 12 mo, respectively, and were 650 kg, considered as a typical Japanese endpoint for steers fed the corn- or hay-based diets for 16 or 20, respectively. The Angus steers achieved the targeted body weights (average of 526.7 and 663.0 kg for the US and Japanese endpoints, respectively; Lunt et al., 2005). The Wagyu steers averaged 453.7 and 588.4 kg for the US and Japanese endpoints, respectively. Part of the difference in final body weights was caused by the 42-kg lesser initial body weights of the Wagyu calves; however, the Wagyu calves also had lower average daily gains (0.86 vs. 0.96 kg/d for the Angus calves), due primarily to slower rates of gain of Wagyu calves on the corn-based diets (Lunt et al., 2005).

After being fed for their respective time periods, the steers in each time-on-feed group were slaughtered on two consecutive days. Immediately following removal of the hide, a section of the *M. longissimus thoracis* and overlying s.c. adipose tissue was removed from the carcass. Samples of s.c. adipose tissue were snap-frozen in liquid nitrogen and stored at −94 °C. Blood samples were collected at exsanguination in tubes containing 15% K_3EDTA, and centrifuged at $1800 \times g$ at 5 °C for 30 min; plasma was stored at −20 °C until analyzed for fatty acid composition. After evisceration, an incision was made distal to the pyloric valve and duodenal contents (approximately 50 g) were collected and stored at −20 °C for analysis of fatty acid composition.

2.2. Total lipid extraction

Total lipid was extracted by a modification of the method of Folch, Lees, and Stanley (1957). Approximately 5 g of digesta, 1 ml of plasma, and 1 g of s.c. adipose tissue were homogenized with 5.0 ml of chloroform:methanol (2:1, vol/vol) and held with shaking at room temperature (approximately 20 °C) for 48 h to extract lipid. The homogenate was filtered through Whatman GF/C filters (Whatman Ltd., Maidstone, England) and rinsed with an additional 10 ml of chloroform:methanol. The extracted lipid was combined with 8 ml of 0.74% KCl and vortexed for 1 min. Once the phases were separated, the aqueous layer was removed and discarded. The lipid layer was transferred to 20-ml scintillation vials and the solvents were evaporated by heating at 60 °C under nitrogen.

2.3. Fatty acid analysis

Approximately 80 mg of each lipid extract was converted to its fatty acid methyl esters (FAME) as described (Morrison & Smith, 1964). FAME analyzed with a Varian gas chromatograph (model CP-3800 fixed with a CP-8200 autosampler, Varian Inc., Walnut Creek, CA), equipped with a fused silica capillary column CP-Sil88 [100 m × 0.25 mm (i.d.)] (Chrompack Inc., Middleburg, The Netherlands), with helium as the carrier gas (flow rate = 1.2 ml/min) (Smith et al., 2002). After 32 min at 180 °C, oven temperature was increased at 20 °C/min to 225 °C and held for 13.75 min. Total run time was 48 min. Injector and detector temperatures were at 270 and 300 °C, respectively. Individual FAME were quantified as g fatty acid/100 g of total FAME identified. Identities of FAME were established by comparison to authentic standards (GLC 96; Nu-Chek Prep, Inc, Elysian, MN, USA). Conjugated linoleic acid isomers were identified by comparison to a commercial preparation (CLA-60; Natural of Hovdebygda, Norway).

2.4. Slip points

Melting points of the s.c. adipose tissue lipids were approximated by determining slip points (Smith et al., 1998). After heating to approximately 45 °C, the lipids were drawn 1 cm into glass capillary tubes. Duplicate tubes were collected for each sample and frozen at −20 °C. After freezing, the capillary tubes were suspended vertically in a chilled water bath with the portion of the tube containing lipid submerged in the water. The water bath was heated at 2 °C/min with constant stirring. Temperature of the water was monitored with a Type K thermocouple (model KTSS-HH, Omega Engineering, Inc., Stamford, CT, USA) attached to a digital thermometer (model 91100-50, Cole-Parmer Instrument Co., Vernon Hills, IL, USA). Slip point is defined as the temperature at which the lipid moved up the capillary tube and reported as the means between duplicates for each sample.

2.5. Cholesterol concentration

Cholesterol concentration of the *M. longissimus thoracis* was analyzed as described (Rule, MacNeil, & Short, 1997; Rule, Broughton, Shellito, & Maiorano, 2002) using gas chromatography. Briefly, 100 g of *M. longissimus thoracis* was freeze-dried and homogenized in a home-style electric grinder. Cholesterol was extracted with 3 ml of ethanol to 100 mg of dried tissue. The lipids were saponified by the addition of 1 ml of 33% (wt/vol) KOH and heating for 60 min in an 80–90 °C water bath. Cholesterol was isolated on an SPB-1, fused capillary column [30 mm × 0.53 mm (i.d.)] (Suppelco, Bellefonte, PA, USA) with column temperature at 250 °C and detector and injector temperatures at 300 °C. Helium was the carrier gas with a 1:3 split ratio. Stigmasterol was used as the internal standard to quantify the total cholesterol.

2.6. Statistical analysis

All statistical analyses were performed by using SPSS version 11 (SPSS Inc., Chicago, IL, USA). Fatty acid composition of plasma and s.c. adipose tissue, slip points, and cholesterol concentrations were compared by ANOVA as three-factor designs that independently compared main effects (breed type, diet, and endpoint) and all possible interactions. The $P < 0.05$ probability level was established for statistical significance.

3. Results

3.1. Digesta fatty acid composition

It was not possible to obtain a representative sample of the hay-based diet for total fatty acid composition, because the steers had free access to the bermuda grass hay and were supplemented with the corn concentrate diet to achieve their desired rate of gain. Therefore, digesta was sampled for each animal at each slaughter interval and analyzed for fatty acid composition. Digesta of the corn-fed steers was higher in palmitic (16:0) and palmitoleic acid (16:1n-7) than digesta from hay-fed steers, whereas digesta of hay-fed was higher in α-linolenic acid (18:3n-3; Table 1). Statistically significant ($P \leqslant 0.05$) differences in myristoleic (14:1n-5), *trans*-vaccenic (18:1*t*11), and α-linolenic acid were detected between breeds types; these fatty acids were greater in Wagyu digesta than in Angus digesta. There was a breed × diet × endpoint interaction for digesta *trans*-vaccenic acid; this fatty acid was greater in digesta of corn-fed Wagyu steers than in corn-fed Angus steers at the US endpoint, but was not different between breed types under any other conditions.

There were significant ($P \leqslant 0.04$) diet × endpoint interactions for digesta palmitic, stearic (18:0), and *trans*-vaccenic acid, total SFA, linoleic (18:2n-6), and α-linolenic acid, the 16:1:18:0 ratio, and total PUFA (Table 1). The concentrations of palmitic and linoleic acid, the 16:1:18:0 ratio, and total PUFA were greater in digesta of corn-fed steers fed to the Japanese endpoint than in corn-fed steers raised to the US endpoint. Conversely, the concentrations of stearic and *trans*-vaccenic acid and total SFA were less in digesta of corn-fed steers fed to the Japanese endpoint than in corn-fed steers fed to the US endpoint. These effects were not observed in hay-fed steers. Digesta concentrations of α-linolenic acid declined in hay-fed steers between the US and Japanese endpoints.

There also were significant breed × diet interactions for myristoleic ($P = 0.03$) and *trans*-vaccenic acid ($P = 0.05$). These fatty acids were higher in digesta of corn-fed Wagyu steers than in digesta of hay-fed Wagyu steers, but did not differ between corn- and hay-fed Angus steers. This was the only significant breed × diet interaction observed in this study.

3.2. Plasma fatty acid composition

Angus steers had higher plasma concentrations of palmitic ($P = 0.05$) and palmitoleic acid ($P = 0.03$) and a higher plasma 16:1:18:0 ratio than Wagyu steers (Table 2). Plasma from steers fed the corn-based diet contained higher concentrations of myristoleic and palmitoleic acid ($P \leqslant 0.02$), but lesser plasma stearic acid than hay-fed

Table 1
Fatty acid concentrations (g/100 g total fatty acids) in digesta of Wagyu and Angus steers fed to US and Japanese endpoints

Item	Months on feed/diet								SE					
	US endpoint				Japanese endpoint									
	8 mo/corn		12 mo/hay		16 mo/corn		20 mo/hay			*P*-values				
	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu		Breed	Diet	Endpoint	$D \times E$[a]	$B \times D \times E$[b]
14:0	0.63	0.61	1.02	1.00	0.50	1.04	0.64	0.71	0.08	0.39	0.38	0.57	0.15	0.48
14:1n-5[c]	0.34	0.95	0.94	0.76	0.29	0.83	0.35	0.49	0.07	0.05	0.81	0.06	0.19	0.48
16:0	19.2	16.8	25.2	26.1	25.4	22.5	23.6	22.3	0.68	0.13	<0.01	0.08	<0.01	0.65
16:1n-7	0.69	0.42	1.18	1.27	0.97	0.72	0.95	0.90	0.08	0.46	0.02	0.98	0.07	0.81
18:0	57.1	48.1	46.0	37.0	27.6	38.5	44.3	40.1	2.22	0.48	0.81	0.03	0.02	0.35
18:1*t*11[c]	2.46^{y}	7.88^{x}	1.81^{yz}	1.25^{yz}	0.46^{z}	1.47^{yz}	1.49^{yz}	2.81^{y}	0.50	0.01	0.08	0.01	<0.01	0.03
18:1n-9	14.8	18.6	12.7	17.4	16.9	17.8	15.4	18.9	0.95	0.12	0.65	0.51	0.72	0.86
18:2n-6	4.76	6.30	10.0	14.1	27.9	16.8	12.9	13.2	1.56	0.58	0.60	<0.01	<0.01	0.36
18:3n-3	0.0	0.25	0.83	1.01	0.0	0.23	0.24	0.48	0.08	<0.01	<0.01	<0.01	<0.01	0.91
16:1:18:0	0.013	0.010	0.031	0.037	0.038	0.021	0.021	0.022	0.003	0.55	0.19	0.64	0.01	0.71
SFA[d]	79.4	73.5	74.1	65.4	54.0	63.6	70.1	66.0	2.03	0.54	0.73	0.02	0.04	0.46
MUFA[d]	15.9	20.0	14.8	19.5	18.1	19.4	16.7	20.3	0.98	0.12	0.81	0.60	0.90	0.84
PUFA[d]	4.76	6.56	11.1	15.1	27.9	17.0	13.2	13.7	1.56	0.65	0.75	<0.01	<0.01	0.36
MUFA:SFA	0.20	0.28	0.22	0.32	0.34	0.34	0.24	0.31	0.02	0.20	0.68	0.26	0.29	0.76

^{xyz} Means with different superscripts are different.

[a] Diet × endpoint interaction. All breed × diet and breed × endpoint interactions $P > 0.10$.

[b] Breed × diet × endpoint interaction.

[c] There was a significant breed × diet interaction for 14:1n-5 ($P = 0.03$) and 18:1*trans*-11 ($P = 0.05$).

[d] SFA = total SFA (14:0 + 16:0 + 17:0 + 18:0 + 18:1*t*11). MUFA = total monounsaturated fatty acids (14:1n-5 + 16:1n-7 + 18:1n-9). PUFA = total polyunsaturated fatty acids (18:2n-6 + 18:3n-3).

Table 2
Fatty acid concentrations (g/100 g total fatty acids) in plasma of Wagyu and Angus steers fed to US and Japanese endpoints

Item	Months on feed/diet								SE					
	US endpoint				Japanese endpoint									
	8 mo/corn		12 mo/hay		16 mo/corn		20 mo/hay			*P*-values				
	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu		Breed	Diet	Endpoint	$D \times E$[a]	$B \times D \times E$[b]
14:0	0.15	0.24	0.96	0.50	0.84	0.58	0.0	0.0	0.11	0.43	0.67	0.59	<0.01	0.31
14:1n-5	0.25	0.42	0.50	0.28	0.61	0.89	0.0	0.0	0.08	0.68	0.02	0.91	<0.01	0.84
16:0	16.7	13.9	15.8	14.6	17.4	13.4	12.3	11.9	0.57	0.05	0.11	0.17	0.13	0.63
16:1n-7	1.31^{x}	1.40^{x}	1.18^{x}	0.25^{z}	1.33^{x}	0.50^{y}	0.18^{z}	0.59^{y}	0.11	0.03	<0.01	0.01	0.69	<0.01
18:0	22.7	20.4	22.2	21.9	18.0	19.1	21.8	21.7	0.42	0.59	0.01	0.02	0.07	0.27
18:1n-9	14.6	12.0	14.2	12.4	16.3	14.9	11.5	10.9	0.68	0.25	0.11	0.94	0.11	0.98
18:2n-6	43.9	51.1	44.7	49.0	45.4	50.4	53.9	54.8	1.34	0.11	0.28	0.15	0.19	0.90
18:3n-3	0.35	0.47	0.48	0.88	0.0	0.22	0.30	0.15	0.09	0.44	0.32	0.06	0.68	0.38
16:1:18:0	0.058^{x}	0.070^{x}	0.053^{x}	0.012^{z}	0.075^{x}	0.026^{y}	0.008^{z}	0.027^{y}	0.006	0.05	<0.01	0.05	0.94	<0.01
SFA[c]	39.6	34.5	39.0	37.1	36.3	33.0	34.1	33.6	0.81	0.11	0.96	0.05	0.59	0.96
MUFA[c]	16.1	13.8	15.9	13.0	18.3	16.4	11.7	11.5	0.73	0.19	0.03	0.85	0.07	0.68
PUFA[c]	44.3	51.6	45.2	49.9	45.4	50.6	54.2	54.9	1.34	0.10	0.25	0.19	0.20	0.86
MUFA:SFA	0.40	0.40	0.41	0.35	0.51	0.50	0.34	0.34	0.02	0.53	0.01	0.39	0.04	0.61

^{xyz} Means with different superscripts are different.

[a] Diet × endpoint interaction. All breed × diet and breed × endpoint interactions $P > 0.20$.

[b] Breed × diet × endpoint interaction.

[c] SFA = total SFA (14:0 + 16:0 + 17:0 + 18:0). MUFA = total monounsaturated fatty acids (14:1n-5 + 16:1n-7 + 18:1n-9). PUFA = total polyunsaturated fatty acids (18:2n-6 + 18:3n-3).

steers ($P = 0.01$). Consequently, plasma from the corn-fed steers had a higher 16:1:18:0 ratio than plasma from hay-fed steers, more MUFA, and a higher MUFA:SFA ratio (all $P \leqslant 0.03$).

Plasma from steers raised to the US endpoint had a higher concentration of palmitoleic acid ($P = 0.01$), less stearic acid ($P = 0.02$), and a higher 16:1:18:0 ratio ($P = 0.05$) than steers raised to the Japanese endpoint. Plasma α-linolenic acid tended to be higher ($P = 0.06$) in steers raised to the Japanese endpoint.

The diet × endpoint interaction was significant for myristic and myristoleic acid (both $P < 0.01$) and the MUFA:SFA ratio ($P = 0.04$), all of which increased with time on feed in the corn-fed steers but decreased in the hay-fed steers. The three-way interaction of breed, diet, and endpoint was significant for palmitoleic acid and, therefore, the 16:1:18:0 ratio (Table 2). Relative to corn-fed steers, hay feeding decreased plasma palmitoleic acid in Wagyu steers raised to the US endpoint, but had no effect in Wagyu steers raised to the Japanese endpoint. The plasma concentration of palmitoleic acid was reduced in Angus steers only in response to hay feeding to the Japanese endpoint.

3.3. Subcutaneous adipose tissue fatty acid composition

Wagyu s.c. adipose tissue contained less myristic and palmitic acid (both $P = 0.01$) than Angus s.c. adipose tissue, whereas oleic, linoleic, α-linolenic, and 18:2*trans*-10,*cis*-12 conjugated linoleic acid, and total PUFA were greater ($P \leqslant 0.04$) in Wagyu s.c. adipose tissue (Table 3). Wagyu s.c. adipose tissue also tended ($P = 0.08$) to have a greater MUFA:SFA ratio than Angus adipose tissue.

Adipose tissue of corn-fed steers contained higher concentrations of palmitoleic, *trans*-vaccenic, and linoleic acid, more total MUFA and PUFA, and higher 16:1:18:0 and MUFA:SFA ratios than adipose tissue of hay-fed steers, whereas adipose tissue of hay-fed steers contained more stearic and α-linolenic acid and more total SFA (all $P \leqslant 0.05$; Table 3). Oleic acid also tended to be higher ($P = 0.08$) in adipose tissue of corn-fed steers. Feeding cattle to the Japanese endpoint increased the adipose tissue concentrations of all MUFA and the 16:1:18:0 and MUFA:SFA ratios (all $P \leqslant 0.01$). Thus, all indices of monounsaturation of fatty acids increased in cattle fed to the Japanese endpoint, relative to the US endpoint. Conversely, palmitic ($P = 0.07$) and stearic acid ($P < 0.01$), and total SFA ($P < 0.01$), decreased in adipose tissue of cattle raised to the Japanese endpoint.

Adipose tissue concentrations of 18:2cis-9,*trans*-11 CLA tended ($P = 0.07$) to be greater in adipose tissue of cattle raised to the Japanese endpoint, and 18:2*trans*-10,*cis*-12 CLA was significantly greater ($P < 0.01$) in cattle raised to the Japanese endpoint (Table 3). The breed × diet × endpoint interaction also tended ($P = 0.06$) to be significant for 18:2cis-9,*trans*-11 CLA, in that this CLA isomer increased only in adipose tissue of hay-fed Wagyu steers fed to the Japanese endpoint. Hay feeding depressed the s.c. adipose tissue concentration of oleic acid at the US endpoint, but had no effect on oleic acid by the time the steers reached the Japanese endpoint ($P = 0.06$).

There was a high, negative correlation ($R^2 = 0.925$) between concentrations of stearic and palmitoleic acid (Fig. 1). Palmitoleic acid was highest in corn-fed steers and, with the exception of one corn-fed, Wagyu steer, was lowest in hay-fed steers. The very highest concentration of palmitoleic acid was observed in adipose tissue of steers fed corn to the Japanese endpoint.

3.4. Slip points

Neither breed type nor diet affected slip points of lipids extracted from s.c. adipose tissue ($P \geqslant 0.14$; Table 4). Slip points decreased by more than 10 °C (38.7 vs. 28.4 °C) between the US and Japanese endpoints. There was a strong, positive correlation ($R^2 = 0.917$) between the concentration of stearic acid and slip points (Fig. 2). Adipose

Table 3
Fatty acid concentrations (g/100 g total fatty acids) in subcutaneous adipose tissue of Wagyu and Angus steers fed to US and Japanese endpoints

Item	Months on feed/diet								SE					
	US endpoint				Japanese endpoint									
	8 mo/corn		12 mo/hay		16 mo/corn		20 mo/hay			*P*-values				
	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu		Breed	Diet	Endpoint	$D \times E$[a]	$B \times D \times E$[b]
14:0	3.88	3.07	3.72	3.11	3.50	3.62	4.06	2.84	0.12	0.01	0.72	0.79	0.91	0.10
14:1n-5	1.14	1.38	0.88	1.08	2.48	2.34	2.30	1.75	0.14	0.77	0.13	0.01	0.80	0.67
16:0	29.2	28.0	30.7	28.5	28.3	27.6	29.1	26.7	0.34	0.01	0.45	0.07	0.43	0.76
16:1n-7	3.13	4.34	2.49	2.63	7.15	7.07	6.38	5.46	0.41	0.87	0.04	<0.01	0.99	0.92
18:0	17.1	15.1	22.0	20.9	7.89	7.67	9.90	9.11	1.26	0.56	0.05	<0.01	0.30	0.83
18:1*t*11	2.12	1.66	2.63	2.64	1.05	1.27	1.49	1.54	0.13	0.80	<0.01	<0.01	0.29	0.37
18:1n-9	39.8	42.3	34.6	37.3	45.5	46.0	43.3	48.6	1.00	0.05	0.08	<0.01	0.06	0.40
18:2n-6	2.73	2.68	1.68	2.24	2.63	2.92	1.87	2.08	0.09	0.04	<0.01	0.73	0.83	0.16
18:3n-3	0.0	0.10	0.25	0.32	0.06	0.21	0.15	0.20	0.03	0.04	<0.01	0.72	0.03	0.68
18:2*c*9,*t*11	0.30	0.45	0.41	0.42	0.55	0.33	0.52	0.64	0.03	0.81	0.16	0.07	0.40	0.06
18:2*t*10,*c*12	0.04	0.26	0.13	0.27	0.32	0.28	0.26	0.46	0.03	0.02	0.32	<0.01	0.90	0.15
16:1:18:0	0.19	0.44	0.11	0.19	1.01	1.04	0.66	0.60	0.08	0.52	0.02	<0.01	0.33	0.83
SFA[c]	52.3	47.9	59.1	55.2	40.7	40.2	44.6	40.2	1.51	0.09	0.03	<0.01	0.19	0.56
MUFA[c]	44.4	48.5	38.4	41.5	55.7	55.8	52.5	56.5	1.45	0.13	0.04	<0.01	0.16	0.51
PUFA[c]	2.74	2.78	1.93	2.56	2.69	3.13	2.01	2.56	0.09	0.01	<0.01	0.84	0.33	0.14
MUFA:SFA	0.85	1.05	0.65	0.80	1.39	1.40	1.18	1.41	0.06	0.08	0.05	<0.01	0.44	0.39

[a] Diet × endpoint interaction. All breed × diet and breed × endpoint interactions $P > 0.20$.

[b] Breed × diet × endpoint interaction.

[c] SFA = total SFA (14:0 + 16:0 + 17:0 + 18:0 + 18:1*t*11). MUFA = total monounsaturated fatty acids (14:1n-5 + 16:1n-7 + 18:1n-9 + 18:2*c*9,*t*11). PUFA = total polyunsaturated fatty acids (18:2n-6 + 18:3n-3).

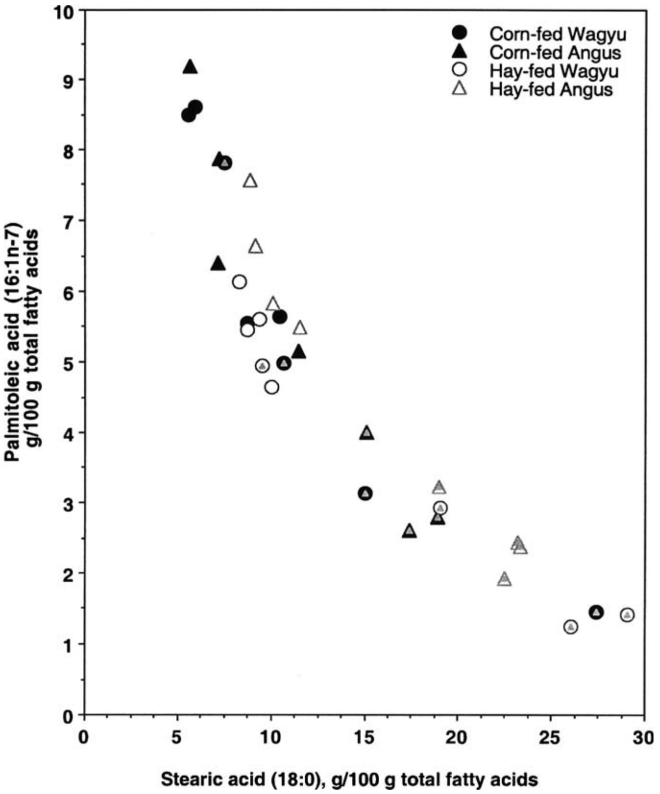

Fig. 1. Palmitoleic acid (16:1n-7) as a function of stearic acid (18:0) in subcutaneous adipose tissue of Wagyu and Angus steers fed corn-based or hay-based diets to US or Japanese endpoints. Closed symbols, corn-fed steers; open symbols, hay-fed steers; circles, Wagyu steers; triangles, Angus steers. Symbols for the cattle raised to the US endpoint contain shaded triangles. $y = 0.015x^2 - 7.96x + 12.32$; $R^2 = 0.925$; $P < 0.001$.

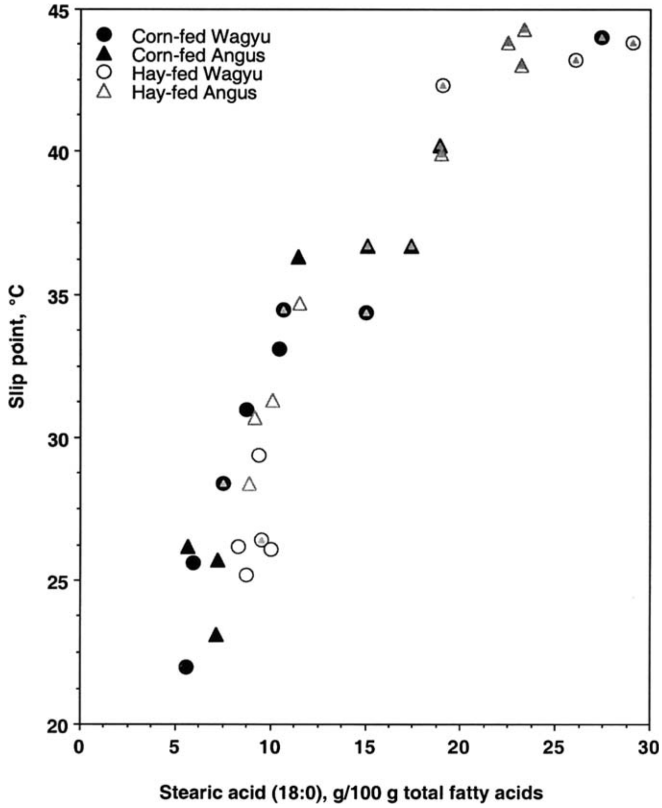

Fig. 2. Slip points as a function of the concentration of stearic acid (18:0) in subcutaneous adipose tissue of Angus and Wagyu steers fed corn-based or hay-based diets to US or Japanese endpoints. Closed symbols, corn-fed steers; open symbols, hay-fed steers; circles, Wagyu steers; triangles, Angus steers. Symbols for the cattle raised to the US endpoint contain shaded triangles. $y = -0.039x^2 + 2.23x + 12.07$; $R^2 = 0.917$; $P < 0.001$.

tissue lipids from cattle of both breed types fed to the Japanese endpoint had the lowest concentrations of stearic acid and consequently the lowest slip points.

3.5. *M. longissimus thoracis* cholesterol

The concentration of cholesterol in the *M. longissimus thoracis* increased ($P = 0.01$) in steers fed to the Japanese endpoint, relative to those fed to the US endpoint (Table 4). There were no effects of breed type ($P = 0.43$) or diet ($P = 0.85$) on *M. longissimus thoracis* cholesterol. There was a significant ($P = 0.03$), though weak ($R^2 = 0.154$) relationship between percentage intramuscular lipid and cholesterol (Fig. 3). There was a stronger ($P = 0.006$; $R^2 = 0.231$) relationship between s.c. oleic acid and *M. longissimus thoracis* cholesterol (Fig. 4).

4. Discussion

We have reported production and carcass characteristics for the cattle used in this study in a separate article (Lunt et al., 2005), and selected results are reported herein. Breed type affected neither overall marbling scores nor USDA quality grades for the Angus (Moderate^{82}; Choice^{86}) and

Table 4
Slip points of lipids from subcutaneous adipose tissue and cholesterol concentrations of *M. longissimus thoracis* of Wagyu and Angus steers fed to US and Japanese endpoints

Item	Months on feed/diet								SE					
	US endpoint				Japanese endpoint									
	8 mo/corn		12 mo/hay		16 mo/corn		20 mo/hay			*P*-values				
	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu	Angus	Wagyu		Breed	Diet	Endpoint	$D \times E$[a]	$B \times D \times E$[b]
Slip point, °C	37.9	35.3	42.8	38.9	27.8	27.9	31.3	26.7	1.29	0.14	0.15	0.01	0.39	0.64
Cholesterol, mg/100 g	72.1	70.8	71.5	68.3	78.4	83.9	78.9	89.3	1.98	0.43	0.85	0.01	0.53	0.64

[a] Diet × endpoint interaction.
[b] Breed × diet × endpoint interaction.

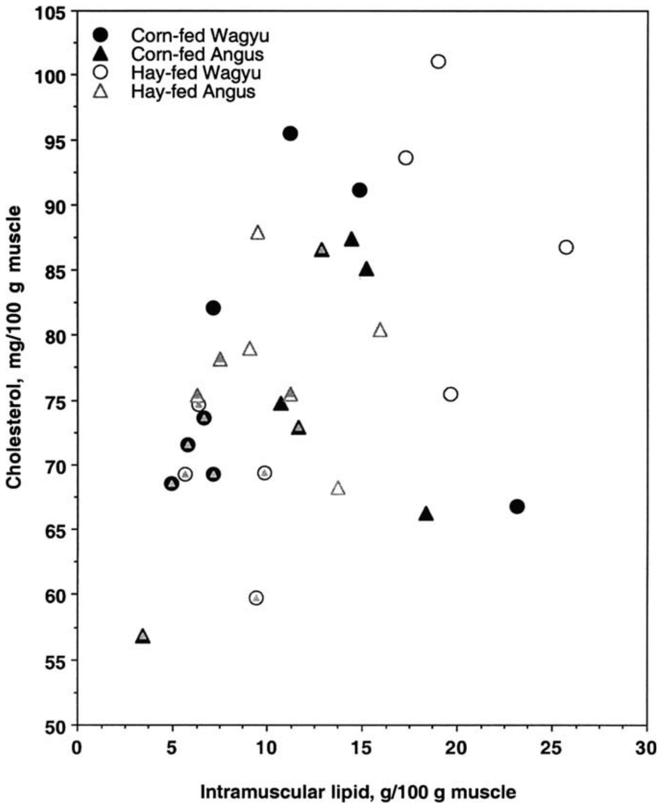

Fig. 3. Relationship between intramuscular cholesterol and intramuscular lipid in *M. longissimus thoracis* of Wagyu and Angus steers fed corn-based or hay-based diets to US or Japanese endpoints. Closed symbols, corn-fed steers; open symbols, hay-fed steers; circles, Wagyu steers; triangles, Angus steers. Symbols for the cattle raised to the US endpoint contain shaded triangles. $y = 0.734x + 68.77$; $R^2 = 0.154$; $P = 0.03$. Data for intramuscular lipid were taken from Lunt et al. (2005).

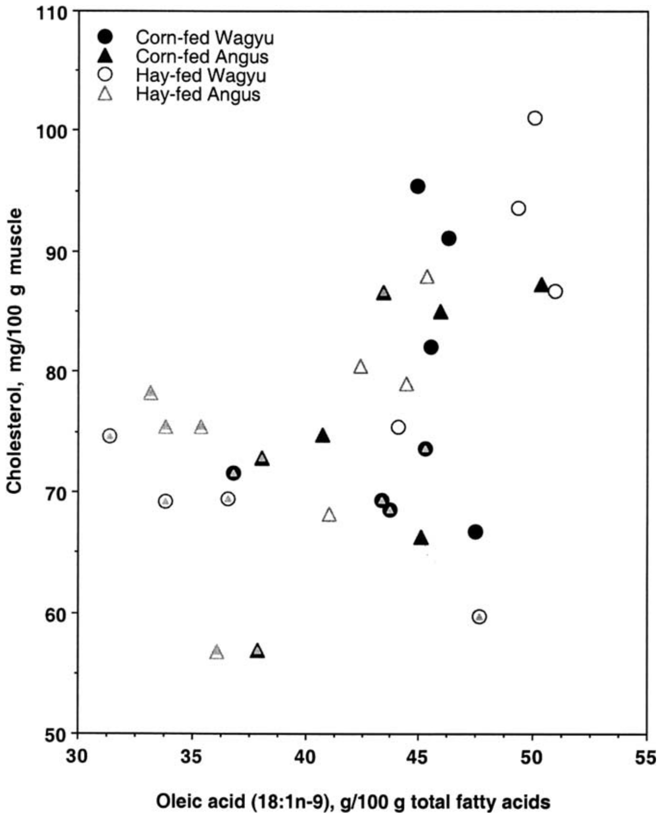

Fig. 4. Relationship between intramuscular cholesterol in *M. longissimus thoracis* and oleic acid (18:1n-9) in s.c. adipose tissue of Wagyu and Angus steers fed corn-based or hay-based diets to US or Japanese endpoints. Closed symbols, corn-fed steers; open symbols, hay-fed steers; circles, Wagyu steers; triangles, Angus steers. Symbols for the cattle raised to the US endpoint contain shaded triangles. $y = 0.955x + 36.39$; $R^2 = 0.231$; $P = 0.006$.

Wagyu steers (Slightly Abundant^{11}; Prime^{03}). Corn-fed steers had significantly greater marbling scores (Slightly Abundant^{51}) than hay-fed steers (Moderate^{46}). Also, steers raised to the Japanese endpoint had higher marbling scores and USDA quality grades (Slightly Abundant^{84}; Prime^{25}) than steers raised to the US endpoint (Moderate^{05}; Choice^{63}). There was a significant breed × endpoint interaction for percentage lipid in the *M. longissimus thoracis*; muscle from Wagyu steers raised to the Japanese endpoint had more extractable lipid (17.2%) than muscle from Angus steers raised to the same endpoint (13.3%) (Lunt et al., 2005). These results were essentially identical to those of our early comparison of forage-fed, Angus and Wagyu steers (Lunt et al., 1993).

In an earlier study, the percentages of oleic acid were 45.2% and 50.2% of total fatty acids in s.c. adipose tissue in Angus and Wagyu steers, respectively, fed a high-roughage diet for 550 d (May et al., 1993). These results are similar to those of the current study for hay-fed Angus and Wagyu steers raised to the Japanese endpoint. Others previously had demonstrated that oleic acid increased with age in feedlot cattle (Huerta-Leidenz et al., 1996; Rule et al., 1997; Waldman, Suess, & Brungardt, 1968), and the results of the current study are consistent with these earlier findings.

It is well documented that Japanese Black and American Wagyu cattle deposit higher concentrations of MUFA in their muscle and adipose tissues than other breed types. Tanaka (1985) reported a higher percentage of oleic acid and a lower percentage of palmitic acid in adipose tissue of Japanese Black steers than in Japanese Shorthorn or Holstein steers. Japanese Black and American Wagyu steers exhibit higher percentages of oleic acid in s.c. and i.m. lipids than Holstein or Angus steers (May et al., 1993; Sturdivant et al., 1992; Zembayashi et al., 1995). The current results are novel in that they indicate that the previously documented differences in oleic acid between Wagyu and Angus steers are expressed regardless of diet or endpoint. Thus, although feeding Wagyu and Angus steers hay-based diets reduced oleic acid, and feeding to the Japanese endpoint increased oleic acid, Wagyu adipose tissue contained a higher concentration of this fatty acid than Angus steers overall.

Alterations in digesta fatty acids may have contributed to the increased unsaturation of s.c. adipose tissue in corn-fed steers raised to the Japanese endpoint. Digesta stearic acid decreased substantially between the US and Japanese endpoints, but only in the corn-fed steers, and a similar tendency was observed for plasma stearic acid. The digesta concentration of *trans*-vaccenic acid also decreased, and linoleic acid increased between the US and Japanese endpoints, again only in corn-fed steers. These observations indicate a depression in the ruminal conversion of linoleic to *trans*-vaccenic acid and ultimately to stearic acid in long-fed steers consuming the corn-based diet. This suggests a reduction with time on feed in those microflora responsible for the isomerization and hydrogenation of linoleic acid in steers consuming the corn-based diet. The lower digesta concentration of stearic acid in corn-fed, Japanese-endpoint steers was not expected, and warrants further investigation.

We did not expect to find breed differences for any of the digesta fatty acids, yet myristoleic, *trans*-vaccenic, and α-linolenic acid were higher in digesta of Wagyu steers than in Angus steers. The Angus and Wagyu weaned steers were purchased from different suppliers, so initial differences in digesta fatty acid composition at weaning would have been expected. However, after a minimum of 8 mo of feeding at the Texas A&M University Research Center at McGregor, initial differences between breed types in ruminal composition and microflora should have been eliminated. The higher concentration of α-linolenic acid in Wagyu digesta ultimately was reflected in the adipose tissue; Wagyu s.c. adipose tissue had a higher concentration of α-linolenic acid than Angus s.c. adipose tissue.

There was a strong, negative correlation between palmitoleic acid and stearic acid for the lipid samples analyzed by Smith et al. (1998). This relationship was shown graphically in a recent review (Smith, Smith, & Lunt, 2004), and is confirmed by the results of the current study (Fig. 2). It is remarkable that such a strong relationship occurs between palmitoleic acid and stearic acid, regardless of breed type, age, or diet. Because palmitoleic acid occurs at low levels in the diet, its concentration in adipose tissue is dictated primarily by the activity of stearoyl-CoA desaturase (or Δ^9 desaturase). The high, negative correlation between palmitoleic acid and stearic acid further suggests that the concentration of stearic acid also is dictated by the activity of stearoyl-CoA desaturase; adipose tissues with high desaturase activity exhibit concomitantly high concentrations of palmitoleic acid and low concentrations of stearic acid. Similar results were reported by Mitsuhashi, Mitsumoto, Yamashita, and Ozawa (1988), who first demonstrated that the proportion of MUFA increased with age in adipose tissues of Japanese Black steers.

In a recent review, Wood et al. (2004) demonstrated the positive correlation lipid melting points and percentage of stearic acid in lamb s.c. adipose tissue. The current study provides additional support for a strong relationship between stearic acid and slip points in bovine adipose tissue. Variation in fatty acid saturation dictates fat firmness, which in turn affects the economics of meat processing and consumer acceptance of meat (Perry et al., 1998). Multivariate analysis that includes melting point in the model (instead of sire breed) indicates that fatty acid composition is related to melting point and environment (Perry et al., 1998). Similarly, Smith et al. (1998) demonstrated large increases in melting points (estimated as slip points) as the percentage of stearic acid increased in s.c. adipose tissue lipids in cattle raised in Japan and Australia. Adipose tissue lipids from Japanese Black cattle raised in Japan contained less than 8% stearic acid, with an average slip point of 22.8 °C. Mitsuhashi et al. (1988) previously reported that, in Japanese Black cattle, the melting point of adipose tissue lipids decreased from 35.5 °C in 14-mo-old steers to 21.2 °C in 28-mo-old steers; they suggested that melting point may be controlled by Δ^9 desaturase. Adipose tissue lipids of other breed types raised in Australia contained over 25% stearic acid, with an average slip point of 45.1 °C (Smith et al., 1998). The Australian cattle had been fed a grain-based diet (which did not include corn), supplemented with 10% whole cottonseed; we suggested that sterculic acid contained in the whole cottonseed depressed Δ^9 desaturase activity (Smith et al., 1998; Yang, Larsen, Smith, & Tume, 1999). However, we cannot rule out the possibility that forages unique to the Australian production environment also contributed to the high stearic acid and slip points. The current study is unique in that the major factors that affect fat firmness, breed type, age, and diet, were controlled within the same study.

We did not anticipate that s.c. adipose lipids from Angus steers would have 16:1:18:0 ratios as high, nor slips points as low, as those from Wagyu steers. However, corn-fed Angus steers raised to the Japanese endpoint accumulated adipose tissues lipids that were remarkably unsaturated. These results confirm the impact of both time on feed and grain feeding in producing more unsaturated, softer fat. It also was unexpected that lipids from one of the corn-fed, US endpoint Wagyu steers would have such a high slip point and low 16:1:18:0 ratio. Otherwise, the highest slip points and lowest 16:1:18:0 ratios were observed in hay-fed, US endpoint steers.

The cholesterol concentrations of bovine muscle and adipose tissue have proven resistant to nutritional (Eichhorn et al., 1986; Rule et al., 1997) and breed effects (Eichhorn et al., 1986; Wheeler, Davis, Stoecker, & Harmon, 1987), but are directly related to marbling score (i.e., amount of intramuscular lipid). Rhee, Dutson, Smith, Hostetler, and Reiser (1982) demonstrated that as US marbling scores increased from Practically Devoid (2.73 g lipid/100 g muscle) to Moderately Abundant (12.08 g lipid/100 g muscle), intramuscular cholesterol increased from 51.77 to 64.74 mg/100 g of muscle [cholesterol = 0.87 * (intramuscular lipid %) + 54.73]. The regression equation derived from the current study contained a lesser slope (0.734 mg cholesterol/g intramuscular lipid) and a higher intercept (68.77 mg cholesterol; Fig. 3). The reduction in slope was caused primarily by unusually low cholesterol values for some of the muscle samples from steers fed corn to the Japanese endpoint.

As reported in Lunt et al. (2005), the highest concentration of *M. longissimus thoracis* intramuscular lipid (20.4 g/100 g muscle) was observed in Wagyu steers fed to the Japanese endpoint, and it was muscle from these steers that contained the greatest concentration of cholesterol (89.3 mg/100 g muscle; Fig. 3). Based on the regression equation of Rhee et al. (1982), we would have predicted an average of 72.5 mg cholesterol/100 g of muscle, far below the observed cholesterol concentration. The greater than predicted accumulation of cholesterol in *M. longissimus thoracis* of hay-fed, Japanese-endpoint steers may have been related to the concentration of oleic acid in the muscle. Fatty acid composition of muscle lipids was not measured in this study. However, we previously reported that s.c. and marbling adipose tissue of 1/2–7/8 American Wagyu steers contained 47.1% and 46.4% oleic acid, respectively, whereas in purebred Japanese Black cattle, s.c. and marbling adipose tissues contained 55.2% and 54.1% oleic acid, respectively (Sturdivant et al., 1992). Thus, concentrations of oleic acid are similar between these two depots.

As indicated in Fig. 4, there was a highly significant and positive relationship between the concentration of s.c. adipose tissue oleic acid and *M. longissimus thoracis* cholesterol. The relationship was only apparent in cattle raised to the Japanese endpoint, in which the highest concentrations of oleic acid and cholesterol were observed. In liver (Goodman, Deykin, & Shiratori, 1964) and intestinal mucosa of rodents (Haugen & Norum, 1976), oleic acid is the preferred substrate for the synthesis of cholesterol esters via acyl-CoA: cholesterol acyl transferase. Although this has not been documented for adipose tissue from any species, oleic acid may similarly promote cholesterol ester synthesis and accumulation in marbling adipose tissue. If this is true, then any production practice that promotes an increase in the concentration of oleic acid (grain feeding or feeding to heavier weights) also would elevate cholesterol beyond that predicted by the increase in intramuscular lipid.

5. Conclusions

The results obtained in the current study reject our hypothesis that fatty acid composition of Wagyu and Angus adipose tissue lipids would be similar when the cattle were fed to the US endpoint. Instead, Wagyu adipose tissue consistently contained higher concentrations of oleic acid and other monounsaturated fatty acids, regardless of diet or endpoint. The reduction in digesta stearic acid in corn-fed steers raised to the Japanese endpoint may have contributed to the lesser amounts of stearic acid, hence lower slip points, observed in the adipose tissue of these animals. Of the three factors tested in this study (breed type, diet, and slaughter endpoint), endpoint had the strongest and most consistent effect on fatty acids of s.c. adipose tissue, and on cholesterol concentrations and melting points of lipids from *M. longissimus thoracis*.

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