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Silage-concentrate finishing of bulls versus silage or fresh forage finishing of steers: Effects on fatty acids and meat tenderness

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ORIGINAL ARTICLE

Silage-concentrate finishing of bulls versus silage or fresh forage finishing of steers: Effects on fatty acids and meat tenderness

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Abstract
The objective of this trial was to assess meat quality in terms of tenderness and fatty acid (FA) composition in *M. longissimus dorsi* and *M. gluteus medius* from bulls finished on *ad lib* silage-concentrates (SIL:CON) vs. steers fed *ad lib* silage (FF) or restricted silage and unrestricted grazing (RES-F). Warner-Brazler shear force value day 1 was lowest for the FF steers ($p < 0.05$). Myofibril fragmentation index (MFI) values were similar after seven days of ageing, showing that ageing compensated for differences in meat tenderness associated with feeding programmes. Total monounsaturated FAs and 18:1c-9 levels were higher in the steer tissue ($p < 0.001$). The SIL:CON bulls had higher polyunsaturated n-6 fatty acids and 18:2n-6 level ($p < 0.001$). Polar lipid 18:2n-6 and n-6 levels were higher for FF than for RES-F steers, whereas the 18:3n-3 level was higher for RES-F than for FF steers ($p < 0.001$). The n-6/n-3 ratio was lowest for the FF steers and highest for the SIL:CON bulls ($p < 0.001$).

Keywords: *Myofibrial fragmentation index, semi-natural grassland, Warner-Bratzler shear force.*

Introduction

Through changes in agriculture land usage in Europe during the last century, semi-natural grasslands and their species diversity have come under increasing threat (Luoto et al. 2009). In Sweden, for example, less than 0.5 million ha of semi-natural grasslands remain, with an estimated loss of 62% of the semi-natural pasture since the early 1920s (Kumm 2004). Currently, there is growing interest in Sweden towards the use of extensive beef finishing systems in an effort to utilize semi-natural grasslands and maintain an open landscape. Grazing these grasslands promotes nature conservation and revitalization of the plant diversity and, through environmental incentive programmes, provides additional financial payment to producers. In Europe there is also a growing public opinion towards animal welfare and producing animals in a way that allows the animals to express their natural behaviour. Extensive grazing systems are regarded as providing better welfare and health for the animals, with less therapeutic interventions than confined feeding systems (Steen et al. 2003). Animal performance from extensive grazing systems is generally poor in terms of feed conversion and average daily gain; however, the feed input costs are minimal in comparison to feedlot finishing (French et al. 2001). In addition, grazing optimizes land usage in arable regions where conventional crop production is not practical, thus providing diversified income for producers.

Regardless of production programmes, the marketability of the meat relies on the consumers' product acceptance and perceived enjoyment from the eating experience. Dikeman et al. (2005) identified the most important factors that govern the satisfaction from a meat eating experience as tenderness, juiciness and flavour. While a number of factors contribute to meat quality, diet has been identified as the most influential

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external component influencing the flavour of beef (Melton 1990). Meat quality from forage finishing systems has been criticized in terms of consumer acceptance due to negative organoleptic properties. Common complaints include less tender meat, darker meat, less marbling and more yellowness of the fat, which is present either as intermuscular or as intramuscular deposits (Varela et al. 2004). A greater phospholipid concentration has been negatively associated with meat flavour, whereas intramuscular triacylglycerols have a positive influence on meat flavour (Dryden and Maechello 1970). Calkins and Hodgen (2007) proposed that a person's eating preference was highly influenced by meat eating experiences during childhood. Such an influence was supported by the preference towards corn-based feedlot finished beef in the United States over Argentinean grass-finished beef (Killinger et al. 2004) or Canadian barley-finished beef (Sitz et al. 2005). On the positive side, regional preferences for forage versus concentrate finished meat exists and is highly dependent on traditional farming practices inherent to the region. Within Europe, preference for feedlot-finished beef was found to be lower than that for pasture-finished beef, which is in line with European beef production practices (Realini et al. 2009). As reviewed by Priolo et al. (2001), European consumers have shown a taste preference towards beef produced under low-intensity production, with favourable correlations towards grassy, milky and sour tastes. The FA composition of beef has a significant influence on consumer acceptability, with both milky and sour flavours being correlated to higher levels of 18:3n-3 (Melton et al. 1982).

Many FAs naturally found in meat are considered to have beneficial properties for human health, in particular n-3 FA (Williamson et al. 2005). Givens et al. (2006) listed anti-atherogenic and anti-inflammatory effects as health benefits for humans associated with increasing the n-3 content of our diet along with feeding practices aimed at increasing the n-3 level and reducing the n-6/n-3 ratio in beef tissue. Forage feeding tends to increase the proportion of 18:3n-3, as well as increase the proportion of its elongase/desaturase products, in particular 20:5n-3 compared with grain feeding (Wood et al. 2008). Additional factors such as the function of the muscle, thus the proportion of "red" or "white" muscle fibre, also has a slight influence on the FA composition (Wood et al. 2003).

Previous studies have compared meat tenderness and FA composition of steers (French et al. 2000, 2001; Fredriksson Eriksson and Pickova 2007) and bulls (Nuernberg et al. 2005; Huuskonen et al. 2010). However, comparisons of meat quality aspects between concentrate-fed bulls and extensively reared steers is currently lacking. The objective of this study was to investigate the effects of extensive forage finishing steer systems compared with indoor concentrate-finishing of bulls on meat tenderness and FA profile.

Materials and methods

Animals

Three groups of newly weaned calves, 75% Charolais breed (initial average age, 7.4 months [standard deviation, SD, 0.4 months], and weight, 297 kg [SD 30 kg]), were moved indoors for the winter housing period between October and April. Animals groups included concentrate-fed bulls (SIL:CON bulls, $n = 9$), full-fed forage steers (FF steers, $n = 9$) and restricted-fed forage steers (RES-F steers, $n = 11$). Individual animals were slaughtered once they reached the respective live weights designated for the finishing group. The SIL:CON bull finishing programme consisted of a 45:55 dry matter (DM) grass-clover silage:barley ration fed *ad lib* (metabolisable energy [ME], 11.9 MJ ME/kg DM; crude protein [CP], 136 g CP/kg DM; neutral detergent fibre [NDF], 340.7 g NDF/kg DM). The SIL:CON bulls were slaughtered at the end of one winter housing period at a live weight of 675 kg. The FF steers received *ad lib* grass-clover silage during a first and a second winter housing period and were on pasture from April until October. The feed value of the silage fed during the second winter housing period was 10.6 MJ ME/kg DM, 159 g CP/kg DM and 530 g NDF/kg DM. The FF steers were slaughtered at the end of the second winter housing period at a live weight of 675 kg. The RES-F steers were fed a restricted grass-clover silage diet during two winter periods and grazed unrestricted during two summer periods. The restricted indoor finishing programme was based on the intake of the FF steers at equivalent live weights at 80% and 90% restriction during the first and second winter housing periods, respectively. The FF and RES-F steers grazed the same pasture during the summer period, while the RES-F steers grazed an additional summer period the following year. The RES-F steers were slaughtered directly from pasture after at least four months of grazing (9.5 MJ ME/kg DM, 145 g CP/kg DM, 555 g NDF/kg DM) during the second pasture period at a live weight of 713 kg to compensate for gut-fill. The pasture used for the steer groups consisted of unfertilized, semi-natural pasture dominated by *Deschampsia cespitosa*. All animals received recommended allotments of vitamins and minerals

according to Swedish recommendations (Spörndly 2003). Samples of offered feed were collected weekly and pooled for lipid analysis. Representative pasture clippings were collected monthly from areas identified as having been previously grazed.

Tissue sample collection

Carcass conformation and fatness were graded at slaughter by the standard EUROP system expanded to 15 numerical levels, for statistical comparison. Meat samples (>500 g) from the anterior end of the *M. longissimus dorsi* (LD) defined by International Meat Purchase Specifications (IMPS) as short-loin, product code #173 (USDA 2010), were collected 24 h after slaughter and stored at -20°C to be used for Warner-Bratzler shear force (WB-SF) analysis. Separate samples from the LD and *M. gluteus medius* (GM), described by IMPS as top sirloin butt cap removed, product code #184B (USDA 2010), muscles were collected, aged seven days and then stored at -80°C to be used for FA and Myofibril fragmentation index (MFI) analysis. Because of an electrical failure at the research facility, aged samples of LD and GM muscle destined for WB-SF analysis were compromised and deemed unsuitable for analysis.

Warner-Bratzler shear force

Shear force samples were thawed 24 h at 5°C before heat treating in a 72°C water bath to an internal temperature of 70°C. Samples were cooled in running water to room temperature. The WB-SF analysis as described by Honikel (1998) was performed by cutting the samples into $1 \times 1 \times 3$ cm strips parallel to the muscle fibre. Values for each measurement were based on the average of 12 samples from each animal measured perpendicular to the muscle fibre using a Texture Analyser HD 100 (Stable Micro Systems Inc., UK) equipped with a WB-SF blade. Blade dimensions include a cutting area of 11×15 mm with a blade 1 mm thick and a speed of 0.83 mm per second. Total and maximum force was used to assess meat tenderness differences between finishing programs. Total force represents the cumulative force necessary for the blade to pass through the sample, whereas maximum force represents the peak force exerted during the analysis.

Myofibrial fragmentation index

Determination of the MFI followed a modified method described by Olson et al. (1976). Briefly, duplicate 0.5 g meat samples were homogenized at 11,000 rpm for 30 seconds in 15 ml cold buffer solution with pH 7.0 (0.1 M KCl, 0.025 M KPO_4, Merck, Germany; 0.001 M EDTA-N_2, Sigma-Aldrich, Sweden). The homogenate was filtered (1 mm mesh) to remove connective tissue. The filter was then rinsed with 5 ml cold buffer. The filtrate was centrifuged at 1000 *g* for 10 min at 4°C (Sorvall super T21, Kendro Lab. Prod, Germany). The supernatant was aspirated, and the remaining pellet was re-suspended in 20 ml cold buffer, vortexed and then centrifuged as before. The supernatant was aspirated, and the recovered pellet was re-suspended in 40 ml cold buffer. Protein concentration was determined using a Peirce BCA protein assay kit (Bio-Rad Laboratories, Sweden). The suspension was diluted with cold buffer to a concentration of 0.5 mg per ml. Absorbance was measured using a spectrophotometer (UV-2401 PC, Shimadzu, Sweden) at a wavelength of 540 nm.

Lipid analysis

Feed lipid extract. Pooled samples of individual feed ingredients collected throughout the trial period were analysed in duplicate following a modified Folch et al. (1957) method. Briefly, concentrate samples were ground through a 0.5 mm screen, while silage and pasture samples were cut into 0.5–1 cm lengths. Feed samples (2.0 g) were soaked in 8 ml H_2O for 12 h and then homogenized (Ultra Turrax T25, Janke & Kunkel IKA Werke, Germany) 3×30 s in 150 ml chloroform:methanol (2:1 v/v). Non-lipids were removed by adding 40 ml (0.11 M) of NaCl solution, the organic solvent was separated and the lipid was determined gravimetrically.

Tissue lipid extraction. Tissue samples were separated from visible intermuscular adipose tissue and extracted for intramuscular lipid content. Lipid extraction followed a modified Hara and Radin (1978) procedure by homogenizing 5 g of fresh muscle tissue in 75 ml of hexane:isopropanol (3:2 v/v) using an Ultra-Turrax. To remove non-lipids, 32.5 ml of 6.67% Na_2SO_4 was added to the homogenate. The solvent was evaporated and lipid determined gravimetrically.

Lipid class analysis. Lipid classes of total lipid were analysed using thin layer chromatography (TLC). As a stationary phase, glass TLC plates pre-coated with silica gel (20×10 cm; Silica gel 60; 0.20 mm layer, Merck, Germany) were used. The analysis was performed according to Olsen and Henderson (1989) with slight modifications. Lipid samples

were applied at a concentration of 1 μg/μl on a TLC plate by a CAMAG TLC Sampler 4 (Camag, Switzerland) in 2 mm bands with an application speed of 250 nl per second; 10 mm between each band, using nitrogen as the spray gas. The plate developer solution was modified to hexane:diethyl ether:glacial acetic acid (85:15:2 v/v/v) to facilitate lipid class separation. Using a Camag TLC scanner 3 (Camag, Switzerland), plates were scanned at a speed of 20 mm per second and a data resolution of 100 μm per step with a slit dimension of 6.0×0.45 mm at a wavelength of 350 nm. Identification of lipid classes was made by comparison to external standard TLC 18-4A (Nu-Chek Prep, USA). The Savatisky-Golay 7 mode and manual baseline correlation were used for data filtering.

Separation of polar and neutral lipids. Tissue neutral and polar lipids were separated by solid phase extraction (SPE). Tissue total lipids (5 mg) were dissolved in 1.5 ml of chloroform. The samples were applied to 500 mg silica SPE columns (Isolute SI, IST, UK) pre-developed with 4 ml of hexane. Neutral lipids were extracted by applying 10 ml of chloroform:2-propanol (2:1 v/v) followed by extraction of polar lipids by using 12 ml of methanol. The solvent was evaporated under N_2. The remaining lipid was re-suspended in hexane and stored at −80°C until FA analysis.

Preparation of fatty acid methyl esters

Polar and neutral lipid fractions were methylated following the procedures of Appelqvist (1968). To each sample, 15 μg of methyl-heneicosanoic acid (Larodan Fine Chemicals, Sweden) was added as an internal reference. First, 2 ml of 0.01 M NaOH in anhydrous methanol was added, shaken and placed in a 60°C heating block for 10 min. Next, 3 ml of 20% BF_3 reagent (Merck, Germany) was added and the samples were reheated for 10 min. Once cooled to room temperature, 2 ml of 20% NaCl and 2 ml of hexane were added. The test tubes were shaken and centrifuged at 600 *g* for 5 min to facilitate the separation of the layers. The fatty acid methyl esters (FAME) were evaporated under nitrogen gas, solved in hexane and stored at -80°C until analyzed.

The FAME were analysed with a gas chromatograph CP3800 (Varian AB, Sweden) equipped with flame ionization detector (FID) using a 50 m BPX 70 fused silica capillary column (ID 0.22 mm, 0.25 μm film thickness; SGE, USA), equipped with an auto-injector with a split ratio set at 1:5. The column temperature programme began at 130°C, held for 5 min, then increased 2°C per minute from 158°C to 220°C and then held for 8 min. Injector and FID temperatures were 230°C and 250°C, respectively. Identification of the FA was achieved by comparing the sample retention times to that of standard reference sample GLC-461 (Nu-Chek Prep Inc., USA). The carrier gas was helium (22 cm per second, flow rate 0.8 ml per minute), and nitrogen was used as the make-up gas. Peak areas were integrated using Star Chromatography Workstation software version 5.5 (Varian AB, Sweden). The percentages of FA were calculated as 100% identified FA.

Statistical analysis

The finishing programme effect was analysed by using one-way analysis of variance (ANOVA) for comparison of carcass characteristics, WB-SF and MFI. Lipid class composition and total and polar FA profiles of the tissues were analysed by using one-way ANOVA with finishing programme as the main effect. Comparisons between LD and GM tissues within the finishing programme for lipid class and FA profile were tested separately by one-way ANOVA using animal as a random variable. All statistical analysis used the MIXED procedure of SAS v9.1 (SAS Institute Inc., Cary, NC, USA).

Results

The average daily gain from weaning to slaughter for the different finishing programmes was as follows: SIL:CON bulls — 1.76 kg per day, FF steers — 0.74 kg per day, RES-F steers — 0.60 kg per day. The FA profile of the individual feed ingredients can be found in Table I.

Carcass characteristics

Carcass characteristics presented in Table II show that the RES-F steers had a higher live weight at slaughter than the SIL:CON bulls and FF steers ($p < 0.001$). However, the carcass weights did not differ between the SIL:CON bulls and RES-F steers. The FF steers had a slightly smaller carcass weight ($p < 0.001$). The SIL:CON bulls had a higher conformation score than did the two steer groups ($p < 0.001$), whereas fat coverage of the carcass did not differ between the finishing programmes.

Tenderness measurements

For meat samples collected at day 1, the total force values (Table III) indicated that the SIL:CON bulls and RES-F steers were similar but had higher ($p < 0.05$) values than the FF steers. Maximum force

Table I. Fatty acid profile (% FAME, SD) of feeds fed during the final four months of the finishing period for the bulls fed *ad lib* silage:concentrates (45:55 DM, SIL:CON bull) and steers fed *ad lib* silage (FF steer) and steers grazing pasture (RES-F steer).

	SIL:CON bull				FF steer		RES-F steer	
	Barley	SD	Silage	SD	Silage	SD	Pasture	SD
Lipid%, as-fed	1.2	0.25	0.9	0.09	1.0	0.47	0.7	0.22
12:0	0.0	0.00	0.4	0.07	0.3	0.02	0.3	0.07
14:0	0.2	0.07	0.9	0.33	0.6	0.01	0.6	0.17
16:0	20.7	0.48	16.4	0.38	14.2	0.36	14.5	1.43
16:1c-9	0.1	0.01	0.3	0.15	0.3	0.06	0.3	0.15
18:0	1.1	0.13	2.0	0.27	1.3	0.02	1.9	0.62
18:1c-9	16.1	3.19	3.8	0.31	2.3	0.29	4.9	2.01
18:2n-6	53.9	1.89	13.2	2.52	15.3	0.27	14.0	0.76
18:3n-3	5.5	0.39	46.3	0.68	50.2	0.90	53.6	5.02
20:0	0.2	0.03	0.6	0.07	0.6	0.01	0.5	0.12
22:0	0.1	0.01	0.9	0.03	0.7	0.02	0.4	0.10
SFA	22.3	0.72	21.1	0.25	17.7	0.42	18.3	2.18
MUFA	16.3	3.18	4.1	0.16	2.5	0.22	5.3	2.07
PUFA	59.4	2.29	59.5	3.21	65.5	1.17	67.6	5.10
18:2n-6/18:3n-3	9.9	0.36	0.3	0.05	0.3	0.00	0.3	0.03

Note: FAME, fatty acid methyl esters; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid; SD, standard deviation.

did not differ between the animals from the different finishing programmes. The MFI values were similar in LD and GM tissue between the finishing programmes following seven days of ageing.

Lipids

Lipid content. The LD and GM tissue lipid content and class composition are shown in Table IV. The lipid content in both LD and GM tissue had a similar finishing programme–related response, however, the content was significantly different only within the GM tissue, with the FF steers and RES-F steers being similar, both having a greater content than the SIL:CON bulls ($p < 0.001$). In both LD and GM tissue, the SIL:CON bulls had higher cholesterol and free FA levels and a lower triacylglycerol level ($p < 0.01$). In addition, in the GM tissue, the SIL:CON bulls had a higher phospholipid level ($p < 0.001$). For each finishing programme, the LD and GM tissues had a similar lipid class profile, except for the lower amount of free FAs in the LD tissue (statistical results not shown).

Fatty acid profile of total lipid. The effect of the finishing programme on intramuscular FA composition

Table II. Carcass characteristics from bulls fed *ad lib* silage: concentrates (45:55 DM, SIL:CON bull) and steers fed *ad lib* silage (FF steer) and steers grazing pasture (RES-F steer) during the finishing period.

	SIL:CON bull ($n=9$)	FF steer ($n=9$)	RES-F steer ($n=11$)	SEM	p
Age, months	13.8^{C}	23.4^{B}	30.3^{A}	0.310	0.000
Live weight, kg	675^{B}	675^{B}	713^{A}	5.495	0.000
Carcass weight[a], kg	397^{A}	358^{B}	385^{A}	4.304	0.000
Dressing,%	58.8^{A}	53.1^{B}	54.0^{B}	0.570	0.000
Conformation[b]	10.2^{A}	7.4^{B}	6.8^{B}	0.344	0.000
Fat class[c]	5.9	7.2	6.4	0.375	0.064

[a]Carcass weight, –2% shrink.
[b]Conformation- EUROP grading system describing muscle definition, 10 = U– and 7 = R–;higher number means more muscling.
[c]Fat class- EUROP grading system describing fat cover, 6 = 2+ and 7 = 3–; higher number means thicker fat cover.
[A–C]Different letters within rows indicate significant difference ($p < 0.05$).

Table III. Warner-Bratzler shear force (WB-SF) measurements of *M. longissimus dorsi* (LD) aged one day and myofibrial fractionation index (MFI) measurements of LD and *M. glutius medius* (GM) aged seven days from bulls fed *ad lib* silage:concentrates (45:55 DM; SIL:CON bull) and steers fed *ad lib* silage (FF steer) and steers grazing pasture (RES-F steer) during the finishing period.

	SIL:CON bull	FF steer	RES-F steer	SEM	p
WB-SF[a] aged 1 day	($n=4$)	($n=6$)	($n=11$)		
Max (N)	61.9	47.6	62.0	6.158	0.128
Total (N mm)	344^{A}	242^{B}	315^{A}	26.38	0.029
MFI, aged 7 days	($n=9$)	($n=9$)	($n=11$)		
LD	132	125	130	4.763	0.570
GM	154	149	153	3.378	0.542

[a]Shear force measurements based on samples collected at processing using limited number of animals.
[A–B]Different letters within rows indicate significant difference ($p < 0.05$).

Table IV. Lipid content (% wet tissue) and lipid classes from bulls fed *ad lib* silage:concentrates (45:55 DM; SIL:CON bull) and steers fed *ad lib* silage (FF steers) and steers grazing pasture (RES-F steer) during the finishing period within *M. longissimus dorsi* (LD) and *M. gluteus medius* (GM).

	LD					GM				
	SIL:CON bull ($n=9$)	FF steer ($n=9$)	RES-F steer ($n=11$)	SEM	p	SIL:CON bull ($n=9$)	FF steer ($n=9$)	RES-F steer ($n=11$)	SEM	p
Lipid,%	2.28	3.25	3.00	0.478	0.363	1.70^{B}	2.64^{A}	2.36^{A}	0.158	0.001
Phospholipid	25.0	20.4	19.1	1.833	0.079	22.5^{A}	18.0^{B}	18.3^{B}	0.842	0.001
Cholesterol	14.5^{A}	11.2^{B}	9.43^{B}	0.718	0.000	13.3^{A}	9.77^{B}	9.88^{B}	0.444	0.000
Free fatty acids	5.74^{A}	3.37^{B}	3.63^{B}	0.541	0.010	9.91^{A}	6.16^{B}	6.38^{B}	0.617	0.000
Triacylglycerols	54.8^{B}	62.7^{AB}	67.9^{A}	2.748	0.008	54.3^{B}	66.0^{A}	65.5^{A}	1.626	0.000

$^{A–B}$Different letters within a row and within a muscle are significantly different ($p<0.05$).

of total lipid in LD and GM tissue is presented in Table V. The overall saturated fatty acid (SFA) level was equivalent between all finishing programmes in both LD and GM tissues. Among the individual SFA, only 16:0 indicated a finishing programme difference. In the GM tissue, there was a higher proportion of 16:0 in the FF steers than in the RES-F steers ($p<0.05$). In the LD tissue, the proportion of 16:0 was higher in the FF steers than in the SIL:CON bulls and RES-F steers ($p<0.01$).

The overall monounsaturated fatty acid (MUFA) level followed the same pattern within both tissues, being lower in the SIL:CON bulls ($p<0.05$) compared with the FF steers and RES-F steers. Among the individual MUFA, the 16:1c-9 proportion in both tissues was higher in the FF steers and RES-F steers than in the SIL:CON bulls ($p<0.001$). In the GM tissue, the 18:1c-9 proportion was highest in the FF steers followed by the RES-F steers, with the SIL:CON bulls having the lowest proportion ($p<0.001$). Within the LD tissue, the 18:1c-9 proportion was similar in the FF steers and RES-F steers, both being higher than in the SIL:CON bulls ($p<0.001$). The 18:1t-11 proportion was highest in

Table V. Total lipid fatty acid profiles (% identified FAME) of bulls fed *ad lib* silage:concentrates (45:55 DM; SIL:CON bull), steers fed *ad lib* silage (FF steer) and steers grazing pasture (RES-F steer) during the finishing period within *M. longissimus dorsi* (LD) and *M. gluteus medius* (GM).

	LD					GM				
	SIL:CON bull ($n=9$)	FF steer ($n=9$)	RES-F steer ($n=11$)	SEM	p	SIL:CON bull ($n=9$)	FF steer ($n=9$)	RES-F steer ($n=11$)	SEM	p
14:0	2.00	2.30	2.22	0.156	0.413	1.71	1.84	1.74	0.125	0.749
16:0	28.5^{B}	29.9^{A}	28.0^{B}	0.386	0.005	26.6^{AB}	27.1^{A}	25.6^{B}	0.426	0.046
16:1c-9	2.49^{B}	3.19^{A}	3.53^{A}	0.190	0.002	2.23^{B}	2.66^{A}	2.68^{A}	0.110	0.013
18:0	16.2	14.7	14.3	0.802	0.221	17.6	15.9	16.8	0.508	0.104
18:1t-11	0.96^{C}	1.64^{B}	2.36^{A}	0.156	0.000	0.83^{C}	1.74^{B}	2.28^{A}	0.146	0.000
18:1c-9	31.9^{B}	36.7^{A}	36.7^{A}	0.905	0.001	30.5^{C}	36.3^{A}	33.7^{B}	0.685	0.000
18:2n-6	7.88^{A}	2.26^{B}	2.57^{B}	0.803	0.000	9.06^{A}	3.22^{B}	4.47^{B}	0.538	0.000
18:3n-3	1.51	1.37	1.45	0.147	0.814	1.67^{B}	1.69^{B}	2.11^{A}	0.122	0.025
CLAc-9,t-11	0.30^{B}	0.39^{B}	0.56^{A}	0.040	0.000	0.28^{B}	0.45^{A}	0.49^{A}	0.035	0.001
20:4n-6	1.69^{A}	0.80^{B}	0.83^{B}	0.210	0.009	2.19^{A}	1.18^{B}	1.48^{B}	0.152	0.000
20:5n-3	0.57	0.58	0.57	0.095	0.997	0.75	0.86	1.04	0.091	0.081
22:5n-3	0.88	0.78	0.63	0.128	0.388	1.13	1.11	1.02	0.091	0.631
SFA	47.8	48.5	46.2	1.020	0.254	47.0	46.4	45.7	0.696	0.391
MUFA	38.0^{B}	44.0^{A}	45.6^{A}	1.004	0.000	35.9^{B}	43.2^{A}	41.2^{A}	0.750	0.000
PUFA	13.1^{A}	6.4^{B}	6.8^{B}	1.375	0.003	15.5^{A}	8.8^{B}	11.0^{B}	0.965	0.000
PUFA/SFA	0.29^{A}	0.13^{B}	0.15^{B}	0.034	0.008	0.34^{A}	0.19^{B}	0.24^{B}	0.025	0.002
n-6[a]	9.90^{A}	3.25^{B}	3.64^{B}	1.051	0.000	11.69^{A}	4.68^{B}	6.38^{B}	0.706	0.000
n-3[b]	2.90	2.73	2.65	0.366	0.890	3.55	3.66	4.17	0.290	0.276
n-6/n-3	3.32^{A}	1.16^{C}	1.37^{B}	0.056	0.000	3.28^{A}	1.27^{C}	1.54^{B}	0.046	0.000

Note: CLA, conjugated linoleic acid; FAME, fatty acid methyl esters; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid.

[a]n−6 = 18:2n−6 + 18:3n−6 + 20:3n−6 + 20:4n−6 + 22:5n−6.

[b]n−3 = 18:3n−3 + 20:5n−3 + 22:5n−3 + 22:6n−6.

$^{A–C}$Values within a row within a tissue followed by a different letter are significantly different ($p<0.05$).

the RES-F steers and lowest in the SIL:CON bulls in both tissues ($p < 0.001$).

The pattern for the overall level of polyunsaturated fatty acid (PUFA) was similar between tissues, being higher in the SIL:CON bulls ($p < 0.01$). The 18:2n-6 proportion followed the same pattern in both tissues, being higher in the SIL:CON bulls than in the steer groups ($p < 0.001$). The proportion of 18:3n-3 was different between finishing programmes only within the GM tissue, with the RES-F steers having a higher proportion than the SIL:CON bulls and FF steers ($p < 0.05$). The SIL:CON bulls had a higher proportion of 20:4n-6 than did the steer groups ($p < 0.01$) in both tissues. The overall PUFA/SFA ratio followed the same pattern in both tissues, being higher in the SIL:CON bulls than in the steer groups ($p < 0.05$). The n-3 level was not affected by the finishing programme in either tissue. The n-6 level was higher for the SIL:CON bulls in both tissues ($p < 0.05$). The overall n-6/n-3 ratio followed the same pattern in both tissues, with the SIL:CON bulls having the highest ratio, followed by the RES-F steers, and the FF steers having the lowest ratio ($p < 0.001$). Comparisons between tissues within individual finishing programme indicated very few differences in the SIL:CON bulls and FF steers (results not shown). Differences between individual FA in the LD and GM tissue of the RES-F steers were more pronounced, possibly being related to lipid storage and mobilization differences between the tissues in relation to grazing energy requirements (i.e. increased locomotion) (results not shown).

Fatty acid profile of polar lipid. Table VI shows the effect of the finishing programme on intramuscular FA composition of polar lipids in LD and GM tissues between finishing programmes. The overall SFA level was unaffected by the finishing programme in both tissues. Among the individual SFA, the 16:0 level was higher for the FF steers than for the SIL:CON bulls or RES-F steers in both tissues ($p < 0.05$). The 18:0 level was higher for the RES-F steers than for the SIL:CON bulls and FF steers in the GM tissue ($p < 0.01$).

The overall MUFA level was different between finishing programmes only in the GM tissue, with the FF steers having a higher level than the SIL:CON bulls and RES-F steers ($p < 0.05$). Within the GM tissue, the 18:1c-9 proportion was highest in the FF steers ($p < 0.01$). The overall PUFA level was different between finishing programmes only within the GM tissue, showing a similarly higher level for the SIL:CON bulls and RES-F steers than for the FF steers ($p < 0.01$). Among the individual PUFA, the 18:2n-6 level was highest for the SIL:CON bulls followed by the RES-F steers, with the FF steer group having the least in both tissues ($p < 0.05$). The 20:4n-6 proportion in GM tissues was higher in the SIL:CON bulls and RES-F steers than in the FF

Table VI. Polar lipid fatty acid profiles (% identified FAME) of bulls fed *ad lib* silage:concentrates (45:55 DM; SIL:CON bull) and steers fed *ad lib* silage (FF steer) and steers grazing pasture (RES-F steer) during the finishing period within *M. longissimus dorsi* (LD) and *M. gluteus medius* (GM).

	LD					GM				
	SIL:CON bull ($n = 9$)	FF steer ($n = 9$)	RES-F steer ($n = 11$)	SEM	p	SIL:CON bull ($n = 9$)	FF steer ($n = 9$)	RES-F steer ($n = 11$)	SEM	p
16:0	22.0^{B}	24.0^{A}	22.5^{B}	0.442	0.010	20.8^{B}	22.3^{A}	20.2^{B}	0.468	0.013
18:0	15.5	14.5	14.9	0.363	0.194	14.0^{B}	14.5^{B}	16.2^{A}	0.404	0.001
18:1c-9	18.7	19.9	17.3	0.937	0.154	18.1^{B}	21.0^{A}	17.2^{B}	0.805	0.007
18:2n-6	20.7^{A}	11.2^{C}	14.0^{B}	0.636	0.000	22.7^{A}	12.0^{C}	15.5^{B}	0.684	0.000
18:3n-3	3.45^{C}	5.45^{B}	6.09^{A}	0.197	0.000	3.66^{C}	5.16^{B}	5.97^{A}	0.207	0.000
20:4n-6	6.45	6.09	6.82	0.240	0.108	7.02^{A}	6.37^{B}	7.10^{A}	0.202	0.034
20:5n-3	2.02^{B}	4.40^{A}	4.74^{A}	0.184	0.000	2.47^{B}	4.64^{A}	4.85^{A}	0.161	0.000
22:5n-3	3.34^{C}	5.85^{A}	4.74^{B}	0.162	0.000	3.41^{C}	5.41^{A}	4.11^{B}	0.139	0.000
22:6n-3	0.28^{C}	0.60^{A}	0.42^{B}	0.036	0.000	0.29^{C}	0.59^{A}	0.39^{B}	0.022	0.000
SFA	38.1	39.3	38.3	0.546	0.329	35.5	37.6	37.3	0.698	0.090
MUFA	21.6	22.9	20.2	0.953	0.144	20.8^{B}	23.8^{A}	20.4^{B}	0.807	0.013
PUFA	37.9	35.2	38.8	1.173	0.103	41.4^{A}	35.7^{B}	40.0^{A}	1.146	0.006
PUFA/SFA	1.00	0.90	1.01	0.043	0.126	1.18^{A}	0.96^{B}	1.07^{AB}	0.052	0.031
n-6	28.9^{A}	18.9^{C}	22.8^{B}	0.845	0.000	31.6^{A}	19.9^{C}	24.6^{B}	0.843	0.000
n-3	9.03^{B}	16.31^{A}	15.95^{A}	0.410	0.000	9.82^{A}	15.80^{A}	15.31^{A}	0.407	0.000
n-6/n-3	3.20^{A}	1.16^{C}	1.43^{A}	0.038	0.000	3.22^{A}	1.26^{C}	1.61^{B}	0.060	0.000

Note: FAME, fatty acid methyl esters; MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid.
$^{A–C}$Values within a row within a tissue followed by a different letter are significantly different ($p < 0.05$).

steers ($p < 0.05$). The 18:3n-3 level was highest for the RES-F steers followed by the FF steers, with the SIL:CON bulls having the least in both tissues ($p < 0.001$). The 22:5n-3 and 22:6n-3 levels were highest for the FF steers, followed by the RES-F steers, with the SIL:CON bulls having the least in both tissues ($p < 0.001$). The overall n-6/n-3 ratio was the same in both tissues, with the SIL:CON bull group having the highest ratio, followed by the RES-F steer group, and the FF steer group having the lowest ratio ($p < 0.001$). There were minor differences between the tissues within all three finishing programmes (results not shown).

Discussion

The trial investigated whether extensive forage finishing of steers would affect the carcass characteristics and meat quality compared with traditional rearing practices commonly used for bulls in a majority of European countries. Differences in live weights and dressing percentages between the animals from the different finishing programmes are likely to reflect the sex and gut fill of the animals at the time of weighing. The carcass conformation class score was different among the finishing programmes, with SIL:CON bulls displaying much heavier muscling characteristics than the steer groups. Regardless of finishing practices, all animals in the trial could be considered finished based on the fat cover of the animals. According to the grid grading system in Sweden, a fat score between 6 and 9 is deemed optimal. Moreover, the lean SIL:CON bulls were at the upper limit of preferred carcass weight in Sweden.

There were no differences among the groups for maximum WB-SF values, although the SIL:CON bulls and RES-F steers seemed more similar to each other than to the FF steer group. Boleman et al. (1997) defined consumer acceptability to vary from what is deemed as "tender" (22–35 N) to "intermediate tenderness" (50–53 N), based on overall meat tenderness as assessed by WB-SF. The maximum shear force value from the SIL:CON bulls (61.9 N) and RES-F steers (62 N) fell outside of the range to what is perceived to be palatable, whereas FF steers (47.6 N) could be regarded as "intermediately tender" according to Boleman et al. (1997). Caution must be taken as we were only able to report WB-SF values from samples collected at day one, whereas meat is normally aged 7 days prior to retail in Sweden. The distinction between the finishing groups for total force values, with the SIL:CON bulls and RES-F steers being similar, although higher than the FF steers, may be a reflection on the fat content of the muscle or a greater rate of tissue turnover due to compensatory gain of the FF steers when fed *ad lib* silage after finishing the low-energy grazing period. Purchas et al. (2002) reported bulls and slow growing animals to have higher WB-SF values compared with steers and animals with high average daily gains. Moreover, Allingham et al. (1998) reported an improvement in muscle tenderness in association with a period of compensatory gain prior to slaughter. A similar pattern observed in the present study was supported by the lower, though not significant, maximum WB-SF value of the FF steers. In addition, muscle lipid content has been positively correlated to muscle juiciness and tenderness, while being negatively correlated to WB-SF measurements (Dryden and Maechello, 1970). On the other hand, a higher calpastatin content in bull tissue (Morgan et al. 1993) and a presumably higher, or less soluble collagen content in the older, leaner RES-F steers would probably have a negative influence on muscle tenderness (Purchas et al. 2002). Dufey (2007) reported that compensatory gain after a period of extensive grazing increased the number and size of muscle fibres, through the activation of satellite cells, and decreased the collagen content in *M. longissimus dorsi*; however, there were no improvements in meat tenderness. The MFI is a useful tool when looking at the effects of meat ageing as the index will become greater as the Z-disk region degrades. Variability in the degree and rate at which the Z-disks degrade between different muscles has been noted by Olson et al. (1976). Both WB-SF and MFI measurements have been shown to be highly associated with muscle tenderness (Veiseth et al. 2001). Based on our WB-SF and MFI values, it was concluded that any differences in tenderness associated with finishing programme were nullified by the ageing period.

Generally, finishing programme does not change lipid class composition in muscles, except when the muscle lipid content is modified (Cordain et al. 2002). In this experiment, the concentration of phospholipids was greater in leaner meat. Hence, differences between finishing programmes are more prominent in the GM tissue due to its lower fat content. In the SIL:CON bulls, reduced fat deposits were reflected by the low amount of triacylglycerol present in both the tissues. In addition, the increase in free FA in the SIL:CON bulls may indicate a greater rate of lipid turnover within the tissues, which would be in line with the physiological age of these animals and higher average daily gain. De Smet et al. (2004) reported that "red" muscles contain more phospholipids due to more mitochondrial membranes in association with the fibres. While both LD and GM muscle are classified as "white" muscles, subtle differences between the muscle fibre

compositions suggest slightly that more red fibres are in association with the LD muscle as reported by Kirchofer et al. (2002). This would support our findings that seemed to indicate a greater proportion of phospholipids associated with the LD muscle across all treatments.

Although there was no taste panel assessment of acceptability, there are a number of inferences that can be made from the FA composition of the tissue. Raes et al. (2003) found a positive relationship between higher MUFA content and flavour intensity. In our study, triacylglycerol increased in relation to the muscle total fat content. There was no effect on the SFA level; however, both the FF and RES-F steers had higher MUFA and 18:1c-9 levels. Furthermore, while FF and RES-F steers were both fed strictly forage, silage feeding led to the highest proportion of 16:0 of all the finishing programmes, similar to the findings of Huuskonen et al. (2010) and French et al. (2000). Increased 16:0 in milk from cows fed silage versus grass has been attributed to the loss of 18:3n-3 during the ensiling process, which may affect the rumen microflora and subsequent fermentation products (Chilliard et al. 2007). Dryden and Marchello (1970) reported sensory panel preference to have a negative relationship to the 16:0 level but a positive relationship to the 18:1c-9 level in *M. longissimus dorsi* muscles. This suggests that inferences regarding meat flavour based solely on the finishing programme are further confounded because of the degree of finish of the animals.

The predominant PUFA in barley is 18:2n-6 whereas that in forages is 18:3n-3, both of which are extensively hydrolyzed in the rumen. Once hydrolyzed, the majority of PUFA are hydrogenated by rumen microbes, with the rate of biohydrogenation increasing in relation to the degree of unsaturation (Bauman et al. 2003). The extent of biohydrogenation is dependent on a number of factors such as the amount of lipid in the diet, partial protection of PUFA by plant cell walls and rumen pH (Chilliard et al. 2007). These factors can have an influence on the rumen microflora and subsequent fermentation products (Vanhatalo et al. 2007). Both the barley FA profile and the level of concentrate in the SIL:CON bull diet would have contributed to the higher 18:2n-6 level within the muscles. Between the finishing programmes, fresh forage had a positive influence on the 18:3n-3 level in both tissues. This was probably due to 18:3n-3 being partially protected by the plant cell wall, limiting the effects of biohydrogenation. Using a European trained sensory panel, Campo et al. (2003) showed that 18:3n-3 was associated with "fishy" and "linseed" odour while 18:2n-6 was associated with "oily" odour, though no attempt was made to discriminate between preferences in that study. Nuernberg et al. (2005) reported a similar relationship between grass-finishing, "fishy" flavour and a higher proportion of 18:3n-3. The perception of a "fishy" flavour may be explained by the increased susceptibility of PUFA towards oxidation with increasing unsaturation (Campo et al. 2006). Moreover, the FA composition has a significant influence on flavour via the volatile compounds released during cooking (Calkins and Hodgen 2007). Warren et al. (2008) found "livery" and "fishy" flavours to be associated more with silage than with concentrate feeding. Similarly Priolo et al. (2001) associated increased intensity of "grass", "sour" and "milky" flavours with forage feeding. These flavours are attributed to the higher proportion of terpenoid-type compounds produced during rumen fermentation of chlorophyll (Melton 1990).

While there were no differences in total PUFA or n-3 levels in total lipids, concentrates feeding increased the n-6 level. A higher human dietary n-6 intake has been linked to pro-inflammatory responses (Calder 2006) and adipogenesis (Ailhaud 2006). However, these correlations have more to do with lifestyle choices than mere meat consumption (Sanders 2000). The majority of PUFA in muscle are associated with phospholipids and are eluted in the polar fraction (Wood et al. 2003). In the present study, silage feeding led to higher levels of 22:5n-3 and 22:6n-3 in the polar lipid fraction, possibly due to competitive inhibition of the desaturase activity due to a higher 18:2n-6 level associated with the fresh forage finishing programme. Fredriksson-Eriksson and Pickova (2007) reported a similar 18:2n-6 and 22:6n-3 result, but an opposite 22:5n-3 finding. As with the total lipids, the n-6/n-3 ratio in the polar lipids was lowest in the FF steers, owing to the low 18:2n-6 level and highest in the SIL:CON bulls, due to the low n-3 level. Based on inferences made from other studies, the results from this study indicate that while forage feeding may result in an FA profile associated with a less desirable eating experience, the health benefits linked with an increased n-3 level may offset any negative organoleptic attributes. The n-6/n-3 ratios were low, and this lower ratio in one component of the diet can help to compensate for the higher ratio found in other foods comprising an average human diet.

Conclusion

In relation to human health, the steer groups would be considered the most optimal production method. The FF steers showed a slight edge over the RES-F

steers in FA profile and n-6/n-3 ratio. Relatively, the influence of the finishing practices on the FA profile of the two tissues was similar, allowing for generalized conclusions regarding the impact of the finishing programme on human health. The lower n-6/n-3 ratio found with the FF steers could be used to promote a more balanced lipid intake that would decrease pro-inflammatory promoters. However, all three finishing programmes produced meat with equivalent SFA content and n-6/n-3 ratios below the recommended 4:1 ratio. Regarding eating quality, the lower total shear force found in the FF steer group at day 1 would infer a more enjoyable eating experience, although extrapolation of the MFI would suggest that ageing minimized the differences in tenderness and most likely would have resulted in meat that would be deemed acceptably tender by the consumer. In conclusion, utilizing extensively reared steers to maintain open-grasslands improves the health quality of the meat lipids without affecting meat tenderness compared with finishing young, cross-bred Charolais bulls indoors.

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