Effects of Time on Feed on Beef Nutrient Composition[1]

S. K. Duckett, D. G. Wagner, L. D. Yates, H. G. Dolezal, and S. G. May[2]

Department of Animal Science, Oklahoma State University, Stillwater 74078-0425

ABSTRACT: Forty-eight Angus × Hereford yearling steers were used to assess the effect of time on feed (TOF) on the nutrient composition of beef longissimus muscle (LM). Steers were fed a high-concentrate diet with the exception of the d-0 group, which served as a grass-fed control, and then were serially slaughtered at 28-d intervals during the 196-d feeding period. Steaks were removed from the 10th rib and trimmed of exterior fat and epimysial connective tissue before nutrient analysis. Intramuscular fat content doubled ($P < .05$) between d 84 and 112 but did not differ ($P > .05$) from d 0 to 84 or from d 112 to 196. This increase in fat content resulted in decreased ($P < .05$) concentrations of moisture, protein, and ash in the LM. Concentrations of Mg, K, and Fe in the LM increased ($P < .10$) with advanced TOF. The increase in the total lipid (TL) content of the LM stemmed from a proportional increase ($P < .05$) in neutral lipid (NL). Polar lipid (PL) remained constant ($P = .33$) throughout TOF. The NL and TL became more unsaturated as TOF increased, primarily due to a linear ($P < .01$) increase in oleic (C18:1) acid concentration. In contrast, the polyunsaturated fatty acid (PUFA) concentration in the PL exhibited a linear ($P < .01$) decrease across TOF. As a result, advanced TOF increased the monounsaturated fatty acid (MUFA) content by 22% and decreased the PUFA content by 72% in the LM. The ratio of hypercholesterolemic (C14 + C16):hypocholesterolemic (MUFA + PUFA) fatty acids was unaffected by increasing TOF from d 28 to 196; however, this ratio was lower ($P < .05$) for grass-fed controls (d 0) than for d 28 to 84 and d 196. Cholesterol content (milligrams/100 grams) changed cubically ($P = .06$) across TOF. Ultimately, by limiting TOF to 112 d, the beef industry could provide consumers a palatable beef product that easily fits into a healthy diet and at the same time diminishes the costs associated with external fat trim.

Key Words: Beef, Cholesterol, Fatty Acids

J. Anim. Sci. 1993. 71:2079–2088

Introduction

Currently retailers trim nearly 42% of all beef retail cuts (Savell et al., 1991). Unfortunately, this practice of trimming the external fat at the retail level has done little to reduce the nearly 1×10^9 kg of excess fat produced each year. Recent estimates indicate that excess fat costs the industry approximately $130 per animal (Nunes, 1992). The industry could avoid unnecessary external fat deposition by identifying the optimum time on feed (**TOF**) needed to produce palatable beef. Research (Greene et al., 1989; Williams et al., 1989; May et al., 1992) shows that increasing TOF results in linear increases in numerical yield grade and s.c. fat thickness, in contrast to quadratic increases in marbling scores and sensory panel ratings. As a result, TOF increased total fat trim (hot fat trimming plus fat removed during fabrication) per carcass (Williams et al., 1989). Upon identification of an optimum TOF, longissimus muscle (**LM**) fatty acid, cholesterol, protein, and mineral content must be examined to safeguard its continued inclusion in a healthy diet. Therefore, the objective of this research was to assess the effect of TOF on the nutrient composition of beef.

Materials and Methods

Forty-eight Angus × Hereford steers, approximately 16 mo of age, were obtained from a native range stocker operation in northwestern Oklahoma. Steers were blocked by weight into eight equally sized groups. Steers were fed a high-concentrate diet (87.5% DM, 1.84 Mcal/kg of NE_m, 1.19 Mcal/kg of NE_g), except for the d-0 slaughter group, which served as a grass-fed control. Groups were serially slaughtered at 28-d intervals (0 to 196 d) at the Oklahoma State

[1]Journal article no. 6417 of the Oklahoma Agric. Exp. Sta., Oklahoma State Univ.

[2]Present address: Dept. of Anim. Sci., Texas A&M Univ., 348 Kleberg Center, College Station 77843.

Received December 22, 1992.

Accepted March 8, 1993.

University Meat Laboratory. Further information on collection of carcass traits and palatability traits and postmortem muscle characteristics has been previously reported (May et al., 1992). One steak (2.5 cm thick) corresponding to the 10th rib was removed from each carcass at 7 d postmortem, vacuum-packaged, and stored at −20°C. After removal of all exterior fat and epimysial connective tissue, the lateral half of each LM was pulverized in liquid nitrogen and stored at −20°C for subsequent chemical analyses.

Duplicate samples were analyzed for nitrogen by the Kjeldahl procedure and multiplied by 6.25 to determine crude protein content, moisture by weight loss after drying at 100°C for 24 h, and mineral content by ashing at 600°C for 8 h (AOAC, 1984). Crude fat content was quantified by extracting with petroleum ether for 8 h (AOAC, 1984). Mineral analyses were conducted by acidifying ash (AOAC, 1984) and then analyzing for Mg, Ca, Fe, K, Zn, and Na using a Perkin-Elmer Model 403 (Perkin-Elmer, Norwalk, CT) atomic absorption spectrometer. The neutral (**NL**) and polar (**PL**) lipids were sequentially separated according to the dry column method of Marmer and Maxwell (1981). Aliquots of NL and PL were freed of solvent and dried at 95°C for 24 h to determine dry lipid weight (AOAC, 1984). The lipid weight of the NL and PL were summed for each sample to obtain a total lipid (**TL**) weight. Phospholipid (**PhL**) content was calculated by determining P content of PL by the modified Fiske-Subbarow procedure (Bartlett, 1959) and multiplying by 25. Both the NL (Slover and Lanza, 1979) and PL (Maxwell and Marmer, 1983) were esterified to yield fatty acid methyl esters (**FAME**). The FAME were analyzed using a HP5890A (Hewlett-Packard, San Fernando, CA) gas chromatograph equipped with a flame-ionization detector and HP7673A (Hewlett-Packard) automatic sampler. Separations were accomplished on a 60-m SP2340 (Supelco, Bellefonte, PA) capillary column (.25 mm i.d. and .2 μm film thickness). Column oven temperature was programmed at 155 to 165°C at .5C°/min, 165 to 167°C at .2C°/min, 167 to 200°C at 1.5C°/min, and held at 200°C for 18 min. The injector and detector were maintained at 280°C. Sample injection volume was 2 μL. Helium was the carrier gas at flow rate of 1 mL/min and a split ratio of 1:100. Data were collected and integrated by HP3365 (Hewlett-Packard) ChemStation software. Peaks were identified by comparisons to reference standards from Alltech (Alltech Associates, Deerfield, IL) and Matreya (Matreya, Pleasant Gap, PA). Fatty acids were quantified by incorporating an internal standard, methyl heneicosanoic (C21:0) acid, into each sample. Total lipid fatty acid profiles were calculated by multiplying the percentage of NL and PL in the TL by each fatty acid. Duplicate 1-mL aliquots of NL were freed of solvent and then redissolved in dichloromethane containing 50 μg/mL of internal standard, stigmasterol, for cholesterol analysis. Samples were separated using a Drug Three Megabore column (Alltech Associates) (.53 mm i.d., 10 m) maintained at a temperature of 285°C with the injector and detector at 300°C and 320°C, respectively. Helium was the carrier gas at a flow rate of 12 mL/min. Cholesterol content was quantified by regression equations obtained from known cholesterol standards and then corrected according to the response of the internal standard.

Statistical analysis of experimental data was performed using the GLM procedure of SAS (1985). The main effect was TOF; the error term was steer within each TOF. Differences between means were compared using Tukey's *t*-tests (Steel and Torrie, 1980). Orthogonal polynomials were computed to determine linear, quadratic, and cubic effects. Regression equations were developed from the regression procedure of SAS (1985). Correlation coefficients were determined by the correlation procedure of SAS (1985).

Results

Carcass Characteristics

Carcass weight, s.c. fat thickness, LM area, and yield grade (Table 1) increased linearly ($P < .01$) during the 196-d feeding period. Marbling score and percentage of kidney, pelvic, and heart fat showed quadratic trends ($P < .05$) across TOF. The carcasses from steers fed for 112 d were the first to attain the mean marbling score (small) required for the USDA Choice quality grade. Marbling scores did not ($P < .05$) increase after 112 d on a high-concentrate diet. Additional carcass characteristics have been reported previously (May et al., 1992).

Proximate and Mineral Composition

Increased TOF resulted in a cubic increase in crude fat content (Table 2) and concomitant linear decreases in moisture and protein content ($P < .01$) in the LM. Ash content in the LM decreased cubically ($P < .05$) as TOF increased; however, individual mineral concentrations did not differ ($P > .05$). The concentrations of Mg and K (Table 3) did show a tendency ($P < .10$) for a cubic increase. Iron concentration also showed a tendency ($P < .10$) for a linear increase across TOF.

Muscle Lipids

Total Lipid. Total lipid content (Figure 1) in the LM doubled between d 84 and 112 but did not differ ($P > .05$) from that measured on d 0 to 84 or on d 112 to 196. This increase in TL stemmed from proportional ($r = 1.0$) increases ($P < .05$) in NL. Concentrations of PL and PhL in the LM did not differ ($P = .33$ and .88, respectively) across TOF. As TOF increased, the

Table 1. Carcass characteristics across time on feed

Item	Marbling score[a]	Fat thickness, mm	Longissimus muscle area, cm^2	Kidney, pelvic, and heart fat, %	Carcass wt, kg	Yield grade
Time on feed, d						
0	254.2^{f}	3.05^{e}	63.3^{e}	1.0^{e}	196.6^{g}	1.4^{f}
28	299.0^{ef}	4.11^{e}	69.8^{de}	1.3^{de}	236.7^{fg}	1.7^{ef}
56	336.0^{def}	6.82^{de}	78.6^{cd}	1.5^{d}	263.7^{ef}	1.7^{ef}
84	372.8^{cde}	9.78^{d}	76.3^{cd}	1.8^{cd}	295.8^{de}	2.4^{de}
112	472.2^{b}	14.60^{c}	82.8^{bc}	2.1^{bc}	327.2^{cd}	2.9^{d}
140	428.3^{bcd}	15.03^{c}	85.7^{bc}	2.4^{b}	353.0^{c}	3.2^{cd}
168	471.7^{b}	18.20^{bc}	84.5^{bc}	2.3^{b}	364.7^{c}	3.7^{bc}
196	464.2^{bc}	21.08^{b}	93.2^{b}	2.2^{bc}	417.4^{b}	4.0^{b}
SEM	21.4	2.0	2.8	.1	9.1	.2
Orthogonal effect[h]	q	L	L	q	L	L

[a]Marbling score: small = 400–499; slight = 300–399; traces = 200–299.
[b,c,d,e,f,g]Means with different superscripts in the same column differ ($P < .05$).
[h]Orthogonal polynomial effect of time on feed: L = linear effect ($P < .01$); q = quadratic effect ($P < .05$).

percentage of TL as PL declined from 25% at d 0 to only 4% at d 196. The NL and TL were highly correlated with marbling score (r = .79). Total lipid values averaged .6% higher than crude fat values. The discrepancy between the crude fat values and the total lipid values reported in this experiment is due to the more efficient extraction of phospholipids when using organic solvents compared with petroleum ether (Maxwell et al., 1980; Lewis et al., 1987).

The saturated fatty acid (**SFA**) content of the TL (Table 4) changed cubically ($P < .05$) as TOF increased, and the highest concentration was recorded at d 56. Myristic (C14:0) acid increased linearly ($P < .01$) and pentadecyclic (C15:0), palmitic (C16:0), nonadecyclic (C19:0), and arachidic (C20:0) acids showed cubic ($P < .05$) decreases. Stearic (C18:0) acid had a 20% linear ($P < .01$) decrease. The monounsaturated fatty acids (**MUFA**) demonstrated a 22% linear increase ($P < .01$) from d 0 to 196. This increase was largely due to a 20% linear increase ($P < .05$) in oleic (C18:1) acid concentration. Myristoleic (C14:1) and gadoleic (C20:1) acids also exhibited linear ($P < .05$) increases. Palmitoleic (C16:1) acid increased quadratically ($P < .05$) over TOF. Concentrations of 10-heptadecenoic (C17:1) acid demonstrated a cubic increase ($P < .05$) with increasing TOF. The polyunsaturated fatty acid (**PUFA**) content changed quadratically ($P < .05$) over TOF, resulting in a 72% decrease from 0 to 196 d. Linoleic (C18:2), mead (C20:3), and clupanodonic (C22:5) acids showed linear ($P < .05$) responses over TOF. Concentrations of 11,14-eicosadienoic (C20:2), arachidonic (C20:4), adrenic (C22:4), and cervonic (C22:6) acids decreased quadratically ($P < .05$). Linolenic (C18:3) and timnodonic (C20:5) acids showed a cubic ($P < .05$) response to increasing TOF.

Together these changes translated into a ratio of hypercholesterolemic (C14 + C16):hypocholesterolemic fatty acids (MUFA + PUFA) that did not differ ($P > .05$) with increasing TOF (d 28 to 196).

Table 2. Composition of the longissimus muscle across time on feed

Item	Moisture, %	Crude protein, %	Ash, %	Crude fat, %	Total lipid, %	Phospholipid, %	Cholesterol, mg/100 g
Time on feed, d							
0	74.58^{a}	21.71^{a}	1.09^{a}	2.09^{b}	2.52^{b}	.56	50.66^{abc}
28	74.08^{a}	21.83^{a}	1.08^{a}	2.62^{b}	3.06^{b}	.47	47.87^{bc}
56	73.32^{ab}	20.51^{ab}	1.07^{ab}	4.10^{b}	4.96^{b}	.50	51.05^{abc}
84	73.64^{a}	21.41^{ab}	1.08^{a}	4.02^{b}	4.09^{b}	.46	44.25^{c}
112	70.45^{bc}	19.50^{b}	$.99^{bc}$	8.67^{a}	9.48^{a}	.47	51.91^{abc}
140	68.93^{c}	20.33^{ab}	$.99^{bc}$	9.35^{a}	9.73^{a}	.51	58.65^{ab}
168	68.59^{c}	20.58^{ab}	$.99^{bc}$	9.64^{a}	9.83^{a}	.51	61.37^{a}
196	67.47^{c}	20.07^{ab}	$.98^{c}$	10.14^{a}	11.65^{a}	.51	50.99^{abc}
SEM	.70	.41	.02	.80	.90	.05	3.80
Orthogonal effect[d]	L	L	c	c	L	NS	c

[a,b,c]Means with different superscripts in the same column differ ($P < .05$).
[d]Orthogonal polynomial effect of time on feed: NS = not significant ($P > .05$); L = linear effect ($P < .01$); c = cubic effect ($P < .05$).

Table 3. Mineral content in the longissimus muscle across time on feed

Item	Mg	Na	K	Ca	Fe	P	Zn
	mg/100 g of tissue						
Time on feed, d							
0	17.78	85.35	329.83	19.55	5.36	226.00	5.66
28	20.96	86.33	315.23	24.98	5.08	188.73	6.70
56	19.31	92.76	321.79	23.45	5.12	198.93	8.11
84	20.75	100.65	336.31	23.17	5.30	185.43	12.17
112	21.97	91 91	324.85	30.50	5.37	189.07	8.43
140	15.44	92.40	295.27	15.05	4.97	216.47	7.48
168	17.71	107 85	283.72	21.02	5.76	204.47	8.94
196	19.66	89.00	332.97	24.33	5.68	202.00	9.41
SEM	1.95	14.01	13.49	6.38	.23	21.61	1.86
Orthogonal effect[a]	c	NS	c	NS	l	NS	NS

[a]Orthogonal polynomial effect of time on feed: NS = not significant ($P > .10$); l = linear effect ($P < .10$); c = cubic effect ($P < .10$).

However, this ratio for the grass-fed controls differed ($P < .05$) from the ratio for some of the grain-fed groups (d 28 to 84 and d 196). This ratio did not differ ($P > .05$) between the grass-fed (d 0) controls and the TOF groups at d 140 or 168. Quantities (grams/100 grams of LM) of total fatty acids (**FA**), SFA, MUFA, and PUFA can be predicted using the following equations: FA (g/100 g of LM) = .0444x + 1.80, R^2 = .82, SE = 2.07; SFA (g/100 g of LM) = .02082x + .9628, R^2 = .79, SE = 1.04; MUFA (g/100 g of LM) = .02276x

Table 4. Fatty acid composition of the total lipid across time on feed

Fatty acid, %	Time on feed, d								SEM	Orthogonal effect[i]
	0	28	56	84	112	140	168	196		
14:0	2.52^{c}	2.68^{bc}	2.88^{abc}	3.15^{abc}	3.45^{ab}	3.56^{a}	3.67^{a}	3.54^{ab}	.19	L
14:1	.78^{b}	.79^{b}	.69^{b}	.74^{b}	.78^{b}	.91^{ab}	1.23^{a}	.96^{ab}	.08	L
15:0	.66^{b}	.86^{ab}	.82^{ab}	.85^{ab}	1.03^{a}	.98^{a}	.90^{ab}	.83^{ab}	.06	Q
16:0	24.84^{b}	26.97^{ab}	26.96^{ab}	27.66^{a}	27.59^{a}	26.70^{ab}	26.80^{ab}	27.16^{ab}	.52	c
16:1	3.32^{c}	3.27^{c}	3.01^{c}	3.15^{c}	3.52^{abc}	3.66^{abc}	4.12^{a}	4.08^{bc}	.17	q
17:0	1.28^{c}	1.69^{bc}	2.04^{ab}	2.10^{ab}	2.48^{a}	2.33^{a}	2.04^{ab}	1.97^{ab}	.12	Q
17:1	.63^{c}	.89^{bc}	1.08^{ab}	1.20^{ab}	1.41^{a}	1.42^{a}	1.41^{a}	1.37^{a}	.08	Q
18:0	17.38^{a}	17.38^{a}	17.80^{a}	15.72^{ab}	15.71^{ab}	14.29^{b}	13.38^{b}	13.92^{b}	.53	c
18:1	34.95^{c}	36.40^{bc}	36.85^{bc}	38.04^{abc}	38.92^{abc}	40.31^{ab}	41.58^{a}	41.86^{a}	.93	L
18:2	6.46^{a}	4.94^{ab}	4.61^{ab}	5.13^{ab}	3.56^{b}	3.96^{ab}	3.36^{b}	2.81^{b}	.57	L
18:3	.93^{a}	.45^{b}	.28^{bc}	.15^{cd}	.10^{bc}	.08^{c}	.05^{c}	.06^{c}	.06	c
19:0	.13^{a}	.21^{a}	.00^{b}	.02^{b}	.08^{a}	.18^{ab}	.17^{ab}	.22^{a}	.04	q
20:0	.49^{a}	.43^{a}	.26^{b}	.22^{b}	.27^{b}	.22^{b}	.20^{b}	.15^{b}	.04	q
20:1	.23^{a}	.26^{ab}	.25^{ab}	.11^{a}	.36^{ab}	.39^{a}	.40^{a}	.46^{a}	.06	L
20:2	.66^{a}	.39^{ab}	.28^{bc}	.28^{bc}	.14^{bc}	.16^{bc}	.13^{bc}	.10^{c}	.06	Q
20:3	.00^{a}	.00^{a}	.00^{a}	.00^{a}	.02^{ab}	.02^{ab}	.03^{ab}	.05^{b}	.01	L
20:4	2.27^{a}	1.15^{b}	.91^{ab}	.94^{bc}	.40^{bc}	.45^{bc}	.38^{bc}	.28^{c}	.19	Q
20:5	.17^{a}	.07^{b}	.02^{bc}	.01^{c}	.00^{c}	.00^{c}	.00^{c}	.00^{c}	.01	C
22:4	.54^{a}	.30^{b}	.21^{bc}	.17^{bc}	.07^{c}	.06^{c}	.04^{c}	.02^{c}	.05	Q
22:5	.22	.21	.09	.09	.05	.06	.03	.04	.04	L
22:6	1.06^{a}	.64^{b}	.44^{bc}	.39^{bc}	.14^{c}	.14^{c}	.11^{c}	.07^{c}	.09	Q
U[f]	.03	.04	.02	.00	.00	.00	.00	.00	.01	L
SFA	47.30^{cd}	50.24^{ab}	50.90^{a}	49.70^{abc}	50.61^{abc}	48.26^{bcd}	47.14^{d}	47.79^{cd}	.86	c
MUFA	39.91^{c}	41.60^{cd}	41.89^{cd}	43.24^{cd}	44.98^{bc}	46.69^{ab}	48.75^{a}	48.73^{a}	1.08	L
PUFA	12.31^{a}	8.15^{b}	6.85^{bcd}	7.16^{bc}	4.48^{cde}	4.93^{cde}	4.18^{de}	3.42^{e}	1.01	q
Ratio[h]	.53^{b}	.60^{a}	.62^{a}	.61^{a}	.63^{a}	.59^{ab}	.58^{ab}	.59^{a}	.02	NS

[a,b,c,d,e]Means with different superscripts in the same row differ ($P < .05$).

[f]Unidentified fatty acid content.

[g]SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.

[h]Ratio of hypercholesterolemic fatty acids:hypocholesterolemic fatty acids = [C14:0 + C16:0]/[MUFA + PUFA].

[i]Orthogonal polynomial effect of time on feed: NS = not significant ($P > .05$); L = linear effect ($P < .01$); Q = quadratic effect ($P < .01$); q = quadratic effect ($P < .05$); C = cubic effect ($P < .01$); c = cubic effect ($P < .05$).

Table 5. Fatty acid composition of the neutral lipid across time on feed

Fatty acid, %	Time on feed, d								SEM	Orthogonal effect[d]
	0	28	56	84	112	140	168	196		
14:0	3.41	2.34	3.28	3.59	3.64	3.79	3.85	3.70	.19	1
14:1	1.10^{ab}	1.01^{ab}	.80^{b}	.88^{b}	.86^{b}	.97^{ab}	1.31^{a}	1.02^{ab}	.09	c
15:0	.76	.96	.88	.92	1.08	.99	.93	.85	.08	q
16:0	27.57	28.22	27.77	29.63	27.51	27.52	27.22	27.40	.60	NS
16:1	3.55^{ab}	3.55^{ab}	3.27^{b}	3.48^{ab}	3.67^{ab}	3.90^{ab}	4.28^{a}	4.21^{a}	.19	L
17:0	1.47^{c}	1.88^{bc}	2.22^{ab}	2.30^{ab}	2.63^{a}	2.33^{ab}	2.12^{ab}	2.02^{bc}	.12	Q
17:1	.59^{c}	.97^{bc}	1.17^{ab}	1.31^{ab}	1.52^{a}	1.44^{a}	1.46^{a}	1.40^{a}	.09	Q
18:0	19.63^{a}	18.42^{ab}	18.68^{ab}	16.10^{bc}	15.62^{c}	14.26^{c}	13.41^{c}	13.92^{c}	.62	L
18:1	38.66	38.97	39.22	40.29	40.23	41.48	42.53	42.44	.87	L
18:2	2.08	1.71	1.81	2.05	2.28	2.26	2.15	1.96	.15	C
18:3	.00	.00	.07	.00	.07	.05	.03	.06	.02	L
19:0	.13^{ab}	.26^{a}	.14^{ab}	.02^{b}	.11^{ab}	.19^{ab}	.18^{ab}	.24^{ab}	.05	q
20:0	.51^{a}	.48^{ab}	.29^{bc}	.25^{c}	.30^{bc}	.22^{c}	.20^{c}	.16^{c}	.05	L
20:3	.00^{b}	.00^{b}	.00^{b}	.00^{b}	.02^{b}	.02^{b}	.03^{ab}	.06^{a}	.00	L
SFA[e]	53.49^{a}	53.45^{a}	53.26^{a}	51.80^{ab}	50.89^{ab}	47.32^{ab}	47.91^{b}	48.29^{b}	.98	L
MUFA[e]	44.22^{b}	44.80^{b}	44.74^{b}	46.10^{a}	46.66^{a}	48.23^{a}	50.00^{a}	49.56^{a}	.96	L
PUFA[e]	2.08	1.71	1.87	2.05	2.37	2.34	2.21	2.08	.16	c

[a,b,c]Means with different superscripts in the same row differ ($P < .05$).
[d]Orthogonal polynomial effect of time on feed: NS = not significant ($P > .05$); L = linear effect ($P < .01$); l = linear effect ($P < .05$); Q = quadratic effect ($P < .01$); q = quadratic effect ($P < .05$); C = cubic effect ($P < .01$); c = cubic effect ($P < .05$).
[e]SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.

+ .6105, R^2 = .83, SE = .99; and PUFA (g/100 g of LM) = .0009x + .2164, R^2 = .58, SE = .08; where x = TOF in days. Using these equations, the possibility exists to predict the fatty acid content of the LM based on TOF for similarly fed Angus × Hereford steers.

Neutral Lipid. The most prevalent fatty acids in the NL fraction (Table 5) were oleic, stearic, and palmitic acids, the sum of which accounted for > 80% of the total fatty acids in NL. The NL was composed of approximately 51% SFA, 47% MUFA, and 2% PUFA, averaged over TOF. The SFA content of the NL decreased ($P < .01$) by 10% as TOF increased from d 0 to 196. This decrease in SFA concentration was due mainly to a 29% decrease ($P < .01$) in stearic acid. The fatty acid chains with odd numbers of carbons (C15:0, C17:0, C19:0) exhibited a quadratic ($P < .05$) response to increased TOF. Myristic acid showed a linear ($P < .05$) increase, whereas arachidic acid showed a linear decrease ($P < .01$). Palmitic acid did not differ ($P > .05$) across TOF. The MUFA had a linear increase ($P < .05$) of 12% with increasing TOF. This increase was due in part to a linear increase ($P < .01$) of 10% in oleic acid. Palmitoleic acid and 10-heptadecenoic also increased linearly ($P < .01$) with TOF. Myristoleic acid showed a cubic decrease ($P < .05$). The percentage of PUFA of the NL showed a cubic effect ($P < .05$) during the 196-d feeding period. Linoleic acid differed cubically ($P < .01$) as TOF increased. Linolenic (C18:3) and mead acids had small increases ($P < .05$) in concentration with TOF. The TOF increased the concentrations of MUFA while decreasing SFA in the NL.

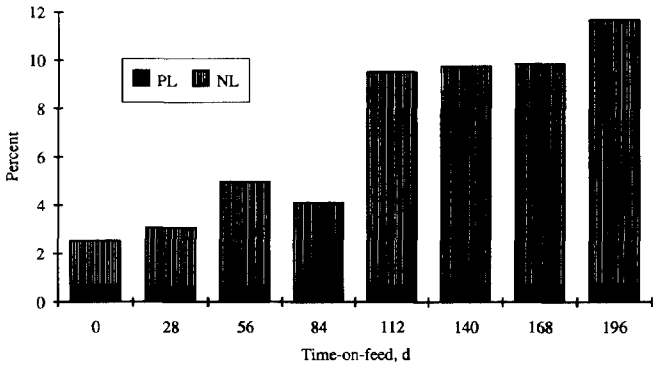

Figure 1. The effect of time on feed on intramuscular neutral (NL) and polar (PL) lipid content. Each bar represents the mean of six animals. Standard errors for the treatment means were .89 for NL and .04 for PL.

Polar Lipid. Oleic, palmitic, and linoleic acids accounted for approximately 60% of the total fatty acids in PL (Table 6). The PL was composed of approximately 38% SFA, 30% MUFA, and 32% PUFA, averaged over TOF. Predominantly, the PUFA in the TL were located in the PL fraction. Comparing grass-fed controls (d 0) to grain-fed steers (d 196), the SFA content showed a linear ($P < .05$) increase of 19%. However, the greatest increase (13%) occurred during the first 28 d on feed (d 0 and 28). Myristic, pentadecyclic, palmitic, and margaric (C17:0) acids all showed linear increases ($P < .05$) with TOF. The MUFA concentration of the LM showed a quadratic

Table 6. Fatty acid composition of the polar lipid across time on feed

Fatty acid, %	Time on feed, d								SEM	Orthogonal effect[h]
	0	28	56	84	112	140	168	196		
14:0	.54^{c}	.67^{bc}	.71^{bc}	.99^{abc}	1.02^{abc}	1.11^{ab}	1.34^{a}	1.20^{ab}	.12	L
14:1	.03^{cd}	.00^{d}	.01^{cd}	.04^{cd}	.07^{bcd}	.13^{bc}	.25^{a}	.17^{ab}	.02	C
15:0	.34^{b}	.47^{ab}	.46^{ab}	.48^{ab}	.57^{a}	.51^{ab}	.48^{ab}	.53^{ab}	.05	l
16:0	19.14	22.50	23.03	22.63	23.47	21.53	21.77	23.68	1.03	c
16:1	2.59^{a}	2.23^{ab}	1.52^{bcd}	1.45^{cd}	1.29^{d}	1.60^{bcd}	2.04^{ab}	2.12^{ab}	.17	Q
17:0	.84	.99	.99	1.08	1.20	1.07	1.07	1.07	.08	l
17:1	.63	.63	.58	.60	.56	.62	.78	.79	.06	q
18:0	12.52	13.29	13.05	13.82	14.00	13.60	13.19	13.78	.58	NS
18:1	26.77^{b}	27.42^{ab}	23.96^{b}	26.33^{b}	25.77^{b}	26.50^{b}	29.47^{ab}	33.16^{a}	1.34	Q
18:2	16.24	16.19	20.31	20.35	20.66	22.14	19.22	15.32	1.54	Q
18:3	2.97^{a}	2.05^{b}	1.45^{c}	.92^{cd}	.52de	.32^{e}	.26^{e}	.04^{e}	.12	Q
19:0	.12^{a}	.00^{b}	.00^{b}	.00^{b}	.00^{b}	.00^{b}	.00^{b}	.00^{b}	.02	C
20:0	.38^{a}	.29^{a}	.08^{b}	.06^{b}	.00^{b}	.04^{b}	.06^{b}	.00^{b}	.04	Q
20:2	2.12	1.74	1.92	1.71	1.90	1.94	1.77	1.58	.18	NS
20:4	7.39^{a}	5.36^{ab}	5.98^{ab}	5.68^{ab}	5.63^{ab}	5.52^{ab}	5.17^{ab}	4.39^{b}	.53	L
20:5	.54^{a}	.34^{b}	.15^{bc}	.05^{c}	.00^{c}	.00^{c}	.00^{c}	.00^{c}	.04	Q
22:4	1.77^{a}	1.36^{ab}	1.40^{ab}	1.07^{bc}	.99^{bc}	.68^{cd}	.56^{cd}	.25^{d}	.14	L
22:5	.74	1.13	.57	.54	.46	.65	.94	.59	.26	NS
22:6	3.46^{a}	3.01^{ab}	2.99^{ab}	2.44^{abc}	2.06^{bcd}	1.72^{bcd}	1.48^{cd}	1.07^{d}	.30	L
U[f]	.12	.18	.16	.04	.00	.03	.00	.00	.05	L
SFA[g]	33.87	38.22	38.32	39.05	40.26	37.86	37.91	40.26	1.46	l
MUFA[g]	30.03^{ab}	30.28^{ab}	26.08^{a}	28.42^{a}	27.69^{a}	28.85^{a}	32.55^{ab}	36.23^{a}	1.47	Q
PUFA[g]	35.22^{a}	31.18^{ab}	34.78^{a}	32.76^{ab}	32.23^{ab}	32.96^{ab}	29.39^{ab}	23.24^{b}	2.55	L

[a,b,c,d,e]Means with different superscripts in the same row differ ($P < .05$).
[f]Unidentified fatty acid content.
[g]SFA = saturated fatty acids; MUFA = monounsaturated fatty acids; PUFA = polyunsaturated fatty acids.
[h]Orthogonal polynomial effect of time on feed: NS = not significant ($P > .05$); L = linear effect ($P < .01$); l = linear effect ($P < .05$); Q = quadratic effect ($P < .01$); q = quadratic effect ($P < .05$); C = cubic effect ($P < .01$); c = cubic effect ($P < .05$).

effect ($P < .01$). Increases in TOF resulted in cubic increases ($P < .01$) in myristoleic acid and quadratic ($P < .05$) increases in oleic acid and 10-heptadecenoic acid. Palmitoleic acid showed a quadratic decrease ($P < .01$) over TOF. The PUFA of the PL decreased linearly ($P < .01$) from d 0 to 196, resulting in a 34% decrease in concentration. Arachidonic acid showed the largest linear decrease ($P < .01$) of 40%. Adrenic and cervonic acids decreased linearly ($P < .01$), whereas linolenic, linoleic, and timnodonic acids showed quadratic ($P < .01$) effects over TOF. The 11,14-eicosadienoic and clupanodonic acids did not differ ($P > .05$) as TOF increased. The PL became more saturated with TOF due to large decreases in PUFA and increases in SFA percentages.

Cholesterol. Cholesterol content revealed cubic trends ($P < .05$) across TOF. The highest concentration was recorded at d 168 (59.19 mg/100 g) and the lowest at d 84 (43.08 mg/100 g). Cholesterol showed moderate associations with TL ($r = .43$), NL ($r = .43$), and marbling score ($r = .32$). Cholesterol content differed ($P < .05$) between quality grades in this study. The LM graded USDA Standard contained 11% less cholesterol than that graded USDA Choice or Select.

Discussion

Regardless of the age or breed of the cattle used, TOF studies (Zinn et al., 1970a; Greene et al., 1989; Wheeler et al., 1989; Williams et al., 1989; Huffhines et al., 1991; May et al., 1992) continue to demonstrate that i.m. fat deposition proceeds in a nonlinear manner. Instead, i.m. fat deposition seems to be a function of the number of days that cattle are exposed to a high-concentrate diet. In this study, approximately 112 d on a high-concentrate diet was needed for these yearling, British-cross steers to reach the U.S. Choice quality grade. Greene et al. (1989) found that only approximately 65 d were needed for purebred Angus steers to reach U.S. Choice grade, whereas Zinn et al. (1970a) reported that 210 d were necessary for purebred Hereford steers fed an 80% concentrate diet to reach Choice grade. Huffhines et al. (1991) reported a plateau in percentage that graded U.S. Choice at 84 d for long-yearling, purebred Hereford steers. In trials with exotic breed-types, Miller et al. (1987) and Wheeler et al. (1989) discovered that extending the feeding period to 168 or 182 d did not result in these cattle reaching the U.S. Choice quality grade. Instead, increasing the TOF to

these end points resulted in unnecessary s.c. fat deposition with no improvement in quality grades. Zinn et al. (1970b), Tatum et al. (1980), Dolezal et al. (1982), and May et al. (1992) all reported that the greatest improvement in palatability occurred within the first 100 d on feed, with little improvement in palatability thereafter. Several researchers (Waldman, 1968; Westerling and Hedrick, 1979; Larick and Turner, 1989, 1990; Mitchell et al., 1991) have found existing relationships between flavor ratings and certain fatty acids present in the LM. Generally, oleic acid has been positively correlated with desirable flavor, whereas PUFA have been positively correlated with off-flavor and aftertaste. Additionally, some SFA (palmitic and stearic acids) have been negatively associated with flavor. Combining the fatty acid composition with the palatability data previously reported by May et al. (1992) revealed that oleic acid was positively associated with tenderness ($r = .33$) and flavor ($r = .39$) ratings from taste panel evaluation and was negatively associated with Warner-Bratzler shear force values ($r = -.50$). In contrast, the PUFA exhibited a negative relationship with tenderness ($r = -.49$) and flavor ($r = -.35$) ratings from taste panel evaluation, and also a positive association with Warner-Bratzler shear force values ($r = .66$). The SFA content exhibited no relationships ($P > .05$) to taste panel ratings or shear force values. These results indicate that the actual quantity of MUFA and PUFA may be better predictors of desirable palatability ratings and shear force values than some of the traditional measures. Ultimately, extending the feeding period beyond 112 d in this trial did not increase i.m. fat deposition or enhance palatability of rib steaks; however, the additional 84 d to d 196 increased s.c. fat thickness by 6.5 mm. These results suggest that one way to decrease waste fat deposition and still obtain a palatable product is to limit TOF to 112 d.

An increase in TOF resulted in increased i.m. fat content and concomitant decreases in mineral, protein, and moisture contents. Bowling et al. (1978), Miller et al. (1981), and Williams et al. (1983) observed similar reductions in moisture content when fat content increased. This decrease would be attributed to the differences in moisture content of fat vs lean. The most substantial increase in i.m. fat content occurred between d 84 and 112 but was not different before d 84 or after d 112. Although LM area and TL follow the same trend across TOF, adjusting TL to the average LM area still results in an increase ($P < .01$) of TL due to increased TOF. Therefore, this increase in TL is not due to the enlargement of the LM area with increased TOF. This doubling of the i.m. fat during this 28-d period suggests the presence of a metabolic signal that triggers triglyceride accumulation by the i.m. adipocytes. Further research is needed to elucidate possible signals that may be regulating i.m. adipocytes to control i.m. fat deposition, while at the same time limiting s.c. fat deposition.

Even though ash content showed a significant decrease as TOF increased, only Mg, Fe, and K showed tendencies for an effect. In comparisons of grain-fed and grass-fed steers, Williams et al. (1983) reported negative correlations between fat and certain minerals (Zn, Fe, P, Na, and K) such that grass-fed steers had increased concentrations of these minerals. However, when evaluating the length of grain feeding, as in this trial, Fe and K were found to increase slightly as fat content increased with TOF. The magnitude of differences in mineral content between grass-fed steers and grain-fed steers may be dependent on forage quality during the growing phase.

The increase in the TL of the LM was due to proportional increases in NL fraction because PL remained constant. Numerous researchers (Bloor and Snider, 1934; Hornstein et al., 1967; Turkki and Campbell, 1967; Link et al., 1970a,b; Hecker et al., 1975; Miller et al., 1981; Larick and Turner, 1989) have also reported that the PhL remains relatively constant throughout growth, probably due to their function as structural components of the cell. Conversely, Larick and Turner (1990) reported an increase in the PhL content at d 54. However, these workers were identifying the composition of PhL in LM from heifers that came off various grazing trials, which may explain the observed differences. The increase in the i.m. fat content in the LM with increased TOF seems to be due to an enlargement of the adipocyte cell with storage reservoirs (triglycerides) vs an increase in adipocyte cell number, because the structural components of the cell (phospholipids) remained constant. This enlargement of the adipocyte resulted in a dilution of the contribution of PhL to the TL with advancing TOF. O'Keefe et al. (1968), Link et al. (1970a,b), and Hecker et al. (1975) also reported similar dilutions of the PhL with increased growth. The consequence of this dilution is evident in the fatty acid composition of TL across TOF.

As indicated in Tables 4 and 5, the NL and PL have very different fatty acid compositions. The NL contains only approximately 2% PUFA, whereas the PL contains approximately 30% PUFA. Other researchers (Terrell and Bray, 1969; Link et al., 1970b; Marmer et al., 1984; Larick and Turner, 1989, 1990) have also noticed that the PUFA are almost exclusively located in the PhL fraction, in which they apparently serve as structural elements of the cells (Bloor and Snider, 1934). Because the percentage contribution of PhL to TL declined greatly with advancing TOF, this ultimately decreased the PUFA content in the LM with increased TOF. However, as the PUFA content in TL was declining with TOF, the MUFA content increased, and the SFA were relatively unaffected. This increase in MUFA resulted from increased concentrations of oleic acid in the NL as TOF increased. Other

researchers (Sumida et al., 1972; Westerling and Hedrick, 1979; Williams et al., 1983; Mitchell et al., 1991) also noted increased concentrations of oleic acid in grain-fed vs forage-fed cattle. In addition, others (Waldman et al., 1968; Westerling and Hedrick, 1979) found significant correlations between animal age and oleic acid concentrations, suggesting that this is due to more of the energy intake being deposited as fat as the animals approach physiological maturity. These reported differences in oleic acid concentrations are suggested to be the result of increased microsomal desaturase activity with increased animal age (Waldman et al., 1968) or of decreased ruminal biohydrogenation with grain feeding (Larick and Turner, 1990). If the microsomal desaturase activity is increased with animal age and physiological maturity, then one would predict mature animals to contain relatively high levels of oleic acid. However, Eichhorn et al. (1986) reported relatively low concentrations (40%) of oleic acid in the muscle of mature cows fed to appetite. Thus, the increased deposition of oleic acid with increased TOF might be better explained by a decrease in ruminal biohydrogenation of fatty acids upon grain feeding. Latham et al. (1972) reported reductions in the number of lipolytic bacteria and in the in vitro lipolytic activity of ruminal fluid, along with the extent of biohydrogenation of unsaturated fatty acids when dairy cows were fed a low-roughage diet. The hydrogenation of linoleic and linolenic acids in cows fed the low-roughage diet was 59 and 63%, respectively, of the hydrogenation of these two acids in cows fed the high-roughage diet. Several bacteria are believed to be responsible for biohydrogenation of fatty acids in the rumen, but most function optimally near neutral pH (Christie, 1981). Therefore, high-concentrate diets that reduce ruminal pH could limit the extent of biohydrogenation in the rumen, ultimately allowing the passage of more unsaturated fatty acids to the small intestine for absorption and incorporation into tissues. Moreover, the increased concentrations of oleic acid with TOF could offer partial explanation for the high concentrations of MUFA reported in Wagyu beef fed over 300 d (Smith et al., 1990). The high MUFA content of Wagyu beef is believed to be due to genetic differences in enzyme activity; however, when Wagyu-cross steers were fed for the same length of time as American-bred steers, no differences in MUFA content were detected (Sturdivant et al., 1992). This would imply that TOF may have more of an effect on the MUFA content of Wagyu beef than do actual genetic differences.

Because increasing TOF resulted in an exchange of the concentrations of PUFA with MUFA in TL, the ratio of hypercholesterolemic:hypocholesterolemic fatty acids remained relatively unchanged by increasing TOF, with the exception that the grass-fed controls had lower ratios than some of the other TOF groups. In this ratio, stearic acid is omitted from the equation because findings by Hegsted et al. (1965), Keys et al. (1965), and Bonanome and Grundy (1987) indicated that stearic acid exerts neither a negative nor a positive effect on plasma cholesterol. More recent evidence (Bonanome and Grundy, 1988) reveals, however, that stearic acid can be as effective as oleic acid in lowering plasma cholesterol levels when either stearic or oleic acid replaces palmitic acid in the diet. The MUFA and PUFA are considered hypocholesterolemic because both are essentially equivalent in lowering plasma LDL cholesterol (Mattson and Grundy, 1985). However, the PUFA also tend to lower HDL cholesterol, and the (*n*-6) PUFA have been associated with enhanced tumorigenesis (Cave, 1991). Thus, the shifting of MUFA for PUFA shown in this study should be perceived as beneficial for human diets designed to lower serum cholesterol.

Cholesterol content in the LM increased cubically as TOF advanced; the highest concentration was reported at d 168. Wheeler et al. (1987) reported no differences in cholesterol content of steers fed for 0, 77, 128, or 182 d. Values reported in this trial, in which a GLC method was used, were lower (52.10 mg/100 g) than those reported by Wheeler et al. (1987), who used a colorimetric procedure (63.32 mg/100 g). Recent evidence (Marshall et al., 1989a,b) suggests that colorimetric analysis may overestimate cholesterol content. The differences noted between the quality grades present in this study should be interpreted cautiously because different numbers of the three quality grades were present in this study.

Based on the results of this study, the optimum TOF would seem to be 112 d to obtain a palatable end product without adding unnecessary external fat thickness. Based on this recommendation, 85 g of cooked rib steak (113 g raw) would provide 44 and 41% of the Recommended Dietary Allowance (RDA, 1989) for protein and iron, respectively, for adult women. Although it would provide significant protein and minerals in a woman's diet, this amount of cooked beef would only supply 8% of the recommended energy intake (2,200 kcal/d). Additionally, only 14% of total fat intake, 20% of saturated fat intake, and 20% of cholesterol intake would be contributed (calculated according to recommendations by the AHA, 1986). Thus, limiting TOF to 112 d would provide consumers with palatable beef products that meet consumers' demands and at the same time diminish costs associated with external fat trim.

Implications

Increasing time on feed results in higher quality and yield grades along with increased s.c. fat thickness. The most substantial increase in i.m. fat deposition came between 84 and 112 d due to increased adipocyte triglyceride storage. Increasing

time on feed results in an exchange of the polyunsaturated fatty acids for monounsaturated fatty acids such that the ratio of hypercholesterolemic to hypocholesterolemic fatty acids remains relatively unaffected. Ultimately, feeding beyond 112 d did not improve quality grade or enhance the palatability of steak, but it did increase waste fat. Furthermore, these results demonstrate the importance of holding time on feed constant to evaluate fatty acid differences.

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